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Spatial co-occurrence of species and language in biodiverse regions: A golden opportunity for conservation

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Abstract

Contemporary Earth is facing a dual-extinction crisis; biologists estimate annual losses of species at least 1000 times that of historic background rates, whilst linguists predict up to 90% of languages could become extinct by the end of the century. Prior research has noted a tendency for biological and linguistic diversity to co-occur in time and space, giving rise to the notion of biocultural diversity. Here we use updated datasets to explore the co-occurrence of biological and linguistic diversity both globally and in those regions which hold the greatest wealth of current biological stock: biodiversity hotspots and high biodiversity wilderness areas. A Biocultural Index was subsequently developed to highlight which regions held the richest biocultural stockpile. Then the cited drivers of biological and linguistic decline were analysed to provide modern-day context to the index. Results indicate that the pattern between language and species is marked: these biodiverse regions account for 62% of investigated languages and 86% of investigated species over just 24% of terrestrial land. Statistical tests for correlation were significant both within and outside biodiverse regions. Reasons for the co-occurrence are complex and seemingly vary between regions, although the strong geographic concordance between language and biodiversity signals some functional connection and opportunity for synergistic conservation. The association between cultural and biological diversity is a golden opportunity for conservation: there is prospect for double payoff when protecting humanity's last biocultural treasure troves if knowledge is combined between linguists, biologists, and the local people who rely on the very lands undergoing the largest changes.

Keywords: biocultural diversity; linguistic hotspots; GIS for biodiversity; biocultural overlap; cultural extinction

(Source: Cristina Mittermeier, 2021)

1. Introduction

Of the challenges faced by modern-day conservationists, tackling global biodiversity loss is one of the foremost. Current extinction rates are exceeding 1000 times that of historical background levels (Ceballos et al., 2015), pushing the world into its sixth mass extinction (Wake & Vredenburg, 2008). Due to its irreversibility, extinction is the severest consequence of the modern biodiversity crisis. Yet, just as undesirable is the lost potential for human-benefiting discoveries: for example, wild species make up the origin of over half of the compounds in all commercial medicines (Chivian & Bernstein, 2008). Only a fraction of the Earth's species have been adequately studied, meaning as they disappear, so too do the vast genetic storehouses that may harbour the next cure for any number of viruses, cancers, or pathogens (Alho, 2008). Thus, it is difficult to overestimate the importance of the last hotspots of biodiversity from a humanitarian or biological standpoint.

Linguistic diversity is in a similar crisis. In some areas, such as the Americas, language loss has experienced a decline of 60% since 1970 (Harmon & Loh, 2010). It is estimated that one language goes extinct every 3.5 months (Rogers & Campbell, 2015) and some linguists predict that by 2100 up to 90% of human languages could fall silent forever (Nettle & Romaine, 2000). For many, linguistic extinction does not evoke outcry: Rupert Murdoch argues that for greater economic efficiency, language homogenisation is necessary (Vines, 1996). Yet, the loss of language signals a loss of difference and a loss of culture. In time, homogenisation would yield people who listen to the same music, eat the same food, and talk the same way. Different beliefs, thoughts, and traditions would become one, and the uniqueness and individuality which makes human culture so rich would fade.

Contemporary research has noted a predisposition for biodiversity and linguistic diversity to co-occur. Inquiries noted that regions holding high biological diversity, such as Mesoamerica, Melanesia, and southern West Africa, also tended to contain high linguistic and cultural diversity (Harmon, 1996; Stepp et al., 2005). Such research gave rise to the notion of biocultural diversity; the sum of the world's differences, including cultural diversity in all its manifestations and biological diversity from genes up to species (Loh & Harmon, 2005). Global linguistic concentrations are marked: almost 70% of the world's languages are spoken over just 24% of terrestrial land, where only one-third of the human population is found (Mittermeier et al., 2004). The general pattern is that of a latitudinal gradient, where language richness increases towards the equator (Collard & Foley, 2002) (Figure 1).

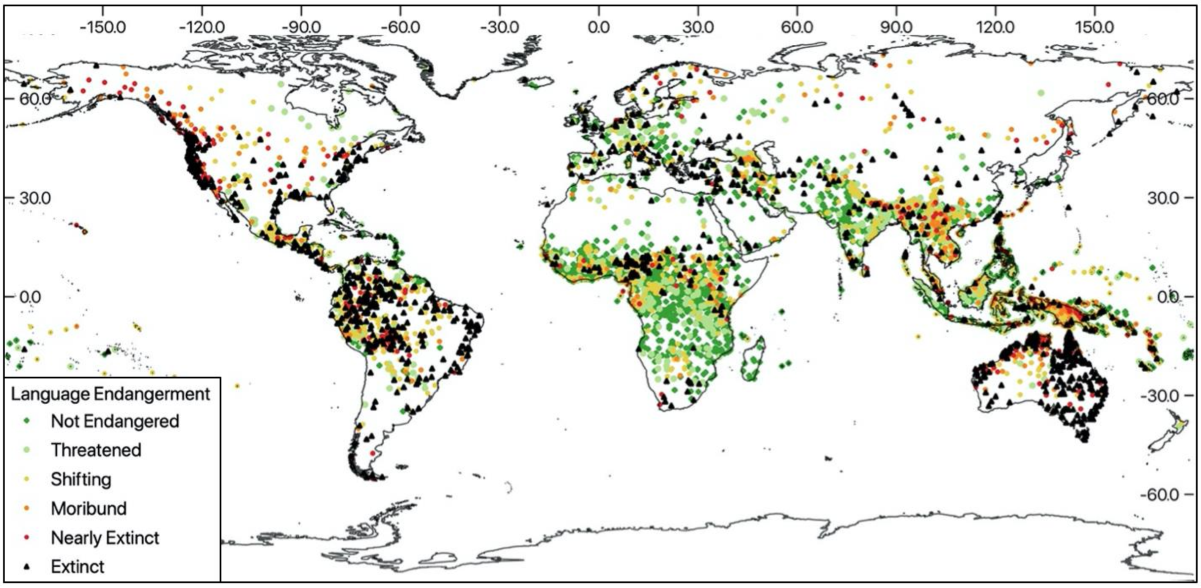

Figure 1: Language endangerment and distribution (Hammarström et al., 2021). Endangerment scale designations derived from Hammarström et al. (2018). Not Endangered = cross generational language; Threatened = some children learn language; Shifting = children not learning language; Moribund = only speakers of oldest generation; Nearly Extinct = infrequently spoken by oldest generation; Extinct = no active speakers. Full descriptions in Supplementary Information.

Many studies have proposed theories on the cause of this relationship. Some propose the ecology of human societies, whereby plentiful diverse resources — meaning a lower ecological risk — reduces any need to communicate with other groups in times of need (Larsen et al., 2000). In support of this ecological risk hypothesis, studies have identified correlations between language diversity and climatic variables such as mean growing seasons (Marsico & Pellegrino, 2013) and environmental productivity (Moore et al., 2002). Substantial irregularity in linguistic diversity with respect to biological diversity across many regions suggests that the underlying mechanisms are complex and could differ from place to place.

Regardless of the causes, of the >7100 languages currently spoken on Earth, over 4800 befall in "hotspots" housing high biological diversity (Gorenflo et al., 2012). The concept of hotspots was first described by Myers (1988), who designated ten tropical forest areas based off extraordinary plant endemism and rapid habitat loss. Through further research and better data availability, this theory culminated into a landmark publication (Myers et al., 2000) which identified 25 biodiversity hotspots from quantitative criteria: each contained >1500 vascular plants as endemics and had less than 30% original vegetation cover remaining. Biodiversity is not evenly allocated on Earth, so regions with high concentrations of endemism offer an exclusive opportunity to protect many unique species that cannot be protected elsewhere. Owing to this, the current 36 hotspots have moved to the forefront of global conservation efforts (Mittermeier et al., 2011). These hotspots — which are under the greatest pressure from human disturbance — highlight where the largest victories could occur regarding global conservation battlegrounds.

In 2003, Mittermeier et al. complemented the hotspot theory by identifying areas they termed high-biodiversity wilderness areas. These areas, in addition to retaining 70% of original habitat cover and harbouring >1500 plant species as endemics, were defined by a human population density of <5 people per km^2. This gave a strategic advantage to conservationists: as hotspots demand immediate and expensive protection to prevent substantial losses, conserving those untrammelled yet biodiverse wilderness areas provided a lower cost, equally as proactive mitigation technique (Brooks et al., 2006). Together, the 36 hotspots and five wilderness areas (Figure 2) shelter 63% of all mammals and 79% of all amphibians as endemics (Mittermeier et al., 2011). As both designations are defined by biological criteria, the parallel with language diversity is a fortunate coincidence for biological and linguistic conservation alike.

Given that these measures of biocultural diversity co-occur in time and space, it is perhaps unsurprising that Loh and Harmon (2014) determined that global language and biodiversity declines had almost perfectly mirrored one another: falling by roughly 30% in around 40 years. Yet, significant regional variability remains. For example, language counts fell by approximately 30% in the Indo-Pacific, whereas species diversity in the region fell by over double that across an identical time frame. This indicates different drivers of change — or different strengths of drivers — between different biocultural hotspots. Drivers of biodiversity decline have been well documented (Clavero et al., 2009; Wood et al., 2013) and it is usually the result of at least one of habitat loss, over-exploitation, alien species invasion, climate change, and pollution (Xu et al., 2019). Over the last 40-50 years, habitat loss has been most rapid across the developing world, confined mostly to the tropics, where the greatest biological diversity is found (Loh & Harmon, 2014). For language and culture, the equivalent measure for habitat would be human population, which has more than doubled since 1970, so is clearly not the problem. There is no cultural analogue to over-exploitation either, so the equivalent to invasive species, language shift, takes residence as the greatest individual threat to language and cultural diversity. Unlike with invasive species, there is no replacement of a human population, instead there is a displacement of smaller language by a larger, more widespread dialect (Gal, 2008). Language shift is driven by a complex array of social, political, and economic factors, including the globalisation of trade and media, migration, and urbanisation. These drivers inherently increase pressure on those languages with thousands or fewer speakers that are already on the periphery of global conversations. Today, the disparity between languages is extreme: half the world speaks one of 24 languages, whilst around 0.1% of the global population, equivalent to a city the size of London, are responsible for keeping 50% of linguistic diversity alive (Loh & Harmon, 2014). Some linguists argue this places language and culture in a far more threatened bracket than biodiversity. The balanced dynamism in the case of species extinction, where new species emerge as old ones die, does not occur in the linguistic realm (Upadhyay & Hasnain, 2017). Nonetheless, the present-day rate of decline in biodiversity is happening far too rapidly for any evolutionary processes to counteract. Ultimately, both linguistic and biological diversity are diminishing at alarming rates as a result of human population growth, growing consumption, and globalisation.

