SATELLITE REMOTE SENSING FOR THE ASSESMENT OF PROTECTED AREAS: A GLOBAL APPLICATION

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Abstract

Unprecedented rates of modern species extinction present a serious challenge in the field of conservation biology. While protected areas (PAs) are regarded as key tools to reduce rates of biodiversity loss, it is unclear to what degree PAs can maintain their ecological integrity while experiencing external pressures from outside of their boundaries. Satellite remote sensing essential biodiversity variables (SRS-EBVs) are indicators of biodiversity that can be produced with large spatial coverages and can be used to measure PAs' capacity to preserve important ecological elements for biodiversity. In this study, I used SRS-EBVs representative of ecosystem structure and function, including productivity, disturbance regimes, ecosystem extent, and ecosystem composition. I tested if PAs preserved these determinants of species survival through time, whether any changes in these variables in PAs were independent of changes in their surrounding areas (buffer zones), and if the management type of PAs influenced either of these patterns. I found that PAs maintained elements of ecosystem structure, including habitat heterogeneity and extent, inside of their boundaries, regardless of changes that occurred in their surroundings. In contrast, PAs were less effective at sustaining elements of ecosystem function and mitigating other forms of human disturbance. Productivity within PAs was the same as that of their surroundings, underscoring the inability of PAs to track shifts in climate regimes that put some species at greater risk of extinction. Fire disturbance trends were maintained across PA boundaries; however, the causes of these fires are unknown, highlighting the importance of supplemental fire census data to tease apart the trends of natural fire regimes compared to harmful burns. Finally, other human pressures thought to be the indirect effects of linear transportation features (ex. edge effects from roads) were observed to have spilled over from buffer zones into PAs. Planning for future development of the global PA network can benefit

greatly from the application of SRS-EBVs. Pairing these data products with foundational ecological conservation principles can build a stronger, more efficient PA network for the preservation of Earth's species.

Résumé

Des taux sans précédent d'extinction d'espèces modernes présentent un sérieux défi dans le domaine de la biologie de la conservation. Alors que les aires protégées (AP) sont considérées comme des outils clés pour réduire les taux de perte de biodiversité, on ne sait pas dans quelle mesure les AP peuvent maintenir leur intégrité écologique tout en subissant des pressions externes provenant de l'extérieur de leurs limites. Les variables essentielles de la biodiversité par télédétection par satellite (SRS-EBV) sont des indicateurs de biodiversité qui peuvent être produits avec de grandes couvertures spatiales et peuvent être utilisés pour mesurer la capacité des AP à préserver des éléments écologiques importants pour la biodiversité. Dans cette étude, j'ai utilisé des SRS-EBV représentatifs de la structure et de la fonction de l'écosystème, y compris la productivité, les régimes de perturbation, l'étendue de l'écosystème et la composition de l'écosystème. J'ai testé si les AP préservaient ces déterminants de la survie des espèces au fil du temps, si les changements de ces variables dans les AP étaient indépendants des changements dans leurs zones environnantes (zones tampons) et si le type de gestion des AP influençait l'un ou l'autre de ces modèles. J'ai découvert que les AP maintenaient des éléments de la structure de l'écosystème, y compris l'hétérogénéité et l'étendue de l'habitat, à l'intérieur de leurs limites, quels que soient les changements survenus dans leur environnement. En revanche, les AP étaient moins efficaces pour maintenir des éléments de la fonction écosystémique et atténuer d'autres formes de perturbations humaines. La productivité au sein des AP était la même que celle de leur environnement, ce qui souligne l'incapacité des AP à suivre les changements dans les régimes climatiques qui exposent certaines espèces à un plus grand risque d'extinction. Les tendances en matière de perturbation par le feu se sont maintenues à travers les limites de l'AP; cependant, les causes de ces incendies sont inconnues, ce qui souligne l'importance des données

supplémentaires du recensement des incendies pour distinguer les tendances des régimes de feux naturels par rapport aux brûlures nocives. Enfin, d'autres pressions humaines que l'on pense être les effets indirects des caractéristiques de transport linéaire (par exemple, les effets de bord des routes) ont été observées comme ayant débordé des zones tampons vers les AP. La planification du développement futur du réseau mondial d'AP peut grandement bénéficier de l'application des SRS-EBV. Associer ces produits de données aux principes fondamentaux de conservation écologique peut créer un réseau d'AP plus fort et plus efficace pour la préservation des espèces de la Terre.

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Introduction

Modern species extinction rates have surpassed background levels by an estimated thousandfold (Pimm et al., 2014; Ceballos et al., 2015). Taxa across a range of environments, including vertebrates and insects, have experienced sharp declines in population sizes and geographic ranges over the past several decades (Leung et al., 2020; van Klink et al., 2020). To date, a total of one million species are estimated to be threatened with extinction and are projected to meet this fate within the next few decades if the drivers of biodiversity loss are left unchecked (Bongaarts, 2019).

