A Critical Assessment of Conservation Outcomes in Indigenous Peoples' Lands and Protected Areas

by

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A thesis submitted

in partial fulfillment of the requirements

for the degree of

Master of Science

(Environment and Sustainability)

in the University of Michigan

August 2023

Thesis Committee:

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Acknowledgements

I would first like to thank my thesis advisor, Dr. Neil Carter. I am grateful your support

and mentorship, and for the opportunity you afforded me to be a part of your lab. Many

thanks to the Conservation and Coexistence Group, especially Dr. Evan Wilson, Dr.

Kirby Mills, Madi Standen, & Amy Zuckerwise, for listening to my thesis updates and

providing feedback on this project from start to finish! Thank you also to my second

reader and advisor Dr. Kyle Whyte for providing thoughtful feedback and for your

perspective on this paper.

Thank you to the Environmental Spatial Analysis lab and Shannon Brines for providing a

helpful space and computers to burn my code through.

Finally, thank you to my partner and family for supporting me in my graduate school

endeavors, as in all other aspects of my life - it means the world!

Abstract

Land tenure – rules governing how people use land – constrain how people interact with natural systems. Different land tenure types therefore have differential effects on sustainability and biodiversity conservation. Notably, Indigenous People's Lands (IPL) and protected areas (PA) – both globally widespread – employ different management practices, yet comparisons of their conservation outcomes are scant. We investigated the relationships between these two land-tenure types and population trends of 2233 vertebrate species in Mesoamerica – a global biodiversity hotspot – controlling for human footprint, spatial autocorrelation of human footprint, and the underlying diversity of different ecosystems from 2000 to 2019. We found that, despite the prioritization of PA establishment in recent decades, proportions of species with decreasing population trends in PAs were comparable to IPLs. Indeed, IPLs supported higher species richness on average than PAs. The intensity and spatial distribution of human impacts appear to moderate these relationships. In areas that had low intensity human pressures at the beginning of the study period in 2000, all spatial configurations of human footprint produced similar outcomes. However, a threshold emerged at human footprint index scores of ~0.40 on a scale of 0-1 (areas transitioning from impacted to heavily impacted), and as pressures intensified beyond this point, the spatial distribution of human footprint was highly determinate of conservation outcomes, with clustered pressures producing worse outcomes than dispersed pressures. Although these geospatial analyses are informative, I encourage future efforts to more deeply and ethically engage local communities when comparing the social-ecological outcomes of different land tenure types.

Introduction

Anthropogenic impacts on the environment, such as climate change, habitat loss, and pollution, are an increasing threat to global biodiversity (Díaz, et al., 2019; Newbold et al., 2015; Maxwell et al., 2016). Land tenure mediates these impacts (Barnes, 2009; Soule, et al., 2000: Tseng, et al., 2021). Land tenure describes the relationships people have with land and the rules that govern these relationships, such as the access to and duration of resource management (FAO, 2002). These relationships can be outlined formally through legal regulation or informally through communal norms (FAO, 2002). Because they often prescribe how natural resources are managed, part of the problem and solution to anthropogenic impacts center on land tenure.

A land tenure type critical to biodiversity conservation are protected areas, the primary objective of which is to the preserve the habitats and the species therein by prohibiting human development within their boundaries (Maxwell et al., 2016; Schuster et al., 2019). Protected areas (PAs) encompass 17% of terrestrial surfaces globally, with efforts to increase this number to 30% by 2030, and 42% of these areas were established within the last decade (Protected Planet, 2020; USDI, 2021). PAs are inherent to the conservation movement as the long-adopted convention for species preservation in the west but international biodiversity targets, namely those outlined under the Convention of Biological Diversity, are responsible for increased PA establishment in recent decades (CBD, 2011; Venter et al., 2014; Watson et al., 2014). The efficacy of PAs has been critiqued, however, due to a hesitancy towards establishing PAs in highly arable lands (Venter et al., 2014; Venter et al., 2018), a failure to intersect with the ranges of some priority species highly vulnerable to extinction (Sánchez-Fernández & Abellán, 2015;

Schuster et al., 2019), fragmentation or limited geographic extent (Baldwin & Beazley, 2019), and varying levels of protection and enforcement which can produce different outcomes across PA categories (Leberger et al., 2020; Locke & Dearden, 2005). In addition, there are larger and more nuanced issues regarding the ways PAs impact people, and in particular, the ways they disproportionately affect Indigenous People. For example, the establishment of PAs are contentious when weaponized through settler colonialist ideologies that displace people and impose a different land tenure regime that limits access to resources, restricts previously uninhibited stewardship practices, and undermines social resilience (Whyte, 2017; Whyte, 2018).

Indigenous Peoples' Lands stewarded by Indigenous People is another land tenure type that has garnered attention for being essential to environmentally just conservation efforts. Indigenous Peoples' Lands (IPLs), ancestral lands stewarded by Indigenous Peoples since time immemorial, are not the exception to PAs, rather they are extraordinarily ubiquitous encompassing 25% of the Earth's surface, intersecting with 40% of lands devoid of high intensity human pressures (Garnett et al., 2018), and representing some of the oldest forms of conservation (Berkes, 2007; O'Bryan *et al.*, 2021). Indeed, many Indigenous cultures reflect cosmological views that unambiguously define a reciprocal relationship between Indigenous rights to self-determinization, communal resilience, and stewardship of the Earth (McGregor, 2016; Sobrevila, 2008; Whyte, 2018). Indigenous Stewardship that manages for the material and immaterial needs of Indigenous Peoples while generating ecologically beneficial outcomes is increasingly well documented such that significant proportions of intact forest landscapes are within IPLs (Fa, et al., 2020) and vertebrate biodiversity in IPLs are at least as rich as

in PAs found in Canada, Brazil, and Australia (Schuster et al., 2019) making IPLs essential to reaching international conservation goals (Leiper et al., 2018; O'Bryan et al., 2021).

The ubiquity of IPLs and the resources behind PAs, which are estimated to be in the billions annually (Balmford et al., 2015; Bruner et al., 2004), hold important implications for how social-ecological conservation is practiced and understanding the conservation outcomes of these different land tenure types is critical for the long-term planning and management. Monitoring biodiversity trends across space and time aids these planning initiatives by enabling actors to track problems and co-develop solutions. To this end, the application of remotely sensed data through geospatial methods have been effectively employed in conservation sciences. Calls to improve the accessibility of remote sensing data and methods in the past decade (Pettorelli et al., 2015; Turner et al., 2015) have increased its use in the assessment of conservation outcomes, for example, by assessing impacts of human pressures on ecosystems and biodiversity (Hansen et al., 2021; Jones et al., 2018; Keys et al., 2021; Leberger et al., 2020; Williams et al., 2020).