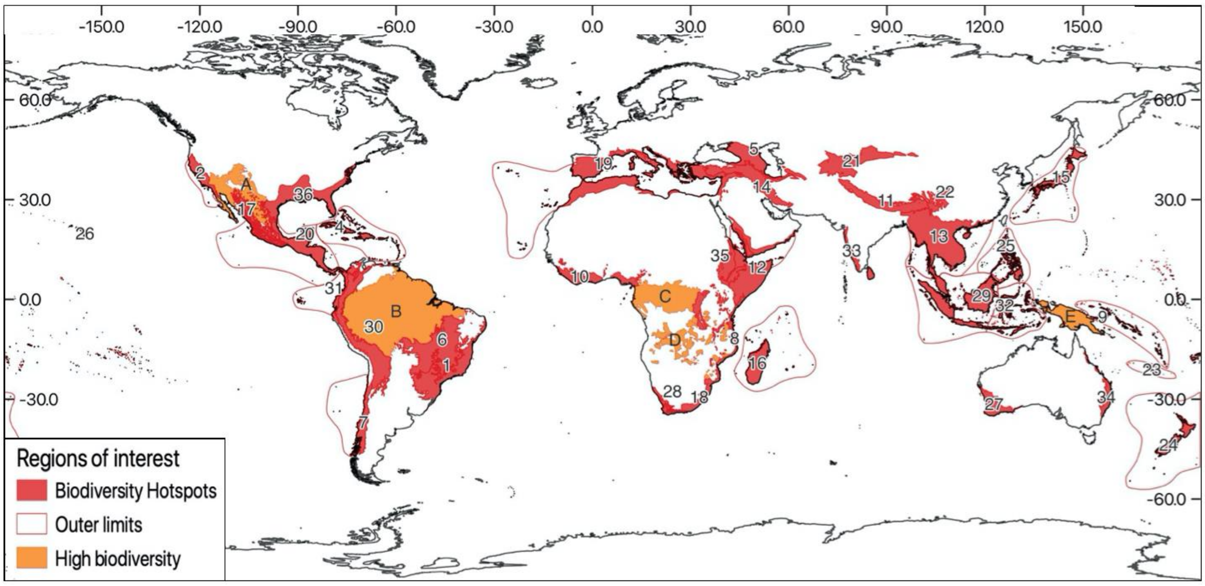

Figure 2: Biodiversity hotspots (1-36) and high biodiversity wilderness areas (A-E). Derived from Myers et al. (2000) and Mittermeier et al., 2003. A: North American Deserts; B: Amazonia; C: Congo Forests; D: Miombo-Mopane Woodlands and Savannas; E: New Guinea. 1: Atlantic Forest; 2: California Floristic Province; 3: Cape Floristic Region; 4: Caribbean Islands; 5: Caucasus; 6: Cerrado; 7: Chilean Winter Rainfall and Valdivian Forests; 8: Coastal Forests of Eastern Africa; 9: East Melanesian Islands; 10: Guinean Forests of West Africa; 11: Himalaya; 12: Horn of Africa; 13: Indo-Burma; 14: Irano-Anatolian; 15: Japan; 16: Madagascar and the Indian Ocean Islands; 17: Madrean

Pine-Oak Woodlands; 18: Maputaland-Pondoland-Albany; 19: Mediterranean Basin; 20: Mesoamerica; 21: Mountains of Central Asia; 22: Mountains of Southwest China; 23: New Caledonia; 24: New Zealand; 25: Philippines; 26: Polynesia-Micronesia; 27: Southwest Australia; 28: Succulent Karoo; 29: Sundaland; 30: Tropical Andes; 31: Tumbes-Choco-Magdalena; 32: Wallacea; 33: Western Ghats and Sri Lanka; 34: Forests of East Australia; 35: Eastern Afromontane; 36: North American Coastal Plain.

Earlier studies have reported the congruence of language and biological diversity (Gorenflo et al., 2012), formed per-country biocultural indices for global comparisons (Loh & Harmon, 2005), and identified multiple drivers of biocultural endangerment (Amano et al., 2014). This investigation deems that the next logical step would be to aim to (i) confirm any analogy of biocultural diversity in hotspots and wilderness areas that Gorenflo et al. (2012) proposed, under the addition of updated language data and a new biodiversity hotspot: the North American Coastal Plain (Noss et al., 2015); (ii) provide a bottom-estimate index of biocultural diversity within biodiverse regions to deliver a snapshot of diversity distribution from which comparisons can be made; and (iii) indicate a spatial change of some major drivers of biocultural decline: show where they are increasing to highlight areas which could come under greater stress in the future. These aims will be achieved through the use of Geographic Information System (GIS) software. As the study of biocultural diversity involves proving relationships and causal factors across space, GIS provides a widely-used tool for such analysis whilst working to guide further enquiry through the establishment of working methods for research (Stepp et al., 2004). Once any links are determined, they can indicate which regions should be prioritised for protection regarding both their biocultural stockpile and the risk of losing it. Knowledge gained could inform policy decisions and further research concerning the protection of biocultural hotspots. The dual extinction crisis could actually become a golden opportunity for conservation: there could be a double payoff concerning the protection of humanity's last biocultural treasure troves if expertise between linguistics and biology are shared. Not only would biological and cultural diversity be preserved in those areas where it first evolved, but the under-threat and under-appreciated traditional knowledge in these regions could become better valued, perhaps being applied elsewhere to further combat the threats to these two pillars of human existence.

2. Method

As with any large-scale mapping project, analysis opened with data acquisition, organisation, and standardisation (Table 1). It was decided early on to rely as little as possible on data defined by political boundaries, and thus to focus on biocultural distribution geographically rather than politically. The resultant spatial database included: biodiversity hotspots and high biodiversity wilderness areas (referred to together as biodiverse regions through this report); biodiversity (amphibian distributions), cultural diversity (language distribution), economy (gross domestic product), poverty (infant mortality rates), and human pressure on the environment (human footprint dataset).

Amphibians have long been regarded as a suitable bioindicator species (Welsh Jr & Ollivier, 1998) owing to their philopatric nature, well-sampled numbers, and sensitivity to aquatic and terrestrial perturbations (Townsend & Driscoll, 2013). Language's suitability as a proxy for cultural diversity lies in its similarities to the evolution of species. Just as the Cambrian explosion redefined the meanings of biological diversity, 70-80,000 years ago humans began to migrate, talk, and generate diversity of language, developing it into the essential medium for expression of culture (Gong, 2010).

Table 1: List of major datasets used in this study

Dataset	**Detail**	**References**
(Language Data) Glottolog world languages	8533 language points and assigned endangerment levels (7917 used in analysis).	Hammarström et al. (2021); Lee and Van Way (2018)
(Species Data) IUCN amphibian red list	Most threatened vertebrate group. Shows 8598 species extents globally as shapefiles.	Rodrigues et al. (2006)
(Spatial Data) Biodiversity hotspots	36 globally recognised hotspot regions and extents as shapefiles.	Noss et al. (2015)
High biodiversity wilderness areas	5 wilderness areas with lower human pressures as shapefiles.	Mittermeier et al. (2003)
(Driver Data) Human footprint	Two raster datasets from 1993 and 2009 on human pressures combining: built environments; population density; electric infrastructure; crop and pasture lands; roads; railways; and navigable waterways.	Venter et al. (2018)
Gross Domestic Product (GDP)	Proxy for economy. Two raster datasets from 1990 and 2015 to derive economic growth over time.	Kummu et al. (2018)
Infant Mortality Rate (IMR)	Proxy for poverty. Two raster datasets from 2000 and 2015 to derive poverty changes over time.	CIESIN (2021)

Data unavailability prevented language extents or speaker numbers from being obtained; however, this was not considered a major limitation. Languages represented by geographical centre-points of the area where speakers live are not particularly problematic on a global scale (Stepp et al., 2004) and aided in maintaining that languages in biodiverse regions were more likely to be endemics. Language richness has been used widely as an indicator of linguistic diversity (Skutnabb-Kangas, 2002; Upadhyay & Hasnain, 2017), yet it does exclude evenness measures. As the focus of our study was exclusively on non-migrant languages, a double-edged mitigation technique to this was to remove the 24 most spoken languages from the dataset. As half the world speaks one of these dialects (Loh & Harmon, 2014), it reduces both evenness and migrant language issues. Languages were then assigned endangerment ranks from the Glottolog language database (Hammarström et al., 2018). Any languages that were secret, unclassified, or without coordinates and endangerment status were removed, resulting in 7917 extinct, sign, and spoken languages for analysis.

Then the database was mapped in QGIS. All explanatory variables were aggregated onto a 2-arc-degree grid, with each grid cell accounting for the number of amphibians or languages found within. Grid-based approaches eliminate data variances from differences in area (Jenelius & Mattsson, 2012). Amphibians and languages were also mapped per biodiverse region, allowing repeat analysis under different spatial confines. Resultant grid-derived values were analysed in GeoDa (spatial analysis software) and tested for correlation via Pearson's and Spearman's correlation coefficients, and also spatial correlation via Moran's I. The results that were bound by biodiverse region extents were used to form a Biocultural Index (Table 2). The Biocultural Index (BI) is equal parts cultural diversity (CD) as language richness, and biodiversity (BD) as amphibian species counts.

$$BI = \frac{CD + BD}{2}$$

To derive scores for CD and BD, a biodiverse region's richness was compared to the global value. For example, with biodiversity, BD is calculated as the log number of species per biodiverse region (B_{br}) divided by the log number of global species (B_{world}).

$$BD = \frac{log\ B_{br}}{log\ B_{world}}$$

Table 2: Biocultural Index workings (full Biocultural Index in Supplementary Information)

Region	Languages (L)	LogL	LogL/ Logworld	Amphibian species (A)	LogA	LogA/ Logworld	Biocultural diversity index
World	7917	3.90	1	8598	3.93	1	1
All hotspots	4877	3.69	0.95	8039	3.91	0.99	0.97
New Guinea (highest)	1009	3.00	0.77	560	2.75	0.70	0.73
Mean	119	2.01	0.53	251	2.40	0.61	0.57
New Zealand (lowest)	2	0.30	0.08	8	0.90	0.23	0.15

A modified use of the species-area relationship (Supplementary Information) allowed for the prediction of expected languages and species per biodiverse region to identify regions with more or less diversity than expected. A Biocultural Index has applied and hypothetical implications. For policymakers, it can act as a framework guiding the allocation of resources when scrutinising biocultural change, and for academics it provides a global context within biodiverse regions, against which more fine-grained analyses can be compared.

Datasets of commonly cited drivers of biocultural decline will then be explored to indicate where the strength or distribution of drivers of biocultural change is developing. Larger pressure on the environment will be inferred from the changes in the driver pressure over time, under the assumption that the drivers have direct influence on biological and linguistic diversity loss on a global scale. This will allow for further inferences to be made in regards to the index, to identify if those areas with the greatest calculated biocultural richness may also be under the greatest pressure.

3. Results

The geographic allocation of languages implies concentrations in expanses of high biodiversity (Figure 3). 4877 (62%) of all language points befell in biodiverse regions whose maximum extents cover just 24% of terrestrial land. New Guinea (1009 languages) dominated counts holding more than double the next highest region: Indo-Burma (428).