Although the drivers of biodiversity loss vary across the globe, habitat loss and degradation have been pinpointed as one of the greatest threats to terrestrial wildlife globally (Newbold et al., 2016; Bongaarts, 2019). While agricultural expansion is the most widespread form of land-use change, growing urban development is a close second, eroding remaining natural and semi-natural habitats. Rates of biodiversity loss are intensified still further by other human actions including species exploitation, pollution, invasive species, and climate change (Barnosky et al., 2011; Urban, 2015; Maxwell et al., 2016; Bongaarts, 2019; Ceballos et al., 2020).

Protected areas (PAs) have the potential to reduce the rate of biodiversity loss by safeguarding suitable habitat for species sensitive to human activities (Watson et al., 2014; Di Marco et al., 2019). However, it is uncertain to what degree PAs keep external pressures outside of their boundaries. PAs certainly can reduce rates of many forms of anthropogenic disturbance. Habitat loss, for example, is known to have a contagious quality, with losses in one area spilling over readily into adjacent locales (Boakes et al., 2010). Although PA networks across continents have demonstrated an ability to mitigate this phenomenon (Geldmann et al., 2013; Kirschbaum et al., 2016; Bolton et al., 2019), intense human land uses in areas around PAs leads to a greater likelihood of land use conversions within them (Leroux & Kerr, 2013). Moreover, this pattern varies geographically and between IUCN categories (Dudley, 2008). As human-caused habitat pressures advance toward PA boundaries globally, there is an increased risk that benefits of PAs for preserving ecosystems and species within their boundaries will fade (Geldmann et al., 2014; Jones et al., 2018). While such examples provide valuable insights into PAs' capacity to provide a bulwark against intensive human land uses, a comprehensive assessment of how well the global PA network has maintained a suite of factors that influence the survival of wildlife while reducing external negative forces has yet to be performed.

To quantify the conservation efficacy of the full PA network, a collection of ecologically meaningful variables available with global coverage is vital. Overall, signatories failed to meet the Convention on Biological Diversity's (CBD) Aichi Biodiversity Target 11 (UNEP-WCMC and IUCN, 2019), and preparation for the post-2020 strategic plan is underway. To measure progress towards achieving the CBD's vision of curbing biodiversity declines, and to ensure that PAs reach their full conservation potential, biologically relevant metrics must be identified and implemented (Watson et al., 2016; Mace et al., 2018). Endorsed by the CBD, Essential Biodiversity Variables (EBVs) are indicators of biodiversity and were originally intended to be used to monitor progress towards achieving the Aichi Biodiversity 2020 Targets (Pereira et al., 2013). While a finalized set of EBVs has not yet been determined, a total of 20 have been proposed (GEO BON, 2017). These EBVs are divided into six categories: genetic composition, species populations, species traits, community composition, ecosystem structure, and ecosystem functioning. Several of these variables, particularly those that fall into the ecosystem structure and functioning categories (Table 1.), require satellite remote sensing platforms for their production and have been named satellite remote sensing EBVs (SRS-EBVs) (Pettorelli et al., 2016). Satellite remote sensing has many conservation applications (Kerr & Ostrovsky, 2003; Rose et al., 2015), offering a cost-efficient method of measuring critical environmental properties across broad spatial extents and at frequent time intervals (O'Connor et al., 2015). These approaches are vital for environmental monitoring across scales ranging from local to global.

SRS-EBVs can be used to assess environmental properties that could contribute to the conservation of species and maintenance of ecosystems. Indicators of ecosystem structure, including habitat extent and heterogeneity, are linked to species richness and population abundance and are common criteria used to monitor the ecological integrity of PAs (Fraser et al., 2009; Nagendra et al., 2013). Ecosystem functions, including primary productivity and ecosystem disturbances, are highly responsive to environmental changes and allow for the monitoring of ecosystem integrity at large scales (Pettorelli et al., 2018). For example, the effect of fluctuations in primary productivity persists through every level of an ecosystem, while changes in disturbance regimes, such as fire cycles, have the potential to modify landscapes and shift the availability of resources that species rely on for survival (CBD, 2013, 2017). Here, I propose to extend the use of SRS-EBVs beyond their original purpose of measuring progress towards Aichi Targets by tracking the trends of four ecosystem structure and function SRS-EBVs both within and outside PAs to test their conservation performance.

In this study, I ask whether differences in PA management practices within long-established PAs are linked with changes in environmental characteristics that can be monitored using SRS-EBVs. Specifically, I expected that if PAs have been effective for conservation, then 1) environmental characteristics within those PAs should show greater stability through time than those measured in surrounding areas, and 2) changes in environmental characteristics within PAs should be independent of human-caused changes in surrounding areas. I also expected that 3) PAs that are designated for more strict conservation purposes should maintain the stability of EBVs within their boundaries to a greater degree than less strict PAs, and 4) that changes in EBVs in strictly managed PAs should be less influenced by environmental changes in surrounding buffer zones relative to less strict PAs.