However, the results of geospatial analyses are not a perfect mirror of Earth's activities. Spatial and temporal scales can warp the accuracy of analyses due to the accessibility, affordability, and feasibility of certain data. But the assemblage and application of geospatial data are also highly influenced by world views (Calzati & Loenen, 2023). Geospatial data often fail to account for the entire context and history from which quantified biodiversity trends and conservation outcomes arise. In particular, land dispossession, intentional suppression of information, administrative bureaucracy, and differing conceptions of ownership, make accurately demarcating boundaries and

outcomes of different land tenure types challenging (Farrell et al., 2021). Despite this, geospatial methods have been used to assess different metrics of biodiversity within IPLs as well as in comparison to PAs across varying spatial scales (Fa, et al., 2020; Garnett et al., 2018; Leiper et al., 2018; O'Bryan et al., 2021; Schuster et al., 2019). While a useful scaffolding for comparing these land tenure types has been created and generalized outcomes are understood, a critical assessment of how methods are employed is needed to better articulate the extent to which geospatial techniques can appreciate the relationships between land tenure, human impacts, and biodiversity conservation.

The objective of this study was therefore to integrate diverse data through a geospatial lens to understand the effect of land tenure on conservation outcomes as a place to engage discussion. To achieve this objective, I overlapped tenure types – PAs and IPLs – with the ranges of terrestrial Mesoamerican vertebrates and modeled conservation outcomes as the proportion of species with decreasing population trends (IUCN, 2022) in each land tenure type. I included covariates for the initial human pressure conditions in 2000, change in intensity of pressures from 2000 to 2019 for our study period, and measures of species richness to account for the variability in underlying diversity across Mesoamerican ecosystems. I expected to observe 1) demonstrable differences in species population trends between PAs and IPLs and 2) that human pressures would mediate these relationships. I discuss my results in the context of the geospatial data and techniques employed to better understand how geospatial methods can be ethically applied to land tenure comparisons.

Methods

Study Region

Mesoamerica covers approximately 2.485 km^2 and includes Mexico, El Salvador, Belize, Honduras, Guatemala, Nicaragua, Costa Rica and Panama. The boundaries for these countries were derived from the Global Administrative Database (GADM, 2022) and merged into a single boundary representing the geographic extent of Mesoamerica. Mesoamerica was selected as the region of study for this research because it is incredibly biodiverse with 59 unique terrestrial ecoregions (Olson et al., 2001) and a resulting high density of protected areas. Additionally, it was a feasibly large geographic area over which to test this proof of concept that had significant areas of land managed or co-managed by Indigenous People (Garnett et al., 2018).

Data Collection and Integration

I pulled protected areas from each country in Mesoamerica from the World Database on Protected Areas (WDPA, 2022) following the methods of Venter *et al.,* 2014 and Butchart *et al.,* 2015. I included IUCN protected area categories I-VI with National or International designation but excluding Proposed areas and UNESCO World Heritage sites as these overlapped with existing nationally designated protected areas. In instances where only the centroid of a protected area was available, I followed the recommendations of the WDPA by excluding records that lacked contributor reported areas and creating circular buffers around the remaining points proportional to the reported area of the site in ArcGIS Pro 3.1 (ESRI, 2022). While the use of generalized buffers introduced some spatial inaccuracies, this method results in a better estimation of actual area protected. I then dissolved overlapping areas into a single spatial boundary

and assigned a unique ID to each unique unit of protected areas for a total of 1619 areas covering 384,186.4 km^2. I did not make comparisons between PA category, as these can produce different environmental and conservation outcomes (Leberger et al., 2020; Locke & Dearden, 2005; Nelson & Chomitz, 2011) and the intent of this study was to compare conservation outcomes between land tenure regimes. By agglomerated all PAs into a single "protected" status, I was able to make comparisons between PAs and IPLS more effectively, but this limited analysis of variability within land tenure types.

I used an aggregated global dataset of Indigenous Peoples' Lands compiled from publicly available records (Garnett *et al.,* 2018). While this data is incomplete, and the delineation of IPL boundaries is controversial, it is the best resource currently available for assessing the spatial extent of Indigenous Peoples' lands at a continental scale. I clipped this data to the spatial extent of Mesoamerica and assigned each individual unit a unique ID for a total of 24 aggregated units of IPLs covering 2,002,238 km^2.

The spatial distribution of species ranges (extent of occurrence) was obtained for all records prior to 2019 from the IUCN's Red List (IUCN, 2022) of terrestrial vertebrate species native to Mesoamerica (n = 1800). The IUCN Red List data is the most cited vertebrate species database in biodiversity studies (Le Saout et al., 2013) but tends to overestimate true occupancy (Pouzols et al., 2014). However, its accuracy improves when used to analyze broader taxonomic groupings where its reliability has been validated (Rondinini et al., 2011; Venter et al., 2014). Therefore, I grouped our species ranges by taxonomic class into mammals, reptiles, and amphibians, analyzing range distributions in the IUCN's available ESRI Shapefile format. The IUCN assigns categorical population trends (increasing, decreasing, stable, or unknown) for each

species according to the contributions of thousands of researchers and working groups (IUCN, 2022; Rondinini et al., 2011). I excluded all species with Unknown population trends but used the remaining three population trend categories as a proxy for conservation outcomes in our analysis because population trends can be reliably applied across a range of habitat types, are an accurate predictor of extinction risk, and are a targetable objective commonly used by PAs (Barnes *et al.*, 2016; Dudley., 2008; Rodrigues *et al.*, 2014).

Terrestrial human pressures were quantified using the Human Footprint Index (HFI) calculated for 2000 and 2019 (Keys *et al.,* 2021). The HFI are aggregated spatial indices calculated from terrestrial human pressures which were assigned a value from 0 to 1 reflecting the intensity of human pressures at a $1km^2$ resolution. The HFI is a comprehensive metric of human pressure that has been widely employed to inform conservation because it includes key drivers of biodiversity loss and can be reliably used to estimate the extent to which human pressure impacts species (Allan et al., 2019; DiMarco et al., 2018; Sanderson et al., 2002; Venter et al., 2016; Williams et al., 2020). I estimated the change in human pressures (Delta HFI) across the 19-year study period by subtracting the HFI value of any given pixel in the 2000 HFI from its spatial counterpart in the 2019 HFI for all of Mesoamerica.

Spatial Analysis

All spatial analyses were conducted using World Mollweide equal area projection. I intersected the ranges of each endangered species with both tenure types using the sf package (Pebesma E , 2018; Pebesma E & Bivand R, 2023) in RStudio version 4.2.2 (Posit team, 2023; R Core Team, 2023), to determine the proportion of any

given species range that overlapped with and were impacted by the management

strategies associated with either PAs or IPLs (O'Bryan *et al.*, 2021; Schuster et al., 2019).

I calculated the size of these areas of overlap and the proportion of a species total range

that they represented. I then excluded all intersections with an area less than 5 km^2 and

less than 25% of a species total range since the management strategies in these areas were

potentially too geographically limited to significantly influence the species population

trend across its entire range. I rasterized each area of intersection between a species range

and tenure type and extracted the underlying HFI in 2000 and the Delta HFI using the

terra package (Hijmans, 2022). Using the Moran's *I* statistic (Bowler et al., 2020), I

calculated the spatial autocorrelation of HFI in 2000 (i.e., how clustered or dispersed

human pressures were in space) and Delta HFI (i.e., the distribution of land use change

from 2000 to 2019) rounding values to the tenth place. Finally, I averaged the extracted

HFI values across every area of intersection so that each intersection polygon had one

value representing the intensity of human pressures in 2000 and change in human

pressures from 2000 to 2019.