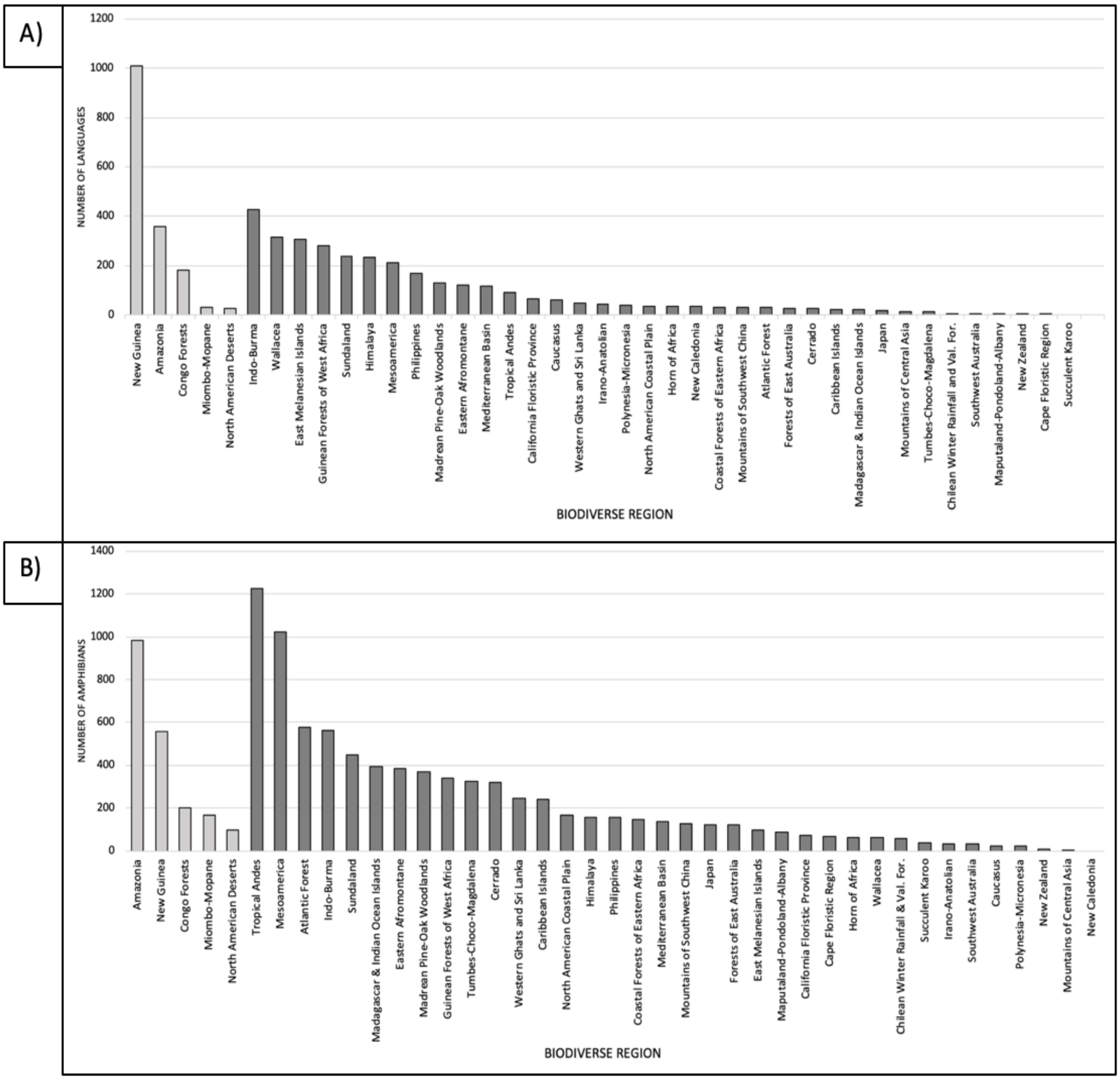

Figure 3: A) Number of Languages per hotspot (dark grey) or wilderness area (light grey); B) Number of amphibian species found in each hotspot or wilderness area

However, when New Guinea is removed from calculations, the biodiverse regions still retain just under half the languages in the world in less than a quarter of its terrestrial land.

Species counts highlighted that 8039 (86%) of amphibians can be found within biodiverse regions. Though, these figures were heavily influenced by the Amazonia, Tropical Andes, and Mesoamerica regions which housed over 40% of all amphibians found in biodiverse regions.

When adjusted for area size, many smaller biodiverse regions replaced larger ones. New Caledonia (35 languages in 18,000 km^2) and Polynesia-Micronesia (41 languages in 46,000 km^2) moved into the top five most linguistically-dense regions, whilst the East Melanesian Islands (306 languages in 99,000 km^2) overtook all other biodiverse regions (Figure 4). Differences between wilderness areas and hotspots appeared large but just stemmed from overall area: Hotspots housed just over double the languages (3274) and area (24.5 million km^2) than wilderness areas (1603; 11.8 million km^2). Comparing biodiverse region species count with number of languages via linear regression suggested a weak but significant, positive relationship: Pearson's $r = 0.39$; $P < 0.02$ and Spearman's coefficient: $r = 0.45$; $P < 0.01$.

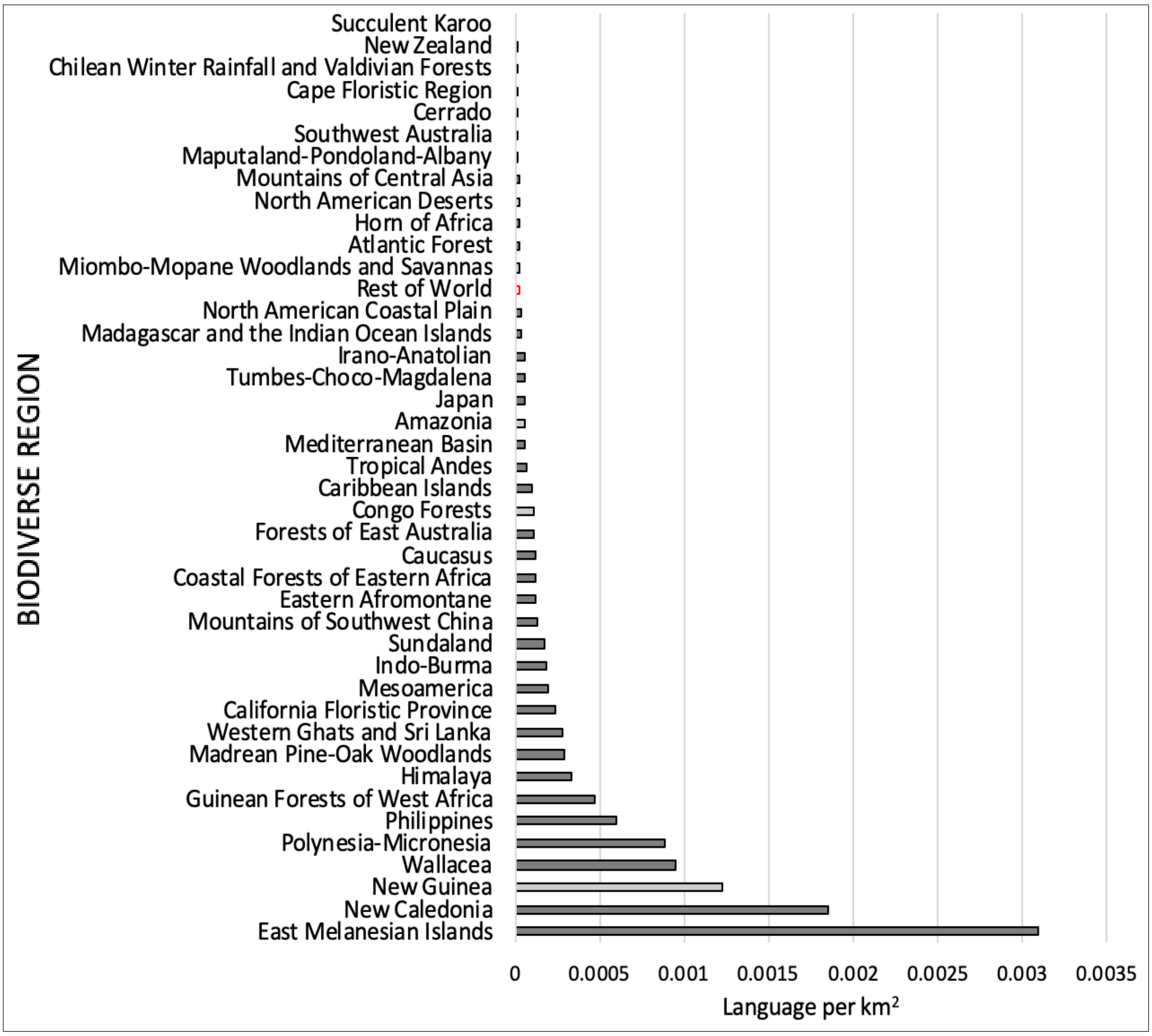

Figure 4: Language per area in biodiverse regions constructed to account for the area bias in results. Twelve Biodiverse Regions hold a lower language density than the global average (shown in red).

When the bounds of the biodiverse regions are discounted, areas of high biodiversity and linguistic diversity generally increase towards the equator, corresponding to areas typically designated biodiverse regions (Figures 5A and 5B), with various densities in the measures of biocultural diversity (Figure 5C). Other than New Guinea and the Amazonia, another cluster appears outside the biodiverse regions to the north of the Guinean Forests of West Africa, where modern-day Nigeria lies.

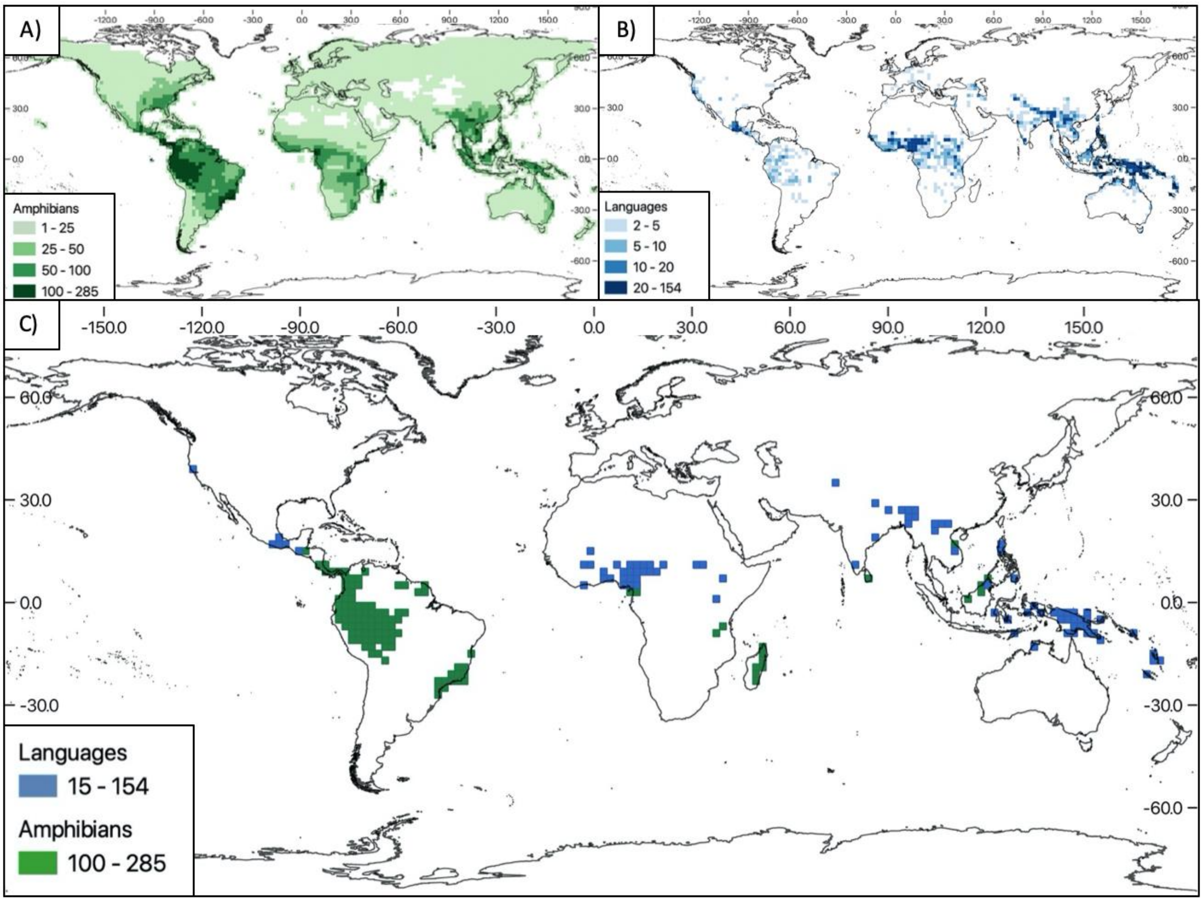

Figure 5: A) Grid-based global distribution of amphibian species, highs of 285 species per grid in the Tropical Andes. B) Grid-based global language distribution, highs of 154 per grid in New Guinea. C) Areas of highest language and species richness.