The first step towards achieving the full conservation potential of PAs is to identify their strengths and weaknesses. Aichi Target 11 brought awareness to the insufficiency of focusing on PA expansion alone; many signatories reached their 2020 goals, yet biodiversity declines persist (Maxwell et al., 2020). Using ecosystem structure and function SRS-EBVs, I identify for which environmental factors PAs act as shields against anthropological impacts, and those where there are gaps in the protection that PA boundaries offer. By maintaining these strengths and addressing weaknesses, the global PA network will only become stronger as we race to reverse modern biodiversity declines.

Methods

All spatial data were projected to the WGS 1984 geographic coordinate system, except for datasets where area was calculated (i.e. proportion of natural land cover). In these cases, data were projected to the Mollweide (world) equal area coordinate system. All geoprocessing was performed using ArcGIS Pro v.2.8.0 (ESRI, 2021).

Protected area and buffer data

PA data were obtained from the World Database on Protected Areas (WDPA), a comprehensive dataset of the globe's PA network (UNEP-WCMC, 2019; UNEP-WCMC and

IUCN, 2019). The WDPA was filtered by both spatial and attribute criteria. For most PAs included in the WDPA, spatial data describing their location and shape are available as polygons which delineate their official boundaries. However, a subset of PAs in the WDPA (~8.5%) lack this information, identifying PA locations using a centroid. Distinguishing between land that is within or outside PA boundaries is necessary in this research, so PAs that lacked clearly delineated boundaries were omitted from the study. In terms of attribute data, the WDPA dataset was filtered further to include only terrestrial PAs recognized by the IUCN (categorized from Ia to VI indicating the level of protection a PA is granted) and established by the year 2000, inclusively. PAs that had one or more coastal boundaries were included in the analysis; however, PAs that were surrounded by water (i.e. islands) were excluded. The filtered dataset included a total of 26,708 individual PAs on all continents except Antarctica, representing 29.12% of the total terrestrial area covered by the WDPA (~7,606,070 km^2; Figure 1A). The IUCN categories of these PAs were reclassified into two broad classes: 1) strict conservation management, represented by categories Ia to IV, and 2) less strict conservation management, represented by categories V and VI (Dudley, 2008).

Buffer zones with a width of 25km were drawn around the perimeters of all PAs in the final filtered dataset (Figure 1A, 1B). A buffer zone width of 25km was chosen so that buffers would be the width of at least one raster cell for EBVs measured at the coarsest resolutions (0.25 decimal degrees). To remove marine and large aquatic areas, buffers were clipped to a single polygon of the world's terrestrial land mass (Natural Earth, 2019).

Essential biodiversity variables

Satellite remote sensing (SRS) data products that have been proposed (CBD, 2017; Pettorelli et al., 2018) for use as EBV measurements of ecosystem structure and function were assembled from an array of sources. Six EBVs have been proposed to measure either ecosystem structure or ecosystem function. However, I focused on four of these EBVs that are available at global extents. These EBVs include 1) productivity, 2) disturbance regime, 3) ecosystem extent, and 4) ecosystem composition. For the data products described below, time series datasets of annual temporal resolution and global coverage were obtained at varying temporal and spatial resolutions (Table 1).

1) Productivity

Productivity is broadly defined by the CBD as the amount of carbon an ecosystem assimilates (CBD, 2017). Many remote sensing products representing productivity, including measurements of primary productivity and vegetation indices, are sensitive to changes in carbon content and are indicative of a habitat's overall health (CBD, 2013, 2017). I collected several of these remote sensing metrics to consider as a representative of this EBV. These products included annual net and gross primary productivity (NPP & GPP) (Running et al., 2011), the fraction of absorbed photosynthetically active radiation (fPAR) and the leaf area index (LAI), including the total annual fPAR and LAI summed across observation periods for the satellite remote sensing measurements, minimum LAI and fPAR, and variability in these measurements (Hobi et al., 2017). I also assembled measurements of annual cumulative and mean normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI2) (Didan and Barreto, 2016a, 2016b). Each is sensitive to sustained changes in carbon flow through an environment and are indicative of an ecosystem's overall health (CBD, 2013, 2017).

GPP and NPP measure the rate at which energy is converted to biomass (g carbon/m^2). While GPP describes the overall rate of conversion, NPP accounts for energy lost through respiration and metabolism (Running & Zhao, 2015). Moderate Resolution Imaging

Spectroradiometer (MODIS) GPP and NPP products are created from pre-existing, satellite-derived products (i.e. land cover, LAI, fPAR). These metrics of GPP and NPP likely underestimate productivity in the most productive areas and may overestimate productivity in areas with limited vegetation cover (Turner et al., 2006; Wang et al., 2017).