Table 1: Description of final variables used in linear models. Methods used to create variables, spatial and temporal resolution, and variable utility to models are included.

Variable	Description	Spatiotemporal Resolution	Model Utility
HFI 2000	Human Footprint Index in 2000 on a scale of 0 to 1.	1 km^2 2000	An estimation of initial human pressures at the beginning of the study period.
Delta HFI	Change in Human Footprint Index from 2000 to 2019 on a scale of -1 to 1. Created by subtracting the Human Footprint Index in 2000 from the Human Footprint Index in 2019 for every raster pixel.	1 km^2 2000 - 2019	An estimation of the 20-year change in human pressures from 2000 to 2019.
Moran's *I* 2000	Spatial autocorrelation of the Human Footprint Index in 2000. Computed from the HFI 2000 values extracted from every intersection between a species range and a tenure unit. The median value from every area of intersection for each tenure unit was calculated.	1 km^2 2000	A measure of how clustered or dispersed human pressures were in space at the beginning of the study period.
Delta Moran's *I*	The change in spatial autocorrelation of the change in Human Footprint Index. Computed from the Delta HFI extracted from every intersection between a species range and a tenure unit. The median value from every area of intersection for each tenure unit was calculated.	1 km^2 2000 - 2019	A measure of the spatial behavior of 20 years of land use change from 2000 to 2019.
Edge Effect	A measure of how powerfully the conditions around the border of a tenure unit will impact it's interior. Calculated as the ratio of a given tenure unit's area to its perimeter.	Shapefile rasterized to 1 km^2	An estimation of how the shape of a tenure unit will influence the degree to which external conditions impact species inside a tenure unit.
Proportion of Range Impacted	The proportion of a species total range that overlaps with and is impacted by a given tenure unit. The ratio of the area of a species range that intersects with a given tenure unit to the species total range.	Shapefile rasterized to 1 km^2 2000 - 2019	A measure of the relative impact a given tenure unit has on an entire species population trend.
Tenure Unit Richness	The total number of unique species with ranges overlapping a given tenure unit	Shapefile rasterized to 1 km^2 2000 - 2019	An estimation of the underlying variability found in different ecosystems across the study region.

Statistical Analysis

      As my primary research interest was the comparison of conservation outcomes between land tenure types, I reorganized the data to the level of individual tenure units. To do so, I averaged the proportions of a species range impacted by each unit of a tenure type, averaged HFI in 2000 and Delta HFI for each area of intersection weighted by the area of that intersection, and found the median value for Moran's *I* in 2000 and change in Moran's *I* from 2000 to 2019 across each tenure unit. I also estimated the underlying diversity and potential changes to community structures across the extent of a tenure unit by calculating the richness of each area as the total number of unique species ranges that intersected with a tenure unit (Schuster et al., 2019), and the edge effect of each unit as the ratio of unit area to perimeter. Using the total area richness, I calculated the proportion of species with increasing, decreasing, and stable population trends in each tenure unit (Table 1). I limited the final response variable for this analysis to the proportion of species with decreasing population trends since our covariates were all measures of human impact and were therefore better suited to predict undesirable conservation outcomes.

      I ran four linear regression models predicting the proportion of species with decreasing population trends in each tenure unit for mammals, reptiles, amphibians, and all taxa classes together. Prior to modeling, I removed outliers following the framework in Benhadi-Marín 2018 and scaled covariates to create the final datasets used in each model (mammal model n = 503, reptile model n = 441, amphibian model n = 451, aggregated taxa model n = 519). I used the Adjusted R^2 to determine model fit and ranked these by AIC score to determine my final models.
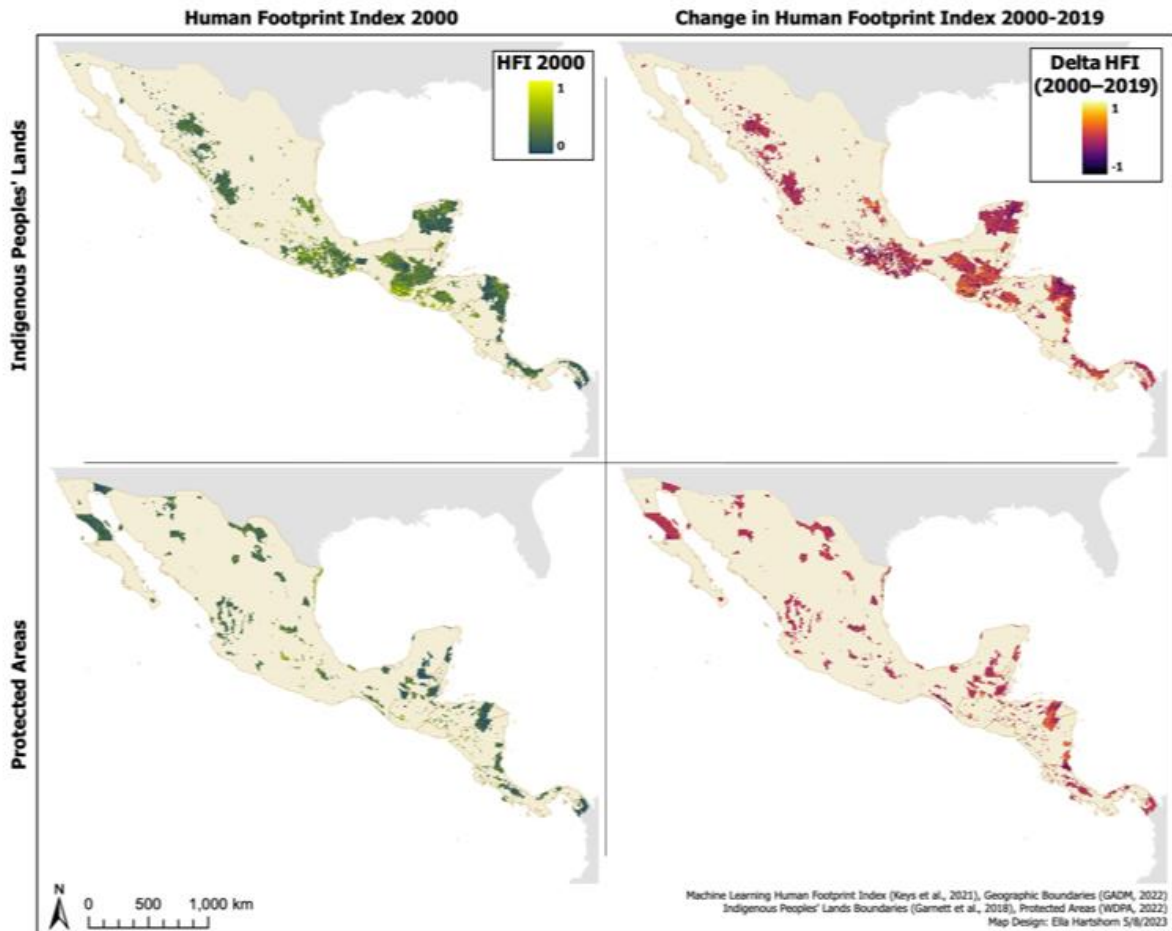
Figure 1: Boundaries of Indigenous Peoples' Lands (top) and Protected Areas (bottom) in Mesoamerica. The Human Footprint Indices are mapped at a 1 km^2 resolution within the tenure units. HFI in 2000 (left) is on a scale of 0 to 1, where 0 represents areas completely devoid of human pressures and 1 represents absolute development. Delta HFI from 2000-2019 (right) is on a scale of -1 to 1, where -1 represents perfectly successful remediation and 1 represents extreme development across the 19-year study period.