Statistically analysing the spatial co-occurrence uncovered a positive Moran's index z-score of 29.5 ($I = 0.239$; $P < 0.001$), meaning there is less than a 0.1% chance that the observed clustering could be down to chance. This observation was supported by linear regression results which uncovered a strong, positive Pearson's r value of 0.68 ($P < 0.001$) and a Spearman's coefficient r of 0.62 ($P < 0.001$). These results show that the correlation between language and species diversity is highly significant globally and led to the further identification of clusters of diversity and statistically significant grid squares.

Under 999 permutations, significant local statistic clusters were found outside the biodiverse regions in northern Argentina and the United States of America (Figure 6), although most clusters transpired within the bounds of the tropics and overlapping decidedly with hotspot boundaries. The cluster map (Figure 7) augments the significance map by indicating the type of spatial association. Here the high biodiversity and high language areas occurred almost exclusively within the Tropic of Cancer and New Guinea. However, the cluster present in the central belt of Africa fell outside most hotspot designated zones, again promoting Nigeria as a linguistically diverse expanse. There appeared to be a western bias for high biodiversity and an eastern bias for high linguistic diversity, exampled by only three grid squares promoting low biodiversity and high language across the entire Americas, and just 12 squares fostering the opposite relationship across all of Asia and Australasia.

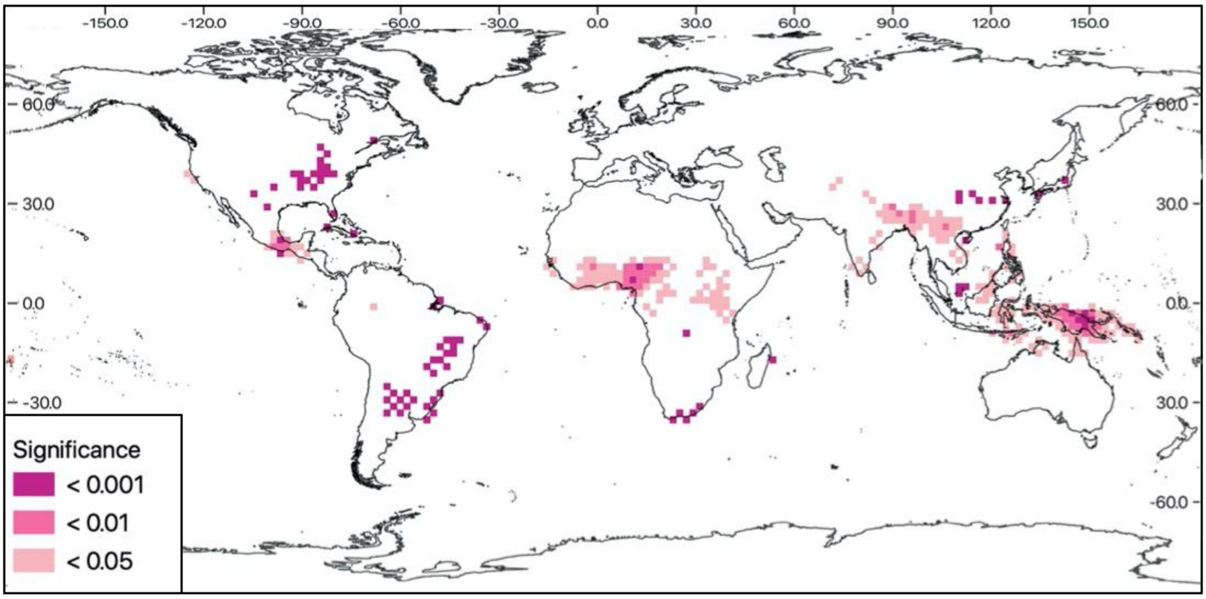

Figure 6: A significance map for the correlation between gridded language richness and species richness globally

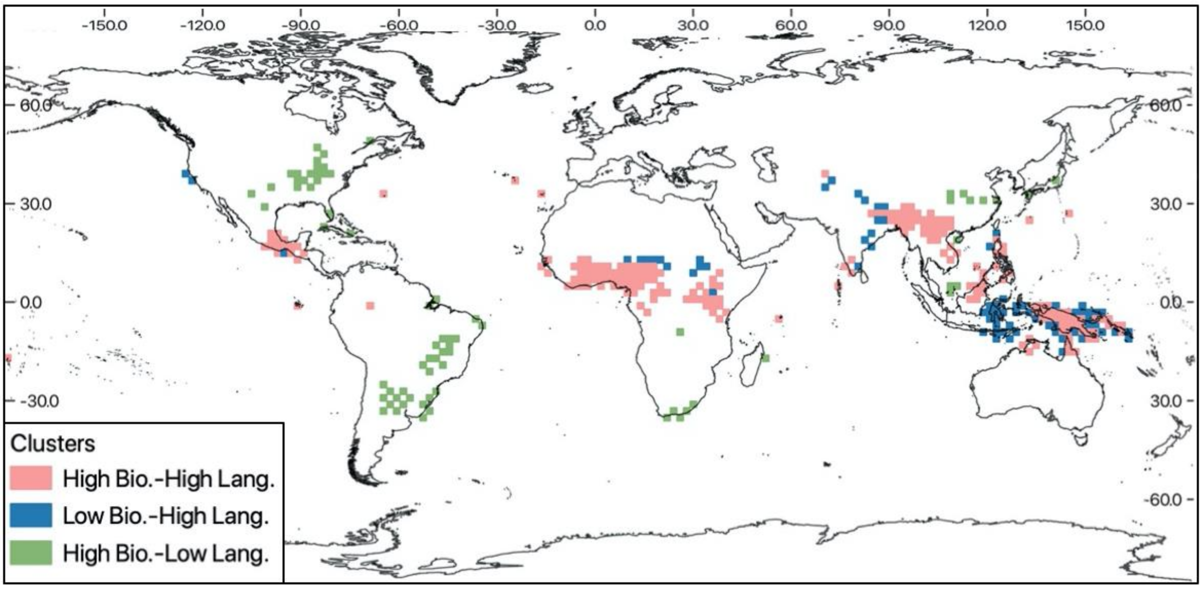

Figure 7: A cluster map extending the correlations demonstrated in Figure 6 by identifying the type of relationship within the grid squares

The Biocultural Index identified seven key regions (Figure 8) with very high Biocultural Index scores: New Guinea (0.73); Amazonia (0.71); Indo-Burma (0.69); Mesoamerica (0.68); Tropical Andes (0.64); Sundaland (0.64); and Guinean Forests of West Africa (0.64). The mean hotspot index score was 0.57, which would hold, on average, 119 languages and 278 amphibian species within its bounds. This dwarfs the mean value for the rest of the world, which in an area the size of the average biodiverse region: 885,300 km^2 (roughly the terrestrial area of Tanzania), would expect to house just 24 languages and 16 amphibian species.

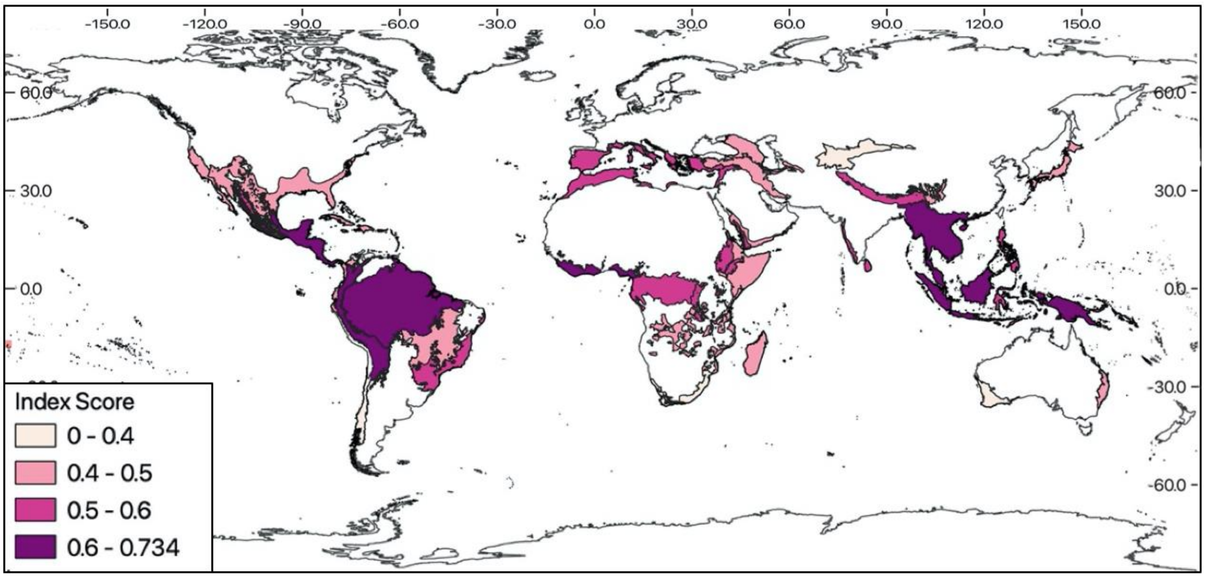

Figure 8: Biocultural index scores of the biodiverse regions as demonstrated on a map. Range: 0.15 (New Zealand) to 0.73 (New Guinea)

The adjusted species-area relationship led to expected diversity calculations which noted regions for their deviation from the biocultural richness that would be expected based off region area. Some regions maintained their positions as leaders in this new ordering: New Guinea (+0.9 log deviation from expected biocultural diversity), Mesoamerica (+0.61), and the Guinean Forests of West Africa (+0.6). However, now areas which covered less terrestrial land showed they house significantly more biocultural diversity than would be expected for a hotspot of their size: East Melanesian Islands (+0.83), and the Philippines (+0.52). Though, the Mountains of Central Asia, New Zealand, and Southwest Australia all fell well below the expected biocultural diversity for biodiverse regions.

When investigating which regions had gone under the largest recent changes in driver magnitude, the GDP (gross domestic product) per capita of six biodiverse regions had more than doubled: Indo-Burma (+156%); Chilean Forests (164%); Himalaya (176%); Guinean forests of West Africa (203%); Western Ghats and Sri Lanka (243%); and the extreme increase of 747% experienced in the Mountains of Southwest China. Australian and North American regions had comfortably the highest mean GDP per capita by 2015, with Southwest Australia reaching over 60,000 USD (GDP per capita in constant 2011 international USD). The top five IMR (infant mortality rate) values in both timestamps were exclusively found in biodiverse regions on the African continent: 88-127 mean deaths per 1000 births in 2000 and 50-72 in 2015. Although, all African countries improved their IMR more than New Guinea, Succulent Karoo, and Indo-Burma, which all only reduced their high IMRs by less than 9 deaths per 1000 births across the 15 years.

Analysing area loss in the biodiverse regions due to all measures of human pressure (Figure 9) showed obvious over-estimates, as total biodiverse region area dropped tenfold from 24% to 2.4% of global terrestrial land cover. We then constructed a high-pressure dataset, where only more direct obstructions to biocultural security endured. Area loss due to the developing human footprint was felt heaviest in the Cerrado, Amazonia, and New Guinea regions, all of which saw estimated losses of over 225000 km^2. Five hotspots retained less than 8% of their original extents, championed by the Western Ghats and Sri Lanka, which was reduced to <1% of original land cover. All high biodiversity wilderness areas retained over half their cover, whereas only four biodiversity hotspots managed this feat.