The NDVI and EVI2 are vegetation indices, standardized between -1 and 1. The NDVI is the normalized transformation of the near infrared (NIR) to red band ratio (Equation 1) and is widely used in ecological research (Kerr & Ostrovsky, 2003; Pettorelli et al., 2005, 2018). The key limitation of NDVI, however, is that it often saturates in regions with dense vegetation, like tropical forests (Huete et al., 2002). The EVI2 (Equation 2) is an optimized vegetation index with improved sensitivity and greater accuracy in high biomass regions. EVI2 omits the need for a blue band signal, which is required for the EVI algorithm. This attribute results in the compatibility of EVI values across different sensors at the expense of minor errors associated with atmospheric aerosols (Jiang et al., 2008). Two annual metrics are provided for NDVI and EVI2: the cumulative value for each index describes the area under the phenological curve for a given year and their annual means represent average annual vegetation quality (Didan et al., 2015).

$$NDVI = \frac{NIR - Red}{NIR + Red} \quad \text{(Equation 1)}$$

$$EVI2 = 2.5\left(\frac{NIR - Red}{NIR + 2.4 * Red + 1}\right) \quad \text{(Equation 2)}$$

fPAR and the LAI can yield measurements that strongly relate to those from vegetation indices. fPAR (Equation 3) describes the proportion of radiation that is available for photosynthesis (PAR; 400 – 700nm) absorbed by green plant material ($PAR_{absorbed}$) to the total amount of PAR emitted by the sun (PAR_{total}); it is a standardized measurement of photosynthetic biomass, ranging from values of zero to one. Interpretation of the LAI (Equation 4) is dependent on the canopy type: while LAI describes the one-sided green leaf area per unit ground area for broadleaf canopies, it represents half of the total needle surface area per unit ground area for coniferous canopies (Myneni, 2020). Like GPP and NPP, fPAR and LAI are derived from SRS data products (i.e. land cover classifications) in addition to direct reflectance data, and errors associated with input datasets persist into these indices (Radeloff et al., 2019). Three annual metrics of fPAR and the LAI are calculated based on the phenological curve for a given year. Cumulative fPAR and LAI describe the sum of all productivity values (the area under the curve), the annual minimum represents the smallest productivity value recorded for a given year, and seasonality refers to the variation in productivity in a year (i.e. it is the coefficient of variation calculated from the standard deviation and the mean of the phenological curve; Radeloff et al., 2019).

$$fPAR = \frac{PARabsorbed}{PARtotal} \quad \text{(Equation 3)}$$

$$LAI = \frac{leaf\ area}{ground\ area} \quad \text{(Equation 4)}$$

2) Disturbance regime

This EBV assesses the pattern of disturbance intensity and frequency. Many ecosystems and the biodiversity that they support are dependent on a consistent disturbance regime for their maintenance through time. A change in this regime can result in the deterioration of an environment and the loss of biodiversity (CBD, 2013, 2017). Fire regimes are common natural disturbances that support the maintenance of certain ecosystems (Shlisky et al., 2007). Unlike other natural disturbance regimes, satellite remote sensing data products that describe fire regime characteristics, such as fire frequency and intensity, with global spatial extents are readily available. Data products of monthly average fire duration (the average number of days a fire burns per cell) and number of ignitions at a 0.25 degree resolution were obtained from the Global Fire Atlas with Characterizations of Individual Fires dataset (Andela et al., 2019a). These data products were derived from the MODIS 500m resolution estimated day of burn product, MCD64A1 v6, where monthly averages were calculated from the fraction of burned area that fell within a 0.25 degree grid cell (Andela et al., 2019b). Monthly files were converted to annual datasets by taking the sum of the twelve months for each year.

In addition to natural disturbance regimes, the explicit assessment of human activity is highly relevant to testing the effectiveness of PAs. Although it is absent from the SRS-EBV list, human disturbances threaten habitats, making their occurrence and intensity important to track through time (Venter et al., 2016a). I assembled Human Footprint data for 1993 and 2009 (Venter et al., 2016b) as a measurement of anthropogenic disturbance. These data integrate built-up environments and infrastructure, impermeable surfaces, population density, agricultural land, and transportation (Venter et al., 2016a).

3) Ecosystem extent

Habitat loss and fragmentation are leading causes of extinction, and measuring changes in the total area of habitats represents a valuable metric of extinction risk (CBD 2013, 2017). For the purpose of this study, I defined ecosystem extent as the proportion of natural land cover for a given PA or buffer zone. Global annual land cover products were obtained from the Climate Change Initiative – Land Cover project (ESA, 2017). From these data, the annual proportion of natural land cover was obtained by first calculating the total area of each PA and buffer zone. All classes of land cover type were then reclassified as either “built or agricultural” (e.g. urban areas and crop land) and “apparently natural” (e.g. tree cover, grasslands, shrub and herbaceous cover; Table 2). Using these reclassified land cover datasets, the total area of natural land cover was calculated for all PAs and buffers. Finally, the proportion of natural land cover was calculated by dividing the area of natural land cover by the total area of the corresponding PA or buffer zone for each year.