Results

Protected Areas represented 11.3% and Indigenous Peoples' Lands 19.2% of terrestrial Mesoamerica. On average, IPLs had a significantly higher species richness per land tenure unit than PAs (t (3.7501) = 22.095, p = 0.001) (Figure 2). This trend was reflected across average taxa specific richness, however the difference was non-significant for amphibians (Figure 4). In IPLs, the proportions of each taxa out of the total species richness were more evenly distributed between mammals (45.0%), reptiles (34.6%), and amphibians (21.3%) than for mammals (56.6%), reptiles (32.0%), and amphibians (13.9%) in PAs.


Figure 2: Species richness (count of all species ranges that intersected with a unique tenure unit) in Indigenous Peoples' Lands (μ = 288.56) and Protected Areas (μ = 140.87).

The best fitting aggregated taxa model with the lowest AIC score (Adj. $R^2 = 0.31$, $F (8, 505) = 29.25$, $p < 2.2e-16$) (Table 2) did not find significant differences between the proportion of species with decreasing population trends in IPLs or PAs ($t (0.48) = 4.04$, $p = 0.66$) (Figure 3). PAs had greater variability in the proportion of species with decreasing population trends than did IPLs. This is likely because I agglomerated all IUCN categories of PAs into a single "protected" management regime because I was not interested in the potentially differing effects of IUCN categories and this agglomeration made the two land tenure types more comparable as IPLs are not categorized.

Table 2: Summary of aggregated species linear regression model predicting the proportion of species with decreasing population trends. Bolded values indicate significant covariates at alpha<0.05.
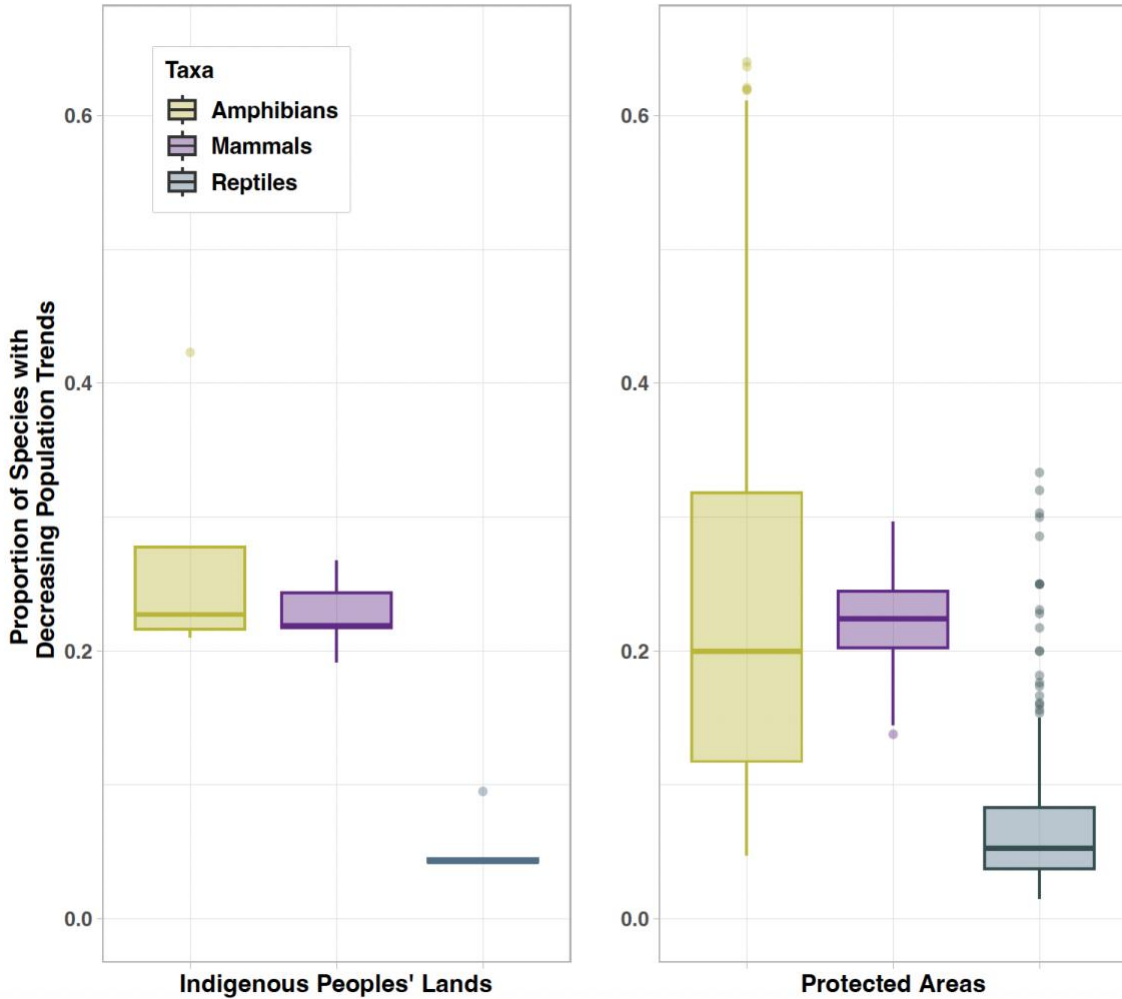
| Coeffcient	Proportion of Species with Decreasing Population Trends		
	Estimates	Conf. Int (95%)	P-Value
Intercept (IPLs)	0.174	0.135 – 0.213	**<0.001**
PAs	0.031	-0.009 – 0.070	0.127
Moran's I 2000	-0.003	-0.006 – -0.000	**0.050**
HFI 2000	-0.003	-0.006 – -0.000	**0.029**
Edge Effect	0.046	0.036 – 0.056	**<0.001**
Proportion of Range Preserved	0.103	0.085 – 0.121	**<0.001**
IPL x Unit Richness	0.019	0.001 – 0.037	**0.034**
PA x Unit Richness	0.003	-0.001 – 0.008	0.131
Moran's I 2000 x HFI 2000	0.003	0.000 – 0.005	**0.036**
Edge Effect x Proportion of Range Preserved	0.116	0.092 – 0.139	**<0.001**
Observations	514		
R^2 / R^2 adjusted	0.321 / 0.309		
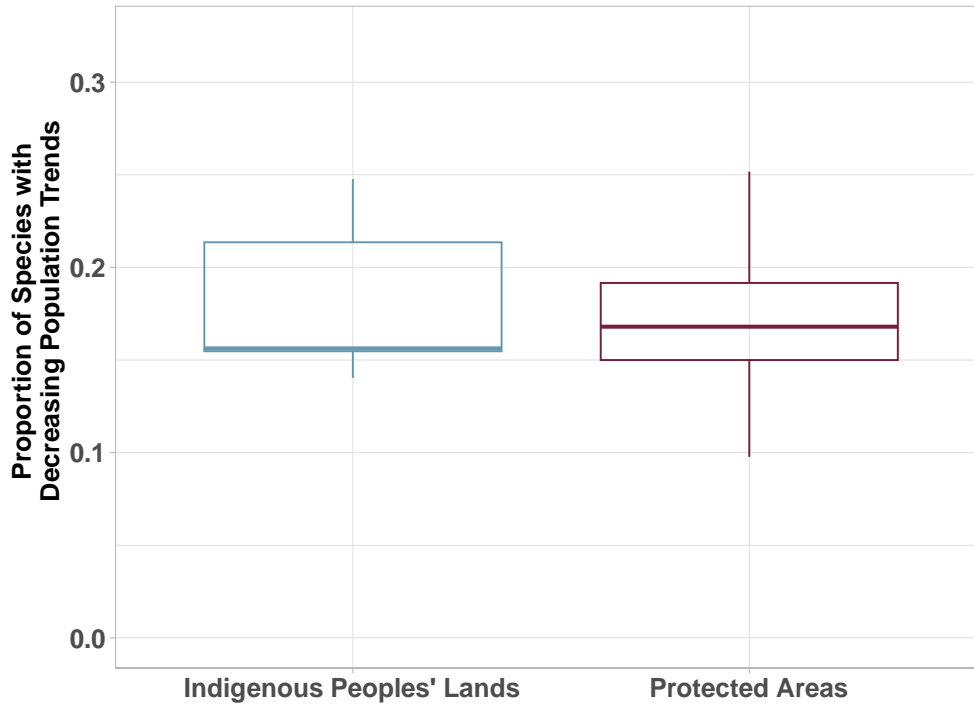
Figure 3: Proportion of species with decreasing population trends in Indigenous Peoples' Lands and Protected Areas. The proportion of species with decreasing population trends was calculated as the number of species with decreasing population trends in each unit divided by that unit's total species richness.