4. Discussion

The results presented here confirm a general clustering of both biodiversity and language towards the equator on a global scale that was backed by statistical results both within and in absence of biodiverse region boundaries. The significant results show a co-occurrence between linguistic diversity and biodiversity that mirrors outcomes of previous research (Loh & Harmon, 2014). The patterns observed in Gorenflo et al. (2012) are confirmed under the addition of the most recent biodiversity hotspots, achieving the first aim of this analysis. Results here show a slightly stronger correlation ($P < 0.02$) within biodiverse regions than Gorenflo et al. (2012) ($P < 0.05$), though this may have been down to use of amphibian species as a bioindicator rather than total vascular plant species per region. Amphibian assemblages are heavily influenced by forest cover and wetland hydroperiod (Herrmann et al., 2005), and as the most common habitat type within biodiverse regions is tropical rainforests (Smith et al., 2001), they may have a stronger association with biodiverse regions than other bioindicators. The second aim was achieved upon construction of the Biocultural Index; the resultant scores provide a bottom-estimate of the biocultural diversity within biodiverse regions. Although all biodiverse regions are defined by their biological characteristics, not all regions are created equal; the Biocultural Index noted great variation in biodiversity between biodiverse regions (0-1024 amphibian species per region). This pattern was again likely influenced by the use of only one biological indicator, as some biodiverse regions, particularly islands such as New Caledonia and New Zealand, fall short in their housing of amphibians despite high levels of endemic plants. The spatial and numerical changes in the drivers of biocultural decline were mapped and analysed to achieve the third aim. In biodiverse regions the infant mortality rate was higher and the GDP per capita was lower than the world average across the whole timeframe, confirming these areas as typically being located in developing countries (Fisher & Cristopher, 2007). Analysis of these datasets and the literature allowed for interpretations on the perceived risk to certain biodiverse regions, allowing for the output of the Biocultural Index to be placed in a contemporary context of evolving human pressure.

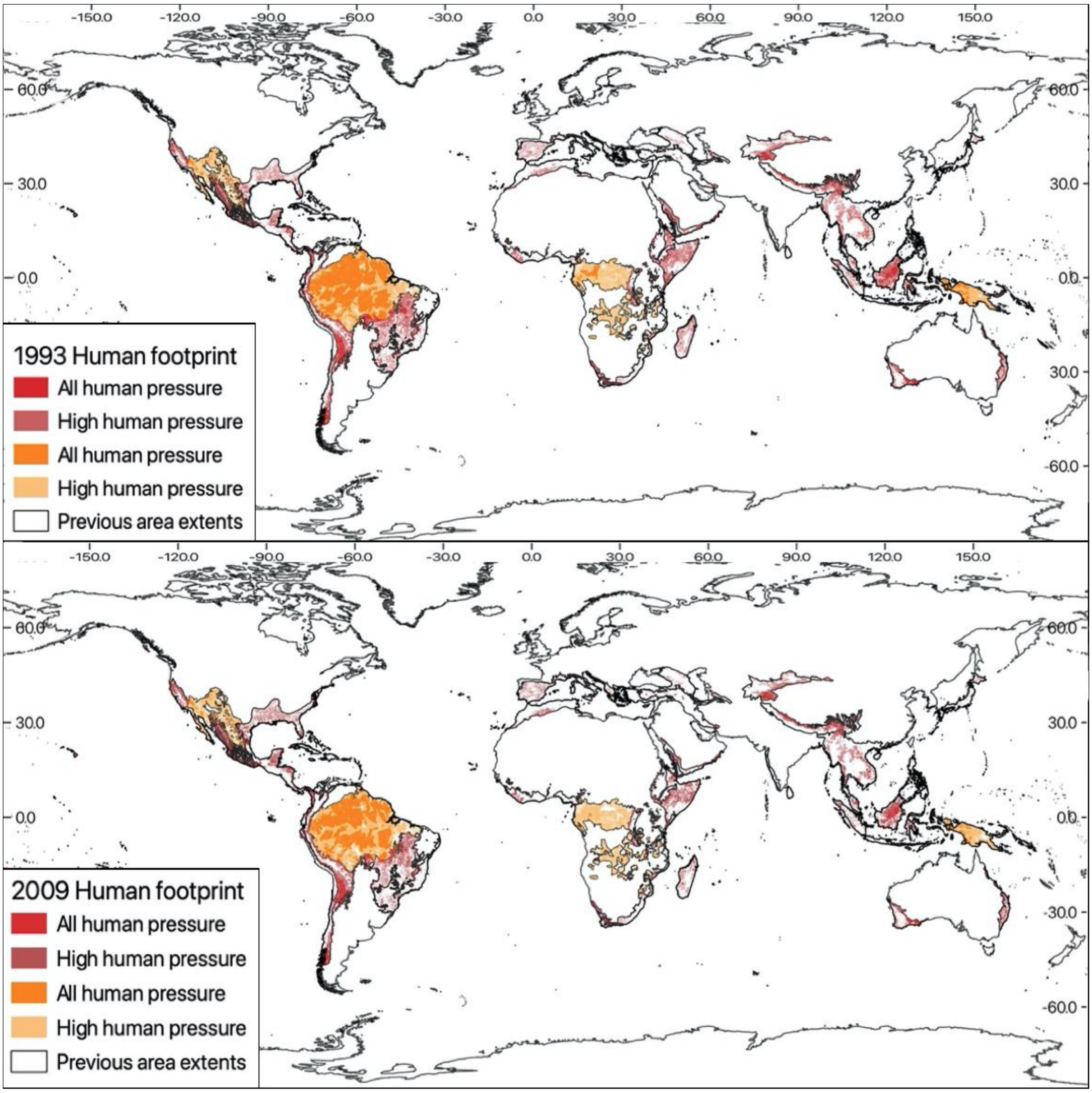

Figure 9: Biodiverse region extent under varying pressure in (A) 1993 and (B) 2009 (Venter et al., 2018). Area remaining untouched by high human pressure fell from 12.4% to 10.9% across the time period as the human footprint grew.

4.1. The global co-occurrence

Despite high biocultural heterogeneity between biodiverse regions, these areas hold a disproportional amount of both language (62%) and species (86%) richness. This value could have been even higher if not for a lower resolution of language data of ±55.5km accuracy with coordinates. A buffer-analysis +55.5km around biodiverse regions found that 5917 (75%) of studied languages then fell within the boundaries, indicating that many languages find their origins in close proximity to biodiverse regions if not within them. If a redeveloped hotspots framework included some aspect of culture within its foundation, perhaps these languages would inhabit the same designation as the biodiversity. Future research could identify bounds of linguistic hotspots — much like Myers et al.'s 2000 paper did with biodiversity — and find exactly where the overlaps lie. Such a process should not be undertaken to demand where biocultural conservation should occur, but rather to indicate which areas may be suitable for research or conservation at smaller scales. Early work identifying language hotspots based off extinction risk was prepared by Anderson (2011). However, his pleas for a comprehensive approach to tackle the language extinction crisis fell on deaf ears. Quantifiable data on language endangerment, speaker extents, and number of speakers are slowly becoming more available. Thus, the prospect of a more developed framework appearing in the future is likely. This would lead to quantification of the extents of language diversity and their relation to biodiversity, allowing researchers and policymakers to go a step further in confronting the twofold-extinction emergency before identifying which regions require immediate attention.

No proportional difference was identified in the language-area relationship between biodiversity hotspots and high biodiversity wilderness areas in our study. This is despite a definitive trait of wilderness areas being a lack of people (<5 people per km^2). Gorenflo et al. (2012) demonstrate that a higher proportion (77%) of the languages spoken in wilderness areas are spoken by <10,000 people than in hotspots (48.5%). However, they did not discuss this pattern. Within our work, there was no estimate of speaker numbers available. Yet, out of active languages, the proportion of threatened dialects was also higher in wilderness areas (65%) than in hotspots (60%). Although not as stark a difference as observed in their paper, this pattern goes some way to explaining why there appears to be no less language richness in areas with fewer people. The languages spoken in wilderness areas have fewer active speakers and can consequently be considered at more risk of extinction. Future research should explore evolving speaker estimates over time to continue to monitor if this pattern arises or changes, to allow for comparisons between ecoregions and subsequent estimates of regional speaker declines over time.

The longitudinal bias (Figure 7) is hypothesised to have occurred partly due to differences in historical suppression of cultural diversity; whereby, for example, native Americans have gone through a long history of war and oppression at the hands of predominantly European settlers (Smith, 2011) causing the linguistic diversity of the Americas to decline. This, coupled with extensive contemporary deforestation and habitat loss in Southeast Asia (Reddy et al., 2018), goes some way to explain the cause of this pattern. An additional consideration should be made regarding the underreporting of language in the Amazonia; incomplete documentation has led central parts of the Amazon to be described as the least understood linguistic expanse on Earth (Dixon & Aikhenvald, 1999). In conclusion, associations between language diversity and species diversity are likely caused by shared causal factors such as climate, landscape, and resource availability (Hua et al., 2019). However, variances at similar latitudes likely occur due to a myriad of historically contingent events that could be culturally unique such as conflict, migration, and religion.

4.2. The Biocultural Index

An index is only as good as the underlying data that is included within it. Inclusion of endemic flora, for example, would have catapulted New Caledonia to the top as it has one of the highest observed rates of floral endemism in the world, with, on average, a new species found every month (Gâteblé et al., 2018). Progressing indices such as the Biocultural Index presented here involves including more data and complexity. Although the purpose of any index is to use simple proxies to signpost more complex phenomena (Loh & Harmon, 2005), this index could benefit from an extra measure of biodiversity (endemic plant richness) and/or cultural diversity (religious diversity). Taken a step further, future research could combine indices with data on drivers of change to create an index of perceived risk of loss as well as biocultural diversity. Such indices highlight areas which were not only of biocultural significance, but could quantifiably relate this to risk of loss. As more and better spatial data become available — for example, number of speakers, species populations, or religion — it will be possible to analyse spatial occurrence of a multitude of measures of biocultural diversity and to explore trends over time. Then the crucial question regarding the rate of global biocultural change could be answered. Whilst such indices are simplistic, they often prove a useful tool for academics, policymakers, and the general public to swiftly order and weigh the importance of biodiverse regions against other designations or ecoregions.

4.3. The driver evolutions

Analysis of the drivers causing biocultural loss helped to identify and predict which regions are under the most stress from humans. Linear distance between human settlements and ecoregions cannot capture the variety of human influences on the environment, such as road incursion, landscape heterogeneity, or river access (Maire et al., 2016). In a certain regard, such linear measures have become obsolete. As the human footprint is so vast, widespread, and multifaceted in the modern era, hardly any unrestricted expanses of environment remain. This consideration is what led to the inclusion of more complex phenomena to act as proxies for drivers of biocultural decline, though this inherently came with more complex assumptions underlying any identified relationships. IMR has been widely used as a proxy for poverty (Zhou et al., 2017), and links between poverty and unsustainable exploitation of habitats have too been shown (Ivić, 2019). For example, an urgent need for food, income, and shelter can lead to rapid degradation of the environment

(Farajollahi et al., 2021). However, some studies signal more multifarious links between IMR and degradation, whereby environmental degradation itself can exacerbate infant mortality in less developed countries (Jorgenson & Burns, 2004). The relationship between the two is likely not to be as one-dimensional as portrayed in our results, and the affiliation may require more studies at a local scale, but is useful in a global context, to achieve a better understanding of this dynamic in future models.

GDP per capita has long been cited as one of the principal drivers of recent language speaker declines (Amano et al., 2014) through associated socioeconomic, political, and educational developments (Austin & Sallabank, 2011). Areas with consistently high GDP per capita, such as Australia and the USA, have been observed to have a positive effect on speaker range size and language extinctions (Amano et al., 2014). This pattern was present within our study, as these two regions only held five non-endangered languages between them whilst also fielding the greatest concentrations of extinct languages (Figure 10). In fact, the Australian language family is the most endangered in the world (Loh & Harmon, 2014), with 94% of its languages either extinct or nearly extinct since 1970. This finding supports the extinction filter hypothesis (Balmford, 1996) whereby language declines in high-GDP regions have already pushed smaller-ranged languages to extinction, so only large-range, major languages remain. This hypothesis, which has also been observed in mammals (Turvey & Fritz, 2011), causes these areas to appear less prone to future language losses than their higher GDP may predict them to be.