4) Ecosystem composition

I measured ecosystem composition as land cover variety, which is an index of habitat heterogeneity (Kerr et al., 2001). Increasingly diverse and complex habitats support a greater number of species by providing a variety of niches (Kerr & Packer, 1997; Tews et al., 2004), and positive relationships between increasing habitat diversity and species richness across a variety of taxa are frequently reported (Stein et al., 2014). Changes in habitat heterogeneity in PAs could, therefore, influence the state of biodiversity within their boundaries. The same global annual land cover products obtained from the CCI-LC project (ESA, 2017) were used to calculate habitat heterogeneity by counting the number of discrete “apparently natural” land cover types (Table 2) in each PA and its associated buffer area for each year.

The candidate variables listed above were tested for correlation for three separate years at equal intervals over the study (2003, 2009 and 2014). A number of candidate variables (the number of ignitions, human footprint, etc.) did not show significant correlation (Table 3) and were used as representative variables for their corresponding EBV. However, measurements of primary productivity (i.e. NPP, GPP, LAI, fPAR, NDVI and EVI) were highly correlated for all three years tested ($r > 0.80$). To address this issue, a principal component analysis (PCA) was performed (Demšar et al., 2013). Due to the varying scales of each variable to be compared, the

PCA was performed on their correlation matrix rather than their covariance matrix. Based on the highest correlation values with the first principal component for each of the three years, cumulative fPAR was selected as the representative variable for primary productivity ($r = 0.94 – 0.97$).

The final variables that underwent processing and analysis for all PAs and their corresponding buffers were the annual: 1) mean cumulative fPAR, 2) mean fire duration, 3) mean number of fire ignitions, 4) mean human footprint, 5) proportion of natural land cover and 6) land cover heterogeneity. Data for each variable were filtered by the PA size to exclude observations where the area of the PA was smaller than the spatial resolution of that particular variable (e.g. mean fPAR data excluded PAs with an area less than $1km^2$ while mean fire duration data excluded PAs with an area less than $780km^2$).

To account for differences in environmental characteristics across biogeographical boundaries, we identified the biome and continent of each PA. Both variables were included in statistical analyses as random effects. Biomes share environmental characteristics (Olson et al., 2001), so PAs and buffer zones within particular biomes could be more likely to respond to environmental changes similarly, relative to PAs in other biomes. The same reasoning could apply at continental extents. I identified the most extensive biome type (usually there was only one) within each PA and buffer pair (based on the biome that occupied the broadest extent) using the World Wildlife Foundation's Terrestrial Ecoregions of the World dataset (Olson et al., 2001), and their continent from the WDPA attribute data (UNEP-WCMC, 2019).

For analyses regarding the mean fire duration and mean number of ignitions, biome types were reclassified into two groups – those with a regular fire regime and those without (Table 4) – to provide a coarse-grained assessment of 'fire regime'. PAs and buffers located in biomes that experience frequent fires could respond to changes in fire regime differently than those found in areas where fire risks are low.

Analysis: EBV change through time in protected areas and buffer zones

Generalized linear mixed models were constructed to determine whether time had a significant effect on each EBV within PAs from 2003 to 2015. To investigate whether the management type of PAs influenced the trend of an EBV through time, the IUCN management class (a two-level factor) was also included as a fixed effect in each model as an interaction term with time (i.e. the year of data collection). For the analysis of mean fire duration and mean number of ignitions, fire regime (a two-level factor) was included as a third fixed effect in a three-way interaction. Outliers were identified using Cook's distance and Cleveland dotplots and removed where appropriate (e.g. extreme values in the predictor variables). The optimal random effects structure was obtained for each EBV using a top-down approach. This was done by constructing a list of models containing all combinations of biome and continent (both, one or the other, or neither) using restricted maximum likelihood estimation (REML) and comparing them using the likelihood ratio test as well as AIC values (Bolker et al., 2009; Zuur et al., 2009). The unique ID of each PA ('WDPA_PID'; UNEP-WCMC, 2019) was also included as a random factor to account for variability among trends of individual PAs and buffers. Various distribution families were used to fit these models depending on the data type of each variable (e.g. beta, binomial, generalized poisson, etc.). Model residuals were tested for the presence of spatial autocorrelation (SAC) using the Global Moran's I statistic. For models in which SAC was found to be significant, the optimal spatial model was found by comparing models' fit with different spatial structures (e.g. gaussian, exponential, and matern) using likelihood ratio tests and AIC values (Dormann et al., 2007). This same procedure was followed to model how each EBV changed through time in buffer zones.