The proportion of species with decreasing population trends was modeled in PAs and IPLs for each taxonomic group (Figure 4). For the three best fitting taxa models (Supplementary Appendix Table S3-S5), I found no differences in the proportion of species with decreasing population trends between PAs and IPLs. Of the 1800 species ranges that intersected with tenure units, 383 were mammals, 618 were reptiles, and 417 were amphibians (Figure 5). Despite this, mammals had the least variability in their results than the other two taxa, potentially because the average mammal range (411,623.42 km^2) was far larger than the average reptile (145,356.29 km^2) or amphibian (64,849.91 km^2) range. Many of the ranges of mammals overlapped with most of or the

entire extent of a given tenure unit producing similar or identical values for many of the

covariates when I averaged results across tenure units.

Figure 4: Proportion of species with decreasing population trends in Indigenous Peoples' Lands and Protected Areas for mammals, reptiles, and amphibians. The proportion of species with decreasing population trends by taxa was calculated as the number of taxa with decreasing population trends in each unit divided by that taxa's total richness in that unit.
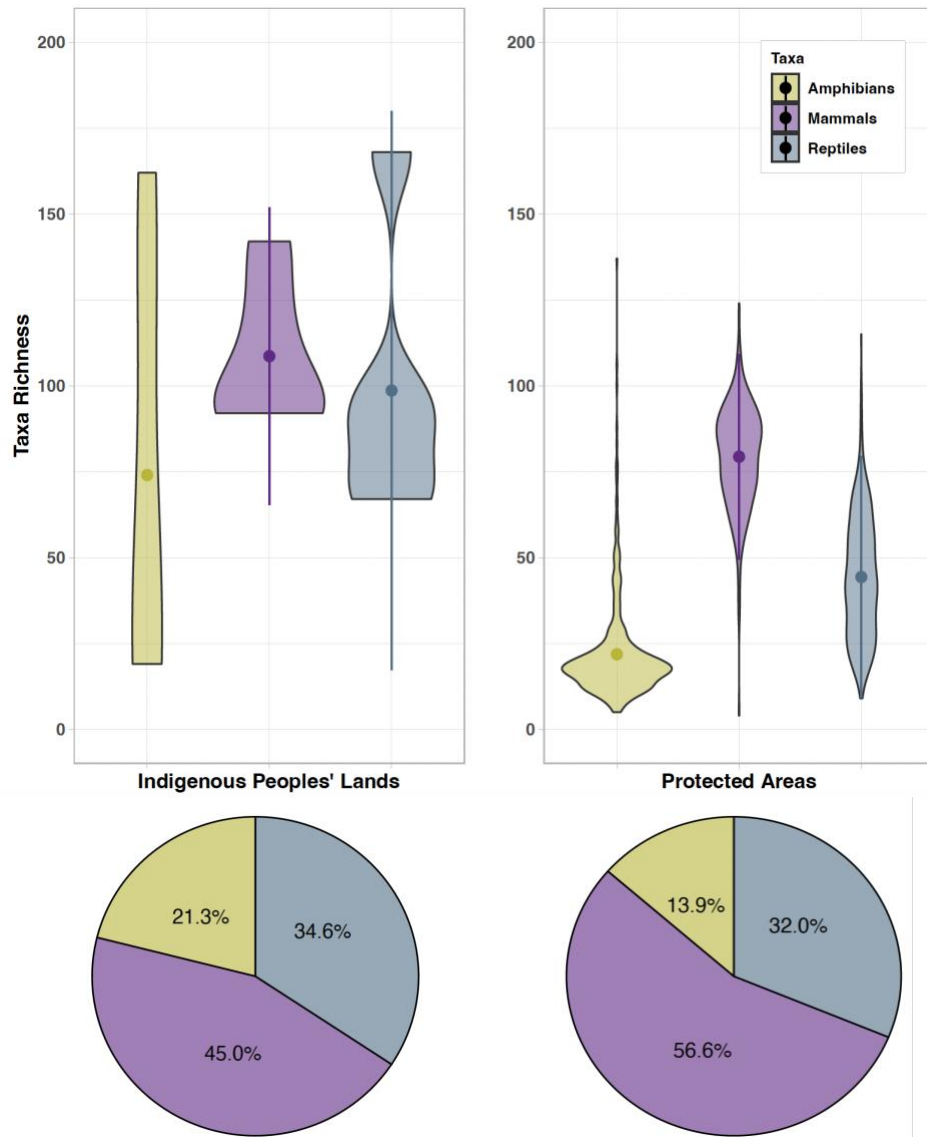
Figure 5: Taxa richness in Indigenous Peoples' Lands (µ mammals = 108.6, µ reptiles = 98.6, and µ amphibians = 74.0) and Protected Areas (µ mammals = 79.3, µ reptiles = 44.3, and µ amphibians = 21.8). Pie charts depict the proportion of mammals, reptiles, and amphibians out of the total average species richness in each land tenure type.