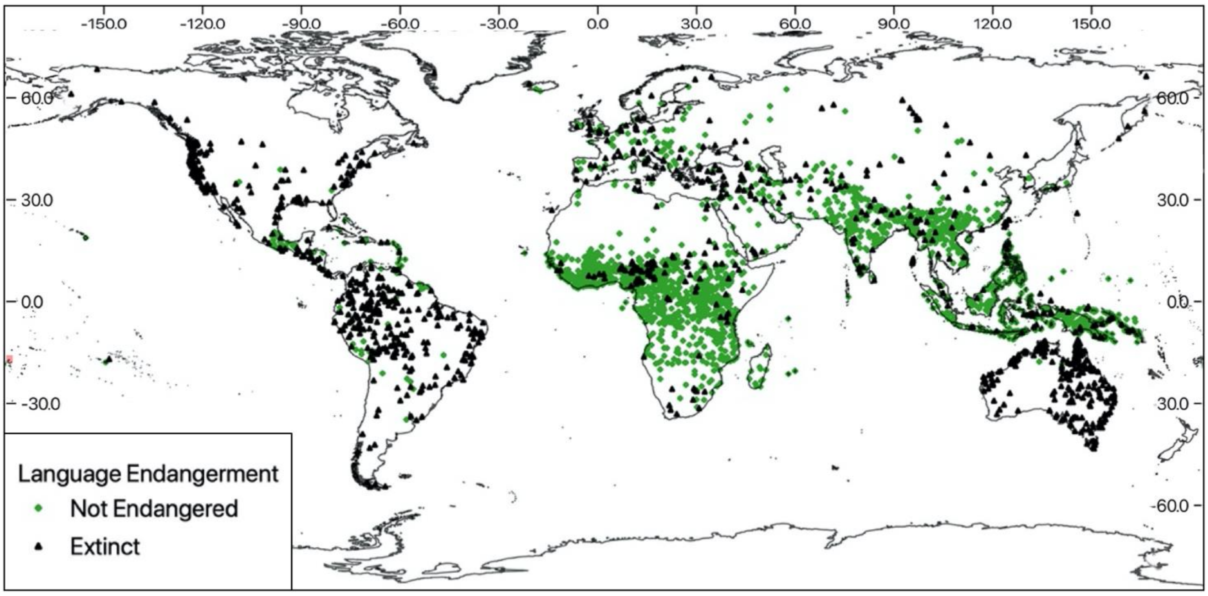

Figure 10: Global distribution of non-endangered and extinct languages where greatest densities of extinct languages share space with less, more widespread, non-endangered dialects

The six biodiverse regions noted for large increases in GDP per capita will have mixed influence due to the extinction filter hypothesis. Indo-Burma, Himalaya, and the Guinean Forests of West Africa all have great linguistic diversity with comparatively few extinctions to date. Rapid rises in GDP here will likely result in increased pressure on the smaller-range languages spoken by fewer people here. Contrastingly, the mountains of Southwest China, Western Ghats, and Chilean forests all house relatively low language numbers with multiple extinctions to date. This results in fewer active languages in these regions. We predict that these areas will experience proportionally less language loss than the other three mentioned. We further theorise that greater deviations between mean regional GDP signal more disparity of wealth, more marginalisation of the poor, and more shifts towards larger cities and languages. This would have a disproportionate impact on habitats and culture than a more uniform GDP rise and should be explored further within biodiverse regions.

The human footprint dataset visualised that there are almost no true wilderness expanses left. We developed a high anthropogenic impression dataset to achieve biodiverse region areas which more closely represented both area estimates from the literature and more direct anthropogenic influence. For example, the constructed high impression dataset mostly excluded navigable waterways, minor roads, rural railways, and some rural pasture lands. This obtained a more realistic expression of biodiverse region extents under the acknowledgement that human influence is so widespread that protecting areas entirely devoid of people would, in essence, just leave Amazonia as the only viable extent of habitat globally. The 2009 area estimate for biodiverse regions was 10.9% of global terrestrial land which fitted well with the Mittermeier et al.'s (2011) 10.2% estimate and thus aided confidence in the approach. The human footprint dataset was specifically designed to spatially represent human pressure on the environment (Venter et al., 2016); thus, its links to biocultural decline are more direct than GDP and IMR. Yet within its construction, pressures were assigned weightings in order of perceived environmental impact. Though, as demonstrated in our research, biodiverse regions are exceptionally diverse and are facing different pressures on varying temporal scales. The prospect of the same weighting being valid across the globe is slim, and it must be acknowledged that different weightings would produce very different outcomes across biodiverse regions.

4.4. Context for biodiverse regions

Notwithstanding the aforementioned debates about driver association with biocultural decline, the driver pressure datasets were used to highlight areas which may be undergoing swelling anthropogenic pressure. Once related to Biocultural Index scores, three major biocultural centres were promoted as regions which hold both exceptional biocultural prosperity and were going through recent, detrimental shifts in pressure under the assumed links with biocultural diversity.

One of these biocultural centres encompassed much of Southeast Asia and Australasia: Indo-Burma; Philippines; Sundaland; East Melanesian Islands; and New Guinea. Between them, they harbour 2151 languages and 1828 amphibians and are undergoing notable increases in human footprint in the modern era. These high biodiversity regions sit at the forefront of human-ecosystem interactions, being home to over 650 million people in an area where rapidly rising GDP levels, but comparatively unimproved IMRs, are signposting a disparity of wealth which may push rural smallholders towards more unsustainable agricultural methods. Southeast Asia's biodiversity-rich forests are undergoing rapid changes in the 21st century (Schmid et al., 2021). Shifting farming practices by local smallholders have long borne the brunt of the blame for deforestation here (e.g., Papenfus, 2000; Rasul & Thapa, 2003). More recently, large-scale commercial crop plantations of commodities such as rubber and palm oil have replaced them as the primary driver of forest loss (Qaim et al., 2020). Often accompanied by investment from China and Vietnam, larger plantations frequently displace smallholders causing further marginalisation of poorer communities and deforestation elsewhere (Hurni & Fox, 2018). Due to the rapidly developing economies and increasing disparity of wealth in these regions, sustainable conservation initiatives require careful land-use planning that supports both people and nature. This is particularly true in nations like Myanmar which havens one of Southeast Asia's last intact forest ecosystems (Woods, 2015), yet, under inappropriate management, could instigate the resurgence of smouldering conflicts (Schmid et al., 2021).

Another biocultural centre was identified across the African continent through the Guinean Forests of West Africa, Congo forests, and Eastern Afromontane. The pressures faced here are incredibly multifaceted, stemming from climate, globalisation, and rapid population growth. The effects of growing global demand for palm oil are becoming increasingly visible on the African continent (Wilcove & Koh, 2010); although significant demand for charcoal from growing urban populations is another major driver of deforestation in these regions (Zulu & Richardson, 2013). The added issue of changing precipitation patterns has caused drying patterns across Africa, especially on the east coast (Omondi et al., 2014). Whilst the Congo forests have not experienced much precipitation change in recent times, the high population growth is putting considerable pressure on these forests and threatening food security (Aukema et al., 2017). Among the most vulnerable populations to climatic changes are African rural communities (Ofoegbu et al., 2017), and the changing dynamics in these regions could cause rapid ecosystem degradation and loss of ecosystem services. Healthy ecosystems are critical for maintaining rural livelihoods and these areas must be preserved for the long-term benefit of the growing African socioeconomic presence. However, a key issue here is the low feasibility of successful transboundary initiatives due to shortcomings in institutional capacities and governance (Mason et al., 2020). Further challenges arise due to ongoing and sporadic cross-border disputes. Conflict across Central and East Africa has already resulted in population declines of several species including elephants (*Loxodonta Africana*) (Beyers et al., 2011). The diminished integrity of some socio-political systems post-conflict means that establishment of successful conservation management through national political institutions is both challenging and unlikely.

The third biocultural centre was identified in South and Central America across the Tropical Andes, Amazonia, and Mesoamerica. The Tropical Andes hotspot has exquisite levels of endemism, being the single most biodiverse hotspot on the planet (Hutter et al., 2017). The Tropical Andes is becoming increasingly fragmented, through mostly agricultural pressures, which is leading to habitat isolation and endangerment of its many species (Rodríguez-Echeverry & Leiton, 2021). Amazonia and Mesoamerica hold 570 languages and 2005 species of amphibian between them. Experiencing similar agricultural pressure to the Tropical Andes, both regions are also undergoing recent political and legislative shifts, which are hindering conservation management. In Mesoamerica, many conservation initiatives have to navigate complex and often contradictory legal frameworks, which leave good legislative intentions frustrated by pre-existing, profit-extracting agendas (Brush, 2013). In the Amazonian region, recent changes in political power inhibit sustainable development due to great influence (often corrupt) from actors interested in more unsustainable practices than conservation (Fearnside, 2018). Just like in all tropical biodiverse regions, the key task in this biocultural centre is to balance an ever-increasing demand for agricultural commodities and economic prowess with conserving biodiversity, delivering critical ecosystem services, and sustaining rural livelihoods (Harvey et al., 2008). Conservation initiatives here have to acutely balance the needs of people and the environment, perhaps creating mosaics with contrasting patterns of production and protection. This way socioeconomic and conservational progress can hopefully be in concordance rather than conflict.

4.5. Limitations and improvements

The biocultural centres, although a useful signpost for those important biocultural hotspots facing significant pressures and challenges, do have some key shortcomings. One major limitation of their transferability involves the constriction to biodiversity hotspots and high biodiversity wilderness areas. Nigeria, for example, was promoted as a region with great biocultural diversity multiple times in our study. The country is incredibly linguistically diverse, holding more languages (400) than the entirety of Europe (Skutnabb-Kangas, 2002), and it holds the largest wetland in Africa: the Niger Delta. However, as only a small section of the country overlaps with a biodiverse region (Guinean Forests of West Africa), this rich pool of biocultural heritage could go unprotected if conservation initiatives limit themselves to hotspot bounds. The 'hotspot' approach is becoming a commonly cited method that transcends modern conservation debates. However, overemphasis on such regions ignores the need for preserving more adaptive variation across a variety of environments (Smith et al., 2001). Climate change threatens large-scale shifts in species and habitat distributions; hence the hotspots of today are unlikely to be the hotspots of tomorrow. On that note, it is important to acknowledge that the analysis in our investigation is purely a contemporary snapshot of linguistic diversity and its links with biological diversity. It is therefore not possible to isolate the direct influence of certain drivers over time with such snapshot studies. Nor can the influence of changing patterns of political complexity over time be accounted for (Currie & Mace, 2009). This is not considered a drawback of this study though, but rather it is considered a reflection of the lack of temporal population change data for human languages. Therefore, although useful for identifying regions of diversity at a global scale, the inherent inflexibility of a hotspot approach demands complementary, adaptable approaches which can evolve through time and space.