Analysis: Net EBV change in protected areas as a function of change in their buffer zones

To determine if change in EBVs that occurred in buffers influenced the state of EBVs in PAs, I calculated the net change of each EBV inside PAs and buffers. Net change was calculated by subtracting data of the last year from the first year of observation for each EBV's unique time period (varies between 2000 and 2016; Table. 1). Net change in land cover heterogeneity was converted to a binary dataset, where a change in the number of land cover types between the first and last year of observation was coded with a value of one and no change was coded as zero.

General and generalized linear mixed models were used to model the net change of each EBV in PAs as a function of the net change of the same EBV in their corresponding buffers. The IUCN management class (two-level factor) was also included as a fixed effect in each model as an interaction term with the EBV net change of buffers to test if management type influenced how EBVs in PAs respond to change in their buffers. For the analysis of mean fire duration and mean number of ignitions, fire regime (two-level factor) was included as a third fixed effect in a three-way interaction (EBV net change in buffers x management type x fire regime). The same modelling approach as above was used to find the model of best fit for each EBV (i.e. addressing outliers, testing for SAC, etc.).

All statistical analyses were run using R 4.0.2 (R Core Team, 2020). Final models for temporal and spatial analyses were fit with REML estimation using the *glmmTMB* package (v.1.0.2.1; Brooks et al., 2017), with one exception (Table 6), and model diagnostics were performed using the *DHARMa* package (v.0.3.3.0; Hartig, 2020). Accounting for spatial autocorrelation in model residuals required the construction of Euclidean distance matrices, where distances between every possible pair of coordinates (i.e. the center of a PA) were calculated. Executing these computations on complete datasets imposed impractical computing requirements. The *glmmTMB* function used to construct models has known issues with parallelization, and estimated run times using a computer cluster were also impractically long. To work around this issue, I executed models using the following procedure: for each variable, I divided the complete dataset into a number of smaller, equal-sized sub-datasets, where observations (i.e. measurements from individual PAs and buffers) were randomized. After running the same model on all subsets for a given variable, I then took the mean of the outputs (coefficients, stand errors, etc.) to get the final averaged model output.

Results

A total of 969 – 12,125 PAs (~4% - 45% of the filtered dataset) were analyzed, depending on the availability and spatial resolution of the data for each variable (i.e. raster data with finer resolutions produced larger datasets than those with coarser resolutions; see Tables 6 and 7 for the sample size of each response variable). The global network of PAs is skewed towards smaller geographic areas (Figure 2), and many were too small to be assessed here with remote sensing data that are available at a global extent.

EBV change through time in protected areas and buffer zones

Primary productivity (mean fPAR) trends through time were comparable for both buffers and PAs. Time had a statistically significant effect on productivity, and there was a small increase in fPAR in PAs and buffers through time. PAs managed for stricter nature conservation showed steeper gains in productivity through time (0.101 ± 0.012 in PAs and 0.099 ± 0.013 in buffers) compared to less strict PAs (0.052 ± 0.036 in PAs and 0.015 ± 0.040 in buffers); however, this effect of management type was not significant (Table 6).

In terms of disturbance regimes, although time had a statistically significant effect on the average fire duration (number of days land burned) in PAs and buffers, these slopes were close to zero (Table 6). From 2003-2015, mean fire duration showed a slight decreasing trend through time, where fires burned approximately 0.982-0.991 (± 1.005-1.011) days less, on average, in PAs and 0.984-0.993 (± 1.009-1.008) fewer days in buffers. Neither the management type of PAs nor the presence of a fire regime influenced the effect of time on fire duration in PAs or buffers. The mean number of fire ignitions over time differed somewhat between PAs and buffers in terms of statistical significance. In terms of biological significance, however, patterns of fire ignition rates through time were similar. The mean number of fires detected in PAs changed significantly through time, and this change varied significantly between PAs with different management types and between PAs in fire-prone versus non-fire-prone regions. In practice, however, the differences in these trends were negligible, and the change in the mean number of ignitions over time in PAs hovered around one per year (0.961-1.005 ± 1.011-1.009; Table 6), regardless of management type or the association of biome type within that PA with fire regimes. In buffers, the temporal trend of the mean number of fire ignitions varied between fire regime groups in terms of statistical significance. However, the effect size is small and likely not biologically relevant (number of ignitions varied between 0.973-0.996 ± 1.019-1.029; Table 6).

Change in the proportion of natural land cover in PAs through time differed from trends observed in buffer areas (Table 6). Time did not have a significant effect on the proportion of natural land cover in PAs, and PA management type did not influence this trend. Conversely, natural land cover extent declined significantly through time at different rates in buffer areas around strictly protected and less strict PAs. The proportion of natural land cover decreased by

~0.12 (±0.008) % in strictly managed PAs' buffers compared to a decrease of ~0.17 (±0.022) % each year in the buffers of less strict PAs. Temporal trends of land cover heterogeneity revealed that time was not related to the number of land cover types in both strict and less strict PAs. Land cover heterogeneity in buffer zones was also not influenced by time, and this trend did not vary between management types (Table 6).