    I furthered explored characteristics across tenure units to better understand how human pressures predicted aggregated species population trends. For the aggregated species model, the effect sizes of all coefficients were small, but the only non-significant variables were PAs and the interaction between PAs and average species richness per
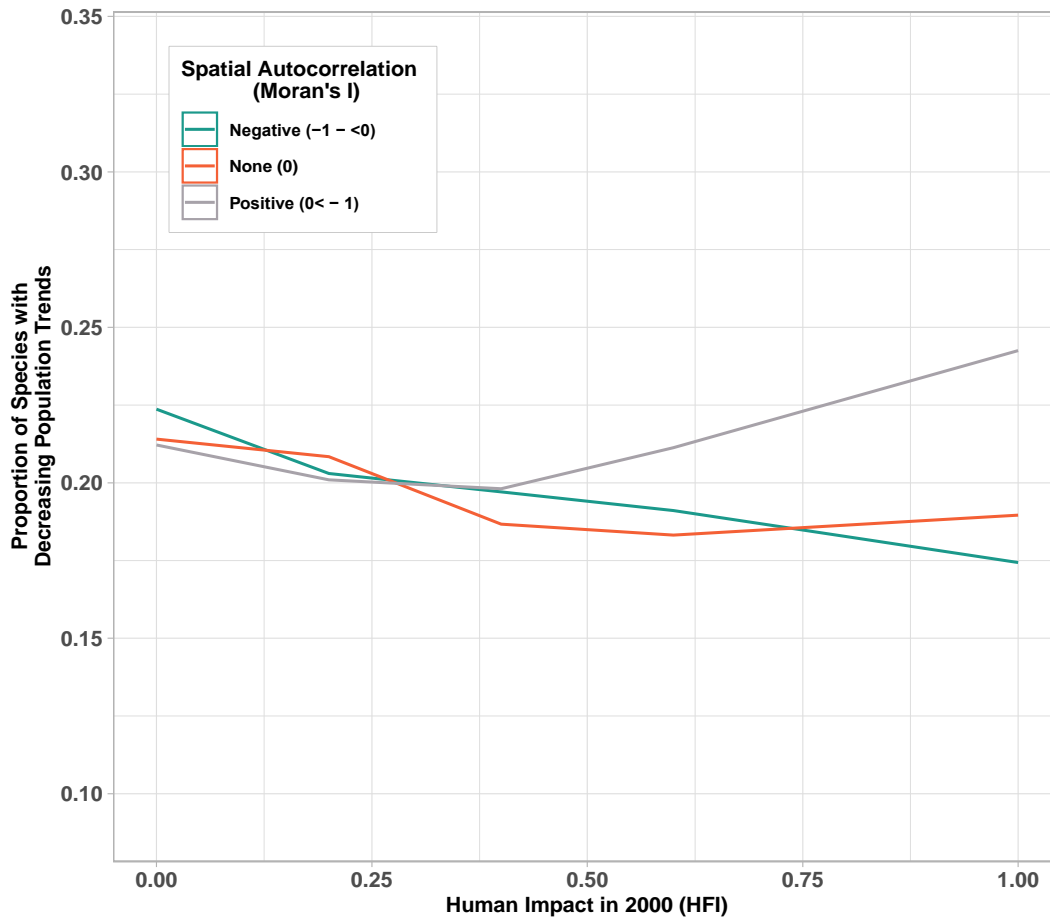
Figure 6: Spline effects plot of the average Human Footprint Index in 2000 and the average Spatial Autocorrelation (Moran's I) in 2000 as they predict the proportion of species with decreasing population trends. HFI 2000 spline knots = 0.2812 & 0.4375 (defined by the points of intersection in original effects plots). Moran's I is on a scale of -1 to 1 where positive numbers represent positive spatial autocorrelation or a clustering of human pressures, zero represents no spatial autocorrelation or a random distribution of human pressures, and negative numbers represent negative spatial autocorrelation of a dispersion of human pressures.

tenure unit (Table 2). The interaction between HFI 2000 and Moran's *I* 2000 indicated

that the initial intensity and spatial distribution of human pressures in 2000 predicted

conservation outcomes twenty years later (Figure 6). In areas with low intensity human

pressures the spatial configuration of impacts did not differently predict proportions of

species with decreasing population trends. As the intensity of pressures increased, a threshold emerged at HFI scores between 0.31 and 0.41, and in areas with initial human pressures greater than this threshold, the spatial configuration of these impacts was highly determinate of conservation outcomes.
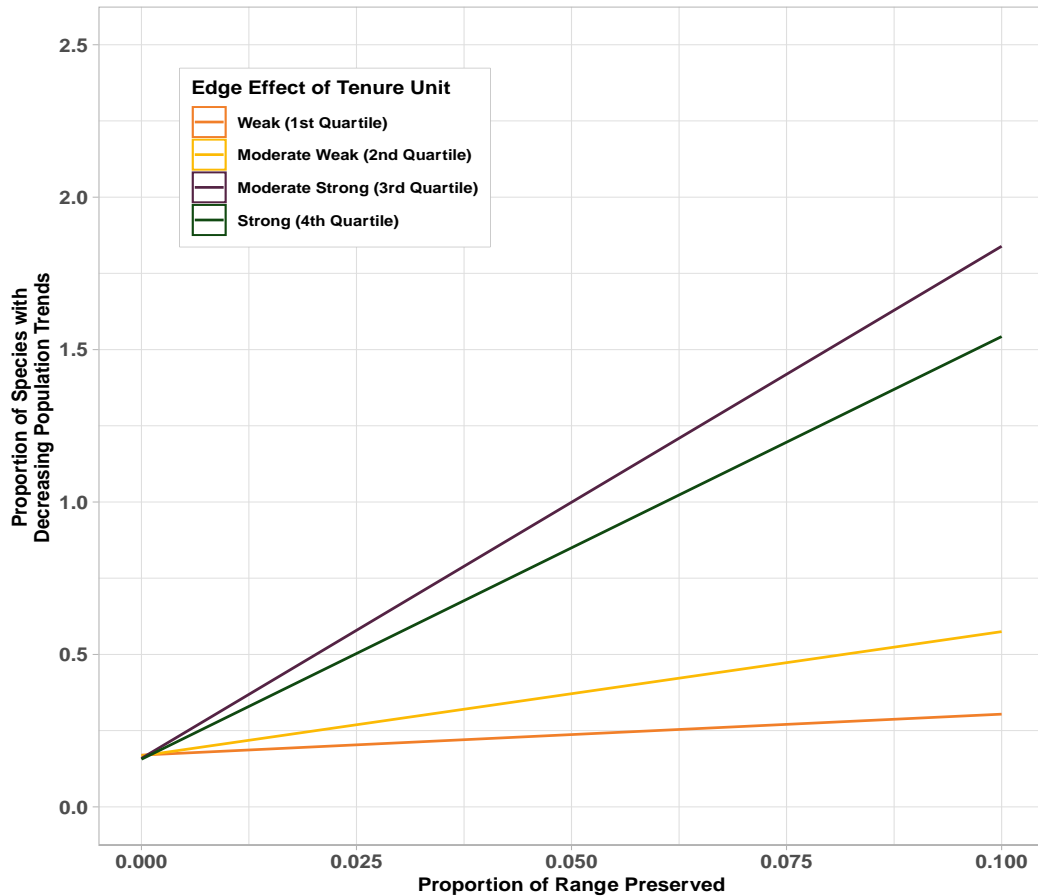
Figure 7: Spline effects plot of the average proportion of a species' range that is preserved by a tenure unit and the average edge effect of that unit as they predict the proportion of species with decreasing population trends. Edge effect is a measure of how powerfully impacts around a unit's boundary effect its interior and is calculated as the ratio of a unit's area to its perimeter. Edge effect spline knots were set at the 1st quartile (0.450), mean (1.161), and 3rd quartile (1.597) which created four bins representing the influence of edge effect as it interacts with proportion of a range preserved at each quartile.