Perhaps a more comprehensive approach would involve protecting areas essential for the origination and preservation of biodiversity or cultural diversity, rather than simply those areas that are currently language or species rich (Erdelen, 2012). Focusing on other priorities for conservation, such as non-tropical biomes and particular rare species, the exclusion of which is a commonly referenced criticism of the hotspot approach (Kareiva & Marvier, 2003), would diversify the habitats under protection and would no doubt yield different patterns of co-occurrence with linguistic and cultural diversity. However, hotspot-focused approaches will likely continue to direct conservation projects in the coming years, and due to the great wealth of biocultural diversity held within them, this is not a bad thing. From socioeconomic viewpoints, these areas still hold disproportionate value. Turner et al. (2007) estimated that the value of the services provided by hotspots is $1.59 trillion annually, over seven times the value per area of the average square kilometre of land globally. Whilst Gibbs and Ruesch (2008) identified these regions hold more than 99 Gt of carbon in living plant tissues, meaning a slowing of habitat destruction here will result in much needed reductions in greenhouse gas emissions that are critical to slow global warming (Yu et al., 2019). Wilderness areas were included within our report to go one step towards diversifying the hotspot approach. Future initiatives may further widen the scope of areas for protection or identify combined, flexible approaches which actively protect the current biocultural clusters whilst allowing for more geopolitical flexibility in its capacity for future protection.

4.6. Securing biocultural hotspots for the future

Securing biocultural and biodiverse regions for future generations is not a simple task; there are many considerations to be made, and due to the incredible diversity within these areas, the subsequent approaches for protection will have to be equally, if not more, diverse. For example, biodiversity hotspots are historical centres of violence. Hanson et al. (2009) uncovered that since 1950, 80% of the world's violent conflicts took place in hotspots, and most also experienced repeated episodes of violence. Such violence is already diminishing the effectiveness of many initiatives and protected areas across Africa (Daskin & Pringle, 2018). Therefore, if conservation in these areas is to be successful, it must somehow be maintained throughout periods of war. Other, less widespread threats include invasive species. Introduced predators have devastated island habitats where species evolved without direct predation, and the threat is still developing in some places, such as feral cat overpopulation on the New Caledonia islands (Palmas et al., 2017). Exploitation for bushmeat or use in traditional medicines continues to threaten species and population dynamics across the developing world, particularly across Africa (Fa et al., 2006). Infrastructure development will continue to hinder biodiverse regions in the future; the majority of the 25 million kilometres of roads anticipated by 2050 will be constructed in developing countries (Maire et al., 2016). The consequences of such expansion, such as accentuated natural resource depletion, have already been well documented in the last wilderness expanses (Barber et al., 2014). A further issue arises due to many biodiverse regions extending across multiple political boundaries. Whilst conservation initiatives are mainly commenced by individual countries, transboundary collaborations can be key for determining successful outcomes (Mazor et al., 2013). Coordinated efforts are required at both regional and national scales (Beger et al., 2015) and can potentially reduce costs of coordination whilst improving the allocation of limited resources (Mazor et al., 2013).

Biocultural conservation therefore faces many challenges, yet adversity breeds opportunity. The establishment and effective management of protected areas must remain the cornerstone of conservation efforts to halt biodiversity loss (Mittermeier et al., 2011). However, this approach often fails to generate sufficient economic incentives for governments to justify park maintenance. We believe that they must continue to adapt to include indigenous populations — and their endangered language and culture — in preservation efforts, rather than state-centric projects devoid of local knowledge. The tendency for biodiversity and cultural diversity to both be high in particular regions suggests that certain cultural practices or systems may be more compatible with the maintenance of biocultural diversity. In the amazon, indigenous lands cover one-fifth of the region (five times the area under legislative protection) and are currently the most important barrier to deforestation (Nepstad et al., 2006). Across the world, minimum estimates of indigenous land (38 million km^2) are still more than double the land protected by legislation, holding within them the lowest levels of urbanisation, agriculture-modified lands, and human population density (Garnett et al., 2018). Synergistic partnerships between smallholder farmers and indigenous populations have proved successful in the Pará state of Brazil (Campos & Nepstad, 2006). The collaboration of smallholders' political and economic ingenuity in establishing profitable agriculture and natives' awareness and knowledge of their ancestral lands benefit both parties in the long run. Such collectives hold huge potential for both agricultural frontier stabilisation (Godar et al., 2012) in the areas where it is encroaching most and also for revitalisation of native tongues and traditional livelihoods (Wilder et al., 2016).

The wealth of indigenous knowledge cannot be overstated; Cámara-Leret and Bascompte (2021) found that over 75% of all medicinal plant services are only known to one language. Here the languages face a greater threat of extinction than the plant species. The same paper found 100% of all unique knowledge in northwest Amazonia is supported by threatened languages, indicating indigenous language loss may be more critical to the eradication of medicinal knowledge than biodiversity loss. If the co-occurrence of linguistic and biological diversity was not fortunate enough for conservationists, the co-occurrence of these regions with perhaps the most strategically aligned groups to vanguard future conservation projects is even more so. Native people have continually endured misuse and seizure of their lands, holding legitimacy as lasting guardians of the environment, especially when compared to more developed actors. Indigenous populations are immensely diverse, and no one method will translate officiously across all global communities. Adaptable frameworks of inclusion, negotiation, and recognition of indigenous people can prove incredibly successful. Where sufficient support is afforded, such as in NGO funded Kayapó reserves in Brazil, forests can remain intact (Zimmerman et al., 2001). Although where there is no investment or consideration of natives' rights, lands can become seriously degraded (Zimmerman et al., 2019). Groups which become empowered through recognition and inclusion can become global frontrunners in conservation. The Kayapó tribe have themselves founded two non-governmental organisations aimed at protecting Brazilian environmental and cultural heritage. They are considered one of the most politically successful indigenous groups globally, fiercely defending indigenous rights and generating upwards of $500,000 annually (Schwartzman & Zimmerman, 2005). Future conservation ventures must realise that a truly balanced and holistic conceptualisation of indigenous peoples is essential to understanding the case-by-case complexities that arise in different conservation partnerships. Furthermore, these plans must be adaptable over space and time. Protecting areas where species and language currently exist is essential. However, allowing for where biocultural diversity may be in the future, and then providing ways to facilitate movement to these new ranges, will be of utmost importance in the coming years.

5. Conclusion

Although different drivers may have given rise to the global co-occurrence of language, culture, and species, similar pressures now appear to be causing cultural homogenisation and biological extinction on a global scale. Economic growth, globalisation, and rising human populations are causing broad changes to bioculturally-rich lands, largely in the form of habitat loss. Biocultural heritage stresses the importance of the recognition of dissimilar worldviews and the benefits of difference. The potential for its loss, and inherently the subsequent loss of indigenous and mainstream knowledge, is daunting. Conserving this diverse knowledge can lead to a superior adaptive capacity for human and biological populations to cope with current and future disturbances. Whilst conservation in these regions is challenged by evolving threats, limited local financial capacity, and insufficient information, it must continue. The disproportionate value biodiverse regions hold for current biology and culture demands their immediate protection, and despite the need for adaptive, flexible approaches, without such safeguard, the consequences will be substantial. If conservations in these areas fail, nearly half of all terrestrial species could be lost, extensive greenhouse gas emissions would occur, and widespread human suffering would be expected due to the loss of critical ecosystem services. Given the extensive influence of the human population, outdated philosophies of conservation in absence of people must be left in the past. Conservation must adopt and develop a shared, holistic framework which integrates biological, indigenous, and linguistic conservation goals in biodiverse regions which can be advanced in other regions across the world. Then we would be one step closer to preserving the differences on this planet which make life on Earth so unique.

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Appendix: Supplementary Information

Table SI1: Glottolog Agglomerated Endangerment Scale (AES) descriptions and equivalent status in other common language endangerment measures. The AES is an agglomeration of the ELCat, UNESCO, and Ethnologue databases.

UNESCO (Moseley, 2010)	**ELCat** (Lee and Way, 2018)	**Ethnologue** (Lewis et al., 2015)	**AES** (Hammarström et al., 2018)	**Description**
Safe	At risk	1 National 2 Regional 3 Trade 4 Educational 5 Written 6a Vigorous	Not Endangered	Language is spoken by all generations and is learnt by children as their first language *(36% of the languages used in this study)*
Vulnerable	Vulnerable	6b Threatened	Threatened	Language is spoken by all generations but only some children learn the language or it is restricted to certain domains (home) *(19% of languages)*
Definitely endangered	Threatened endangered	7 Shifting	Shifting	Language is spoken by older generations but children are not learning it as their first language *(23% of languages)*
Severely endangered	Severely endangered	8a Moribund	Moribund	Language is only spoken by oldest generation e.g. grandparents *(5% of languages)*
Critically endangered	Critically endangered	8b Nearly extinct	Nearly extinct	The youngest speakers are grandparents who speak the language infrequently *(4% of languages)*
Extinct	Dormant awakening	9 Dormant 9 Reawakening 9 Second language 10 Extinct	Extinct	There are no active speakers of the language left *(13% of languages)*

Shown below are the calculations used to form the Biocultural Index as used in this study. Steps are a modified version of the index created in Loh and Harmon (2005).

The Biocultural Index (BI) is a combination of equal parts cultural diversity (CD) in the form of language richness, and biodiversity (BD) in the form of amphibian species counts.

$$BI = \frac{CD + BD}{2}$$

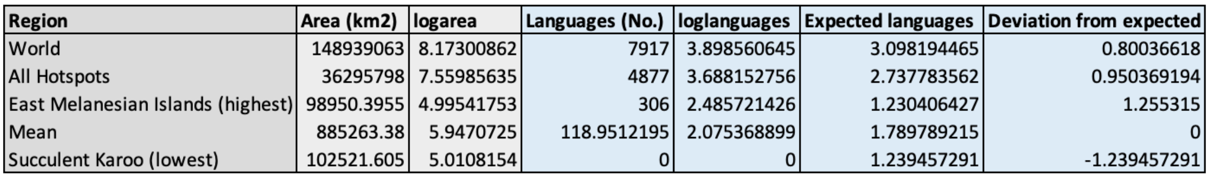
To derive scores for the two component indicators (CD and BD), the specific biodiverse region's richness value was directly compared to the global value. For example, for cultural diversity, CD is calculated as the log number of languages (L) in a biodiverse region by the log number of languages in the world.

$$CD = \frac{log\ L_{br}}{log\ L_{world}}$$

Where L_{br} is the number of languages in a biodiverse region and L_{world} is the total number of languages in the world. Data were set to a logarithmic scale to account for data skewness.

To compensate for the fact that larger biodiverse regions tend to house greater cultural and biological diversity than smaller ones simply because of greater area, an expected diversity index was calculated through a modified use of the species area relationship.

Table SI2: Area-adjusted Biocultural Index example for languages



Region	Area (km2)	logarea	Languages (No.)	loglanguages	Expected languages	Deviation from expected
World	148939063	8.17300862	7917	3.898560645	3.098194465	0.80036618
All Hotspots	36295798	7.55985635	4877	3.688152756	2.737783562	0.950369194
East Melanesian Islands (highest)	98950.3955	4.99541753	306	2.485721426	1.230406427	1.255315
Mean	885263.38	5.9470725	118.9512195	2.075368899	1.789789215	0
Succulent Karoo (lowest)	102521.605	5.0108154	0	0	1.239457291	-1.239457291

The expected diversity was calculated from the standard formula for the species-area relationship.

$$\log S = c + z\ logA$$

Where S = species number, A = area, and c and z are constants derived from observation. The same formula was used to derive expected values for both the indicators of cultural diversity and biological diversity.

The constants c and z were found via scatter-plots. The log number of species and number of languages in biodiverse regions were plotted against the log area of the biodiverse regions. A line of best fit and accompanying y and R^2 values provided the c and z values.