Net EBV change in protected areas as a function of change in their buffer zones

The productivity (mean fPAR) change in PAs was significantly influenced by the change in productivity in their corresponding buffers. This relationship did not differ significantly between strict (slope = 0.833 ± 0.023) and less strict (slope = 0.841 ± 0.067) PAs (Table 7).

The relationship between the mean fire duration (mean number of days that land burned) of PAs and buffers was not significantly different between PA management types. The fire regime, however, demonstrated a significant influence on this relationship (Table 7). In regions with regular fire disturbances, the duration of fires in PAs was less than that in their buffers (strict: slope = 0.687 ± 0.204; less strict: slope = 0.869 ± 0.537) compared to the fire duration in PAs in non-fire prone regions, which was approximately equal to their surroundings (strict: slope = 0.944 ± 0.093; less strict: slope = 0.942 ± 0.242). The relationship between the mean number of fires (measured as the mean number of fire ignitions per year) in PAs and their corresponding buffers was significantly different between each combination of PA management type and fire regime group (Table 7). Less strict PAs located in non-fire-prone regions were influenced the least by their buffer zones (slope = 0.691 ± 0.233), followed by strict nature conservation PAs in fire-prone regions (slope = 0.866 ± 0.277). The two remaining groups of PAs – strict, located in a non-fire prone region (slope = 0.956 ± 0.146), and less strict, located in a fire-prone region (slope = 1.051 ± 0.434) – were influenced more by their buffers. The intensity of human disturbances (mean human footprint) in buffers also significantly influenced the degree of human disturbance in PAs, and this effect was similar between strictly managed (slope = 0.892 ± 0.027) and less strictly managed (slope = 0.939 ± 0.076) PAs (Table 7).

When the proportion of natural land cover changed in buffers, there was a significant change in their corresponding PAs. Strictly managed PAs were influenced less by their buffers (slope = 0.286 ± 0.045) compared to less strictly managed PAs (slope = 0.468 ± 0.127); although, this effect of management type was not statistically significant (Table 7). In contrast, detected change in land cover heterogeneity in buffers did not significantly influence the probability of land cover heterogeneity change in PAs, and this pattern was approximately the same between strict and less strict PAs (Table 7).

Discussion

The global PA network is an essential conservation tool for harbouring threatened terrestrial wildlife (Gray et al., 2016). However, PAs are far from meeting their full conservation potential (Watson et al., 2014), and there are important gaps in understanding the extent to which PAs limit the contagion of environmental changes in surrounding areas. Using a set of proposed SRS-EBVs, I tested the stability of the temporal and spatial trends of biologically important variables in PAs and their surroundings, and whether the management regime of PAs influenced either of these trends. Our results reveal that the current PA network appears effective at maintaining elements of ecosystem structure and reducing some forms of human-induced global change, but less efficient at supporting ecosystem functions and mitigating other types of human pressures.

The current PA network effectively maintained elements of ecosystem structure. PAs were particularly successful at maintaining habitat variety through time, and this was comparable to trends in their surroundings (Figure 7B). Spatial analyses also suggest that PAs are resilient against change in land cover variety even if it occurs in their surroundings (Figure 7A). The diversity of habitat types represented by remotely sensed land cover variety is an important determinant of species richness (Kerr et al., 2001; Jetz & Rahbek, 2002), where greater land cover variety translates to greater niche diversity, making an area habitable for more species (Tews et al., 2004). While habitat characteristics of PAs can reflect past and present actions of humans, including those of indigenous groups whose activities are essential for conservation in many landscapes (Fa et al., 2020), PAs limit the risks of rapid changes in habitat heterogeneity. While this trend does not imply that species richness is higher or lower in PAs, PAs maintain habitat heterogeneity, changes to which might be expected to lead to human-induced biodiversity change.