The interaction between the average edge effect (unit area / unit perimeter) and the average proportion of a species range preserved or impacted by a unit (proportion of a species range overlapping a tenure unit / species total range) indicated that as this proportion increases, the proportion of species with decreasing population trends also increases (Figure 7). This relationship is mediated by the relative magnitude of edge effect were units in the first and second quantiles (weak and moderately weak edge effect) produced lower proportions of decreasing species as range preserved increased. Units with edge effect in the upper third and fourth quantile (moderately strong to strong edge effect) produced greater proportions of species with decreasing population trends. This indicated that when a unit impacts a greater proportion of species ranges, the conditions in and around that unit are increasingly determinate of its overall population trends.

Discussion

My analysis resulted in three main insights: 1) Indigenous Peoples' Lands supported greater species richness for all three assessed taxonomic groups, 2) Indigenous Peoples' Lands and Protected Areas had comparable rates of decreasing species population trends, and 3) the interaction between initial spatial autocorrelation and human pressures in 2000 moderated conservation outcomes across tenure type. These results contribute to a better understanding of how the stewardship and management practices associated with IPLs and PAs influence conservation outcomes while highlighting opportunities to further engage in alliance building between two land tenure types that represent 30.5% of Mesoamerica.

The results of the spatial overlap of land tenure units and vertebrate ranges in Mesoamerica indicated that Indigenous Peoples' Lands hosted greater species richness than protected areas. In PAs, mammals were more represented, accounting for 56.6% of all species with intersecting ranges, compared to amphibians (13.9%) and reptile (32.0%). The disparity in PA conservation outcomes for amphibians and reptile populations, which are experiencing the greatest biodiversity loss of vertebrate species across the globe (Cordier et al., 2021; Gibbons et al., 2000) and specifically within Mesoamerica (Mayani-Parás, et al, 2019), are particularly concerning. As viability of amphibian and reptile habitats outside of PAs are projected to diminish under future global climate change scenarios (Mi et al., 2023), my results may also indicate bias in the funding and establishment of PAs, which have already been shown to be preferential to charismatic mammal preservation (Colléony et al., 2017; Monsarrat & Kerley, 2018). However, mammals only accounted for 45.0% of total richness in Indigenous Peoples' Lands and, the remaining representation was more evenly distributed between reptiles (34.6%), and amphibians (21.3%). The ethos of reciprocal relations core to Indigenous Stewardship, may foster conservation outcomes more equally across taxonomic diversity than protected areas, which can lead to more robust and resilient ecosystems (Gagic et al., 2015; Hooper et al., 2005; Olivier et al., 2015).

My models of conservation outcomes between land tenure types, indicated there was no significant difference in the proportion of aggregated or taxa specific species with decreasing population trends found in Indigenous Peoples' Lands and protected areas. These results were unexpected given the prioritization of PAs in the last decade, especially since, historically, many of the actions associated with the establishment of

PAs are directly responsible for the current vulnerability and impoverishment of Indigenous Peoples (Stevens, 2014; Whyte, 2017). For example, Indigenous Peoples Lands are at some of the highest risks of environmental pollution (Fernández-Llamazares et al., 2020) and these risks are further perpetuated by the depletion of easily accessed natural resources which spurs development into resource rich but sparsely populated Indigenous Lands (Garnett et al., 2018; Fernández-Llamazares et al., 2020). Impoverishment and a lack of land tenure security have been linked to diminishing conservation and sustainable development outcomes (Barnes, 2009; Soule, et al., 2000: Tseng, et al., 2021). Yet despite global evidence that Indigenous Peoples Lands are specifically targeted by development operations, often intentionally subverting Indigenous rights, my results indicate that these lands continue to harbor more biodiversity than protected areas while producing similar rates of species depopulation in Mesoamerica. These results are consistent with other studies, which have shown that IPLs are critical refugia for threatened and non-threatened mammals (O'Bryan et al., 2021) and that IPLs can support greater vertebrate richness than PAs in Canada, Australia, and Brazil (Schuster et al., 2019). My central conclusion is that, against many social odds, IPLs produce conservation outcomes better than or at least comparable to PAs in Mesoamerica, so successful conservation efforts in the future should center in rights based equitable partnerships and Indigenous lead conversations.

My results also indicated that, across tenure type, undesirable conservation outcomes appear to be moderated by the magnitude and spatial autocorrelation of initial human pressures in 2000 but not by the change in human pressures from 2000 to 2019. While significant effort has been made to track global increases in human pressures over

the last two decades (Keys et al., 2021; Venter et al., 2016; Venter et al., 2016; Williams et al., 2020), my results suggested that early impacts to systems may be more predictive of long-term population trends. While HFI scores in 2000 were on average lower than in 2019, these initial pressures may have created more severe shocks to systems that ultimately resulted in greater decreases in the populations of species that were unable to adapt to new stressors (Mimura et al., 2017).

The spatial autocorrelation of initial human pressures in 2000 did not differently determine conservation outcomes when the intensity of this pressure was initially low. However, beyond the identified threshold of HFI scores 0.31 - 0.41, which were indicative of areas in a transition from being moderately impacted to highly impacted (DiMarco et al., 2018; Garnett *et al.,* 2018; Watson & Venter, 2019), human pressures that clustered in space (positive spatial autocorrelation) produced higher proportions of species with decreasing population trends. The identification of such a threshold can be essential for recognizing tipping points in coupled social and ecological systems (Kelly et al., 2015) which can better inform management decisions (Hilton et al., 2022; Stevenson, 2011). Additionally, the emergence of a relatively high threshold is somewhat encouraging as it indicated that systems are resilient to multifunctional use in space as long as impacts remain moderate. More specifically, the spatial configuration of multifunctional use in IPLs and PAs fall on somewhat opposite ends of a land-sparing (concentrated zones of high yield agriculture set apart from natural areas) and land-sharing (lower impact agricultural use interspersed with natural features) paradigm (Grass et al., 2019). Although typically employed in agricultural contexts, this paradigm can be used to categorize the conservation strategies associated with PAs and IPLs when it is

applied as a spectrum rather than a binary (Kremen, 2015; Majgaonkar et al., 2019). PAs are more representative of land-sparing, with fortressed blocks designated for protection that are separated from areas of human use, whereas IPLs are more representative of land-sparing in which lands are managed for human use that supports biodiverse non-human populations. My results suggest that even if an area experiences significant human pressures, severe decreases in species population trends can be mitigated by dispersing intensified impacts across space, as is often the case with Indigenous stewardship. The land-sparing paradigms of protected areas may still be necessary to protect many biodiverse and irreplicable habitats, but my current results suggest that IPLs can and should be integrated into broader-scale goals for conserving biodiversity amid human activities. Indeed, the resources and institutional support afforded to PAs may be key for facilitating partnership networks with Indigenous Peoples' Lands. Voluntary partnership networks modeled around Indigenous Stewardship are not only essential to achieving conservation outcomes, but also offer a more wholistic approach to meeting global biodiversity targets, which include improving engagement and further integrating diverse and Indigenous Knowledge into conservation efforts.