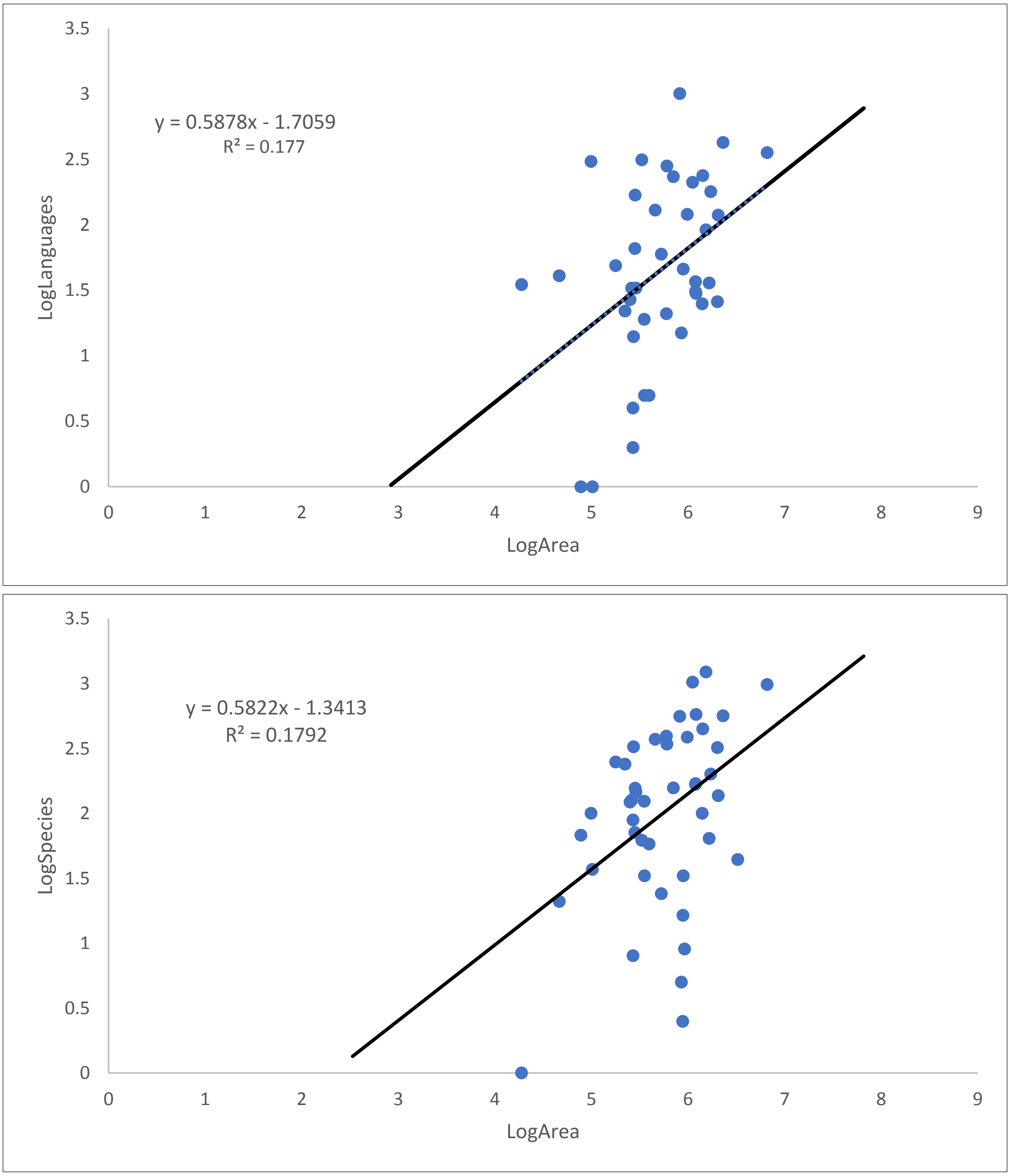


Figure SI1: Languages-area and species-area scatter plots

The deviation values were calculated by subtracting the expected log language (or species) number from the observed log language (or species) number.

Table SI3: Full Biocultural Index with expected diversity included

Region	Languages (No.)	loglanguages	LD index	Expected logLanguage	Deviation from expected	Amphibian species (No.)	logamphibians	SD index	Expected logAmphibians	Deviation from expected	Biocultural Index	BI deviation
World	*7917*	*3.8985606*	*1*	*3.098194465*	*0.80036618*	*8598*	*3.93439744*	*1*	*3.623156312*	*0.311241129*	*1*	*0.5558037*
All Hotspots	*4877*	*3.6881528*	*0.946*	*2.737783562*	*0.950369194*	*8039*	*3.90520203*	*0.9926*	*3.230984121*	*0.674217908*	***0.969304393***	*0.8122936*
New Guinea	1009	3.0038912	0.7705	1.77088184	1.233009326	560	2.74818803	0.6985	2.178873979	0.569314048	**0.734507888**	0.9011617
Amazonia	358	2.553883	0.6551	2.303428166	0.25045486	981	2.99166901	0.7604	2.758351063	0.233317944	**0.707735837**	0.2418864
Indo-Burma	428	2.6314438	0.675	2.034634503	0.596809266	564	2.7512791	0.6993	2.465869902	0.285409202	**0.687133419**	0.4411092
Mesoamerica	212	2.3263359	0.5967	1.849594475	0.476741386	1024	3.01029996	0.7651	2.264523182	0.745776775	**0.680920053**	0.6112591
Tropical Andes	92	1.9637878	0.5037	1.92987741	0.033910417	1226	3.08849047	0.785	2.351881068	0.736609402	**0.644359159**	0.3852599
Sundaland	239	2.3783979	0.6101	1.910584199	0.467813701	448	2.65127801	0.6739	2.330887639	0.320390375	**0.641971099**	0.394102
Guinean Forests of West Africa	282	2.4502491	0.6285	1.692621148	0.75762796	341	2.53275438	0.6437	2.093716547	0.439037832	**0.636123704**	0.5983329
Madrean Pine-Oak Woodlands	130	2.1139434	0.5422	1.621874839	0.492068514	371	2.56937391	0.6531	2.016735704	0.552638206	**0.597645429**	0.5223534
Eastern Afromontane	121	2.0827854	0.5342	1.816106545	0.266678826	386	2.5865873	0.6574	2.22808412	0.358503184	**0.595836893**	0.312591
Himalaya	234	2.3692159	0.6077	1.731517756	0.637698102	157	2.19589965	0.5581	2.136040927	0.059858726	**0.582922056**	0.3487784
Congo Forests	180	2.2552725	0.5785	1.960623625	0.29464888	201	2.30319606	0.5854	2.3853368	-0.082140742	**0.581944225**	0.1062541
East Melanesian Islands	306	2.4857214	0.6376	1.230406427	1.255315	100	2	0.5083	1.590769055	0.409230945	**0.572968419**	0.832273
Philippines	169	2.2278867	0.5715	1.498767765	0.72911894	156	2.1931246	0.5574	1.882779793	0.310344805	**0.564443578**	0.5197319
Wallacea	315	2.4983106	0.6408	1.539582713	0.958727841	62	1.79239169	0.4556	1.927191567	-0.134799878	**0.548199256**	0.411964
Atlantic Forest	30	1.4771213	0.3789	1.870345277	-0.393224023	579	2.76267856	0.7022	2.287102653	0.475575911	**0.540537407**	0.0411759
Mediterranean Basin	119	2.075547	0.5324	2.005282836	0.070264125	137	2.13672057	0.5431	2.433931613	-0.297211046	**0.537737566**	-0.1134735
Western Ghats and Sri Lanka	49	1.6901961	0.4335	1.380904589	0.309291491	248	2.39445168	0.6086	1.7545299	0.639921781	**0.521068936**	0.4746066
Cerrado	26	1.4149733	0.3629	2.000405406	-0.585432058	321	2.50650503	0.6371	2.428624358	0.077880674	**0.500011161**	-0.2537757
Madagascar & the Indian Ocean Islands	21	1.3222193	0.3392	1.689257718	-0.367038424	393	2.59439255	0.6594	2.090056714	0.504335836	**0.499284345**	0.0686487
North American Coastal Plain	37	1.5682017	0.4023	1.867212159	-0.299010435	169	2.2278867	0.5663	2.283693427	-0.055806723	**0.484255072**	-0.1774086
Caribbean Islands	22	1.3424227	0.3443	1.438371885	-0.095949204	239	2.3783979	0.6045	1.817061513	0.561336388	**0.474425958**	0.2326936
Miombo-Mopane	31	1.4913617	0.3825	1.86637365	-0.375011957	167	2.22271647	0.5649	2.282781025	-0.060064554	**0.473743094**	-0.2175383
Coastal Forests of Eastern Africa	33	1.5185139	0.3895	1.50385265	0.01466129	146	2.16435286	0.5501	1.888312785	0.276040071	**0.469808339**	0.1453507
California Floristic Province	66	1.8195439	0.4667	1.497331551	0.322212384	71	1.85125835	0.4705	1.881217013	-0.029958664	**0.468626792**	0.1461269
Tumbes-Choco-Magdalena	14	1.146128	0.294	1.489034018	-0.342905982	325	2.51188336	0.6384	1.872188258	0.639695103	**0.466214588**	0.1483946
Mountains of Southwest China	33	1.5185139	0.3895	1.478119523	0.040394417	126	2.10037055	0.5338	1.860311921	0.240058625	**0.461677194**	0.1402265
Forests of East Australia	27	1.4313638	0.3672	1.468022578	-0.036658814	122	2.08635983	0.5303	1.849325181	0.23703465	**0.448719428**	0.1001879
North American Deserts	25	1.39794	0.3586	1.908120969	-0.510180961	100	2	0.5083	2.328207336	-0.328207336	**0.433457774**	-0.4191941
Japan	19	1.2787536	0.328	1.555454485	-0.276700884	124	2.09342169	0.5321	1.944462043	0.148959643	**0.43004425**	-0.0638706
Horn of Africa	36	1.5563025	0.3992	1.949750546	-0.393448046	64	1.80617997	0.4591	2.373505528	-0.567325554	**0.429136678**	-0.4803868
Irano-Anatolian	46	1.6627578	0.4265	1.792939352	-0.13018152	33	1.51851394	0.386	2.202875314	-0.684361374	**0.40623201**	-0.4072714
Caucasus	60	1.7781513	0.4561	1.658885785	0.119265465	24	1.38021124	0.3508	2.057008248	-0.676797007	**0.403455404**	-0.2787658
Polynesia-Micronesia	41	1.6127839	0.4137	1.037441563	0.575342293	21	1.32221929	0.3361	1.380799122	-0.058579827	**0.374876765**	0.2583812
Maputaland-Pondoland-Albany	4	0.60206	0.1544	1.487015399	-0.884955408	89	1.94939001	0.4955	1.869991748	0.079398259	**0.324952469**	-0.4027786
Chilean Winter Rainfall and Val. For.	5	0.69897	0.1793	1.58386899	-0.884898985	58	1.76342799	0.4482	1.975380581	-0.211952588	**0.313748571**	-0.5484258
Southwest Australia	5	0.69897	0.1793	1.556825858	-0.857855854	33	1.51851394	0.386	1.945954268	-0.427440329	**0.282623849**	-0.6426481
Mountains of Central Asia	15	1.1760913	0.3017	1.781667793	-0.605576534	5	0.69897	0.1777	2.190610446	-1.491640442	**0.239664687**	-1.0486085
Cape Floristic Region	1	0	0	1.168869175	-1.168869175	68	1.83250891	0.4658	1.52380882	0.308700093	**0.232883045**	-0.4300845
Succulent Karoo	0	0	0	1.239457291	-1.239457291	37	1.56820172	0.3986	1.600617528	-0.032415804	**0.199293761**	-0.6359365
New Caledonia	35	1.544068	0.3961	0.807583638	0.736484406	0	0	0	1.130684918	-1.130684918	**0.198030528**	-0.1971003
New Zealand	2	0.30103	0.0772	1.486036773	-1.185006777	8	0.90308999	0.2295	1.868926879	-0.965836892	**0.153376364**	-1.0754218