PAs also mitigated habitat loss. Regardless of management type, PAs maintained the extent of natural land cover better than their surrounding areas through time (Figure 6C). Significantly less habitat loss was also detected in the buffer zones of strict nature conservation PAs compared to the amount of loss observed in the surrounding areas of extractive PAs. Less strict PAs (IUCN categories V and VI) are located in regions that experience intense human interaction and resource extraction (Dudley, 2008) that are likely at greater risk of losing natural land cover, which may explain this pattern. PAs generally tend to be located in areas that are already at lower risk of human pressures like forest clearing (Joppa & Pfaff, 2010), and more strict PAs (categories Ia-II) are especially biased towards these regions (Joppa & Pfaff, 2009; Ferraro et al., 2013), which is also a likely cause for the observed difference in habitat loss between buffer types. Spatial analyses revealed that some loss of habitat extent in buffers spills into adjacent PAs; however, PAs demonstrated an ability to reduce the amount of habitat loss compared to that measured in their buffers (Figure 6A, 6B). These results suggest that PAs consistently provide a positive service of preserving more natural habitat compared to unprotected land, even in highly worked landscapes. Similar conclusions have been made in other recent studies, where national PAs established between 2000 and 2012 were found to have reduced forest loss by 72% relative to estimated loss if these lands were not protected (Shah et al., 2021). The strength of this effect, however, is likely influenced by PA location. PAs have historically been placed in regions with low economic or agricultural value rather than targeting hotspots of threatened species. This has led to overestimation of effective protection that PAs grant (Joppa & Pfaff, 2009; Venter et al., 2018). For example, the protective effect of strict PAs has been shown to have less of an impact on maintaining natural land cover compared to less strict PAs because they tend to be placed in areas under comparatively less pressure (Joppa & Pfaff, 2011). Even in areas of high pressure, however, PAs have demonstrated an ability to reduce natural land cover loss (Shah et al., 2021), though habitat losses (i.e. land use changes to non-indigenous human activities) can also accrue within PAs (Françoso et al., 2015; Clerici et al., 2020; Geldmann et al., 2020), and this variation is captured in our analysis. Yet, perhaps the most obvious function of PAs is to prevent habitat losses or reduce rates of loss, and, at a global scale, PAs perform this function capably.

PAs did not alter trends in ecosystem function that depend strongly on broad-scale climatic conditions relative to surrounding areas. I focused on metrics of productivity, specifically the fraction of photosynthetically absorbed radiation (fPAR) (Figure 3). Over the study period, temporal and spatial patterns of mean fPAR were similar in both strict nature conservation and less strict PAs compared to their buffers. Productivity levels are closely linked to climate (Xu et al., 2019) and nutrient availability (Wieder et al., 2015). While PAs effectively limit habitat changes, they do not limit climate change-based changes within their boundaries, nor in surrounding areas, however rigorously they are managed for biological conservation. Interpretation of trends in fPAR (and other remote sensing vegetation indices) is not straightforward in the context of conservation. While these data products are reliable metrics for landscape productivity (Coops et al., 2018), productivity varies enormously by land cover type, and PAs clearly reduce rates of land cover change relative to surrounding lands while fPAR is comparable. The conversion of a tropical forest, for example, to an oil palm plantation has enormous consequences on ecosystem function and biodiversity (Qaim et al., 2020) but effects on productivity alone are challenging to interpret. Ensembles of biodiversity metrics, such as that envisioned within the context of the EBV framework, are necessary to provide insight into the impacts of environmental changes within and around PA networks. The static boundaries of PAs inhibit them from tracking changes in these important climatic determinants of species' survival (Hannah, 2008; Kharouba & Kerr, 2010), Instead, PAs support species on the move in response to changing climates by acting as stepping stones of important microrefugia to facilitate shifting ranges to more suitable habitat (Lehikoinen et al., 2019). This supports proposals for integrating climate change-informed adaptations to the global PA network; to better serve biodiversity in the future, bigger and better-connected PAs that include regions of low climate change vulnerability are essential (Hannah, 2008; Robillard et al., 2015; Coristine et al., 2016).

PAs did not alter fire dynamics within their boundaries (Figure 4). Temporal trends of fire duration and occurrence were stable in PAs and comparable to trends observed in their buffer zones, regardless of the management type or presence of a fire regime. Net changes in these fire metrics were also approximately equal in buffers and PAs, with some exceptions. The maintenance of fire regimes inside PAs may indicate that ecosystem functions, including natural disturbances, can be sustained across broad landscapes. However, the interpretation of these trends becomes less clear when considering the uncertainty of the causes of detected fires. Although we have controlled for broader climatic and ecosystem regimes, the causes of fires – natural or human-started – are unknown. Controlled burns are a common conservation practice within PAs and are often used as a method to protect against more severe fires that would otherwise be dangerous and difficult (or impossible) to control (Fidelis et al., 2018; Eloy et al., 2019; Radford et al., 2020). Fire suppression is another common park management practice with the purpose of maintaining resource supply for extraction (ex. timber) or to preserve natural features (Alvarado et al., 2018; Bolton et al., 2019). While we have demonstrated that satellite remote sensing data provides unparalleled spatial and temporal breadth of fire disturbance data, it is limited in pinpointing fire causes. Future work should supplement remote sensing data with fire census data to separate naturally occurring fire regimes separate harmful, uncontrolled burns. As the field of remote sensing continues to develop in technological and methodological abilities, other forms of natural disturbances may become detectable at global extents too (McDowell et al., 2015; Senf et al., 2017), allowing for a greater understanding of how PAs affect a diversity of disturbance regimes.

Finally, PAs managed for both strict and less strict nature conservation failed to prevent the spill-over of other anthropogenic pressures from their surroundings. The degree of