Finally, my results underscore challenges of comparing outcomes across land tenure types when relying on geospatial methods such as the overlap between geographic boundaries and projected species ranges. Mismatches in space (mammals with ubiquitous ranges across Mesoamerica, amphibians with highly isolated ranges, and incomplete delineation of Indigenous Peoples' Lands) as well as mismatches in time (IUCN range records were from 2000 to 2019, protected areas had varying dates of establishment, and

unclear timelines of Indigenous sovereignty over land use) likely result in a failure to fully characterize the relationships between land tenure and biodiversity trends.

I found that the proportion of species with decreasing population trends increased with the interaction between the severity of a tenure unit's edge effect and the proportion of a species range that overlapped with that unit. While this suggests that the shape of a tenure unit as well as the conditions in and around that unit influence depopulation rates, the average land tenure unit overlapped with <10% of species ranges. However, many species ranges, particularly mammal ranges, overlapped with the multiple distinct PAs and IPLs. The agglomerated power of this multi-land tenure protection network, while fragmented, may have beneficial effects that aggregate across space in a way not captured by this study's individual land tenure unit of analysis. This highlights opportunities for comparing land tenure types by assessing the conservation status of subpopulations endemic to a single land tenure unit rather than for the entire species range. That said, biodiversity trends have been found to be highly correlated between taxa in the tropics and subtropics (Leal et al., 2010; O'Bryan et al., 2021), indicating that these estimates are still a beneficial starting point for conversations around the comparison of land tenure types. However, given that relationships of land tenure and biodiversity are highly nuanced, a geospatial lens should be cautiously applied to identify trends and open dialogue to engage communities which ensures that narratives created with high-level geospatial methods reflect the context and history of on-the-ground realities.

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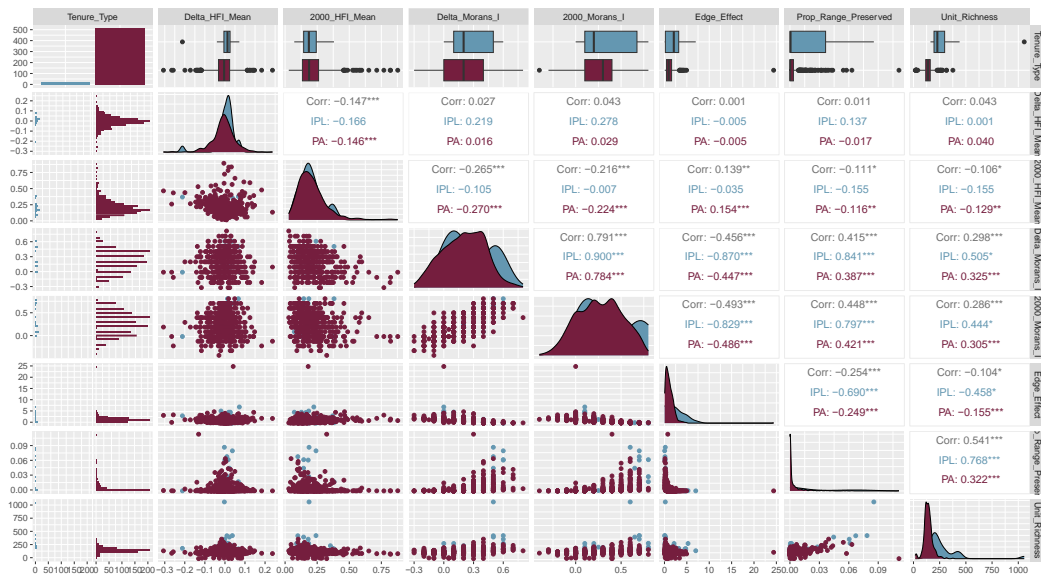
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Supplementary Appendix

Table S1: Correlation, distribution and histogram plots of aggregated species data color coded by Indigenous People's Lands (blue) and Protected Areas (maroon). Correlation coefficients calculated using Pearson's r between all variables included in the model (black), all variables excluding Protected Areas (blue) and all variables excluding Indigenous Peoples' Lands (maroon). Asterix next to correlation coefficients denotes the level of significant.

Table S2: Correlation, distribution and histogram plots of taxa specific data color coded by mammals (purple) and reptiles (dark green), and amphibians (yellow). Correlation coefficients calculated using Pearson's r between all variables included in the model (black), all variables and just mammals (purple), all variables and just reptiles (dark green), and all variables and just amphibians (yellow). Asterix next to correlation coefficients denotes the level of significant.

Table S3: Summary of mammal linear regression model predicting the proportion of species with decreasing population trends. Bolded values indicate significant covariates at alpha<0.05.

Coeffcient	Proportion of Mammals with Decreasing Population Trends		
	Estimates	Conf. Int (95%)	P-Value
Intercept (IPLs)	0.215	0.188 – 0.241	**<0.001**
PAs	0.008	-0.019 – 0.035	0.556
Unit Richness	0.008	0.003 – 0.012	**0.001**
HFI 2000	-0.010	-0.013 – -0.007	**<0.001**
Delta Moran's I	0.002	-0.001 – 0.005	0.119
HFI 2000 x Delta Moran's I	-0.004	-0.006 – -0.001	**0.002**
Observations	498		
R^2 / R^2 adjusted	0.148 / 0.139		

Table S4: Summary of reptile linear regression model predicting the proportion of species with decreasing population trends. Bolded values indicate significant covariates at alpha<0.05.

Coeffcient	Proportion of Reptiles with Decreasing Population Trends		
	Estimates	Conf. Int (95%)	P-Value
Intercept (IPLs)	0.101	0.060 – 0.142	**<0.001**
PAs	-0.040	-0.081 – 0.002	0.060
Proportion of Range Preserved	0.007	0.002 – 0.011	**0.002**
Unit Richness	-0.032	-0.039 – -0.026	**<0.001**
Moran's I 2000	0.005	-0.000 – 0.009	0.051
Proportion of Range Preserved x Unit Richness	0.007	0.003 – 0.012	**0.001**
Observations	441		
R^2 / R^2 adjusted	0.202 / 0.193		

Table S5: Summary of amphibian linear regression model predicting the proportion of species with decreasing population trends. Bolded values indicate significant covariates at alpha<0.05.

Coeffcient	Proportion of Amphibians with Decreasing Population Trends		
	Estimates	Conf. Int (95%)	P-Value
Intercept (IPLs)	0.201	0.082 – 0.319	**0.001**
PAs	0.069	-0.049 – 0.186	0.254
Proportion of Range Preserved	0.168	0.131 – 0.205	**<0.001**
Edge Effect	0.060	0.036 – 0.084	**<0.001**
Unit Richness	0.047	0.026 – 0.069	**<0.001**
Moran's I 2000	-0.015	-0.029 – -0.000	**0.049**
HFI 2000	0.012	-0.001 – 0.024	0.064
Proportion of Range Preserved x Edge Effect	0.192	0.138 – 0.246	**<0.001**
Moran's I 2000 x HFI 2000	0.019	0.007 – 0.030	**0.002**
Observations	447		
R^2 / R^2 adjusted	0.261 / 0.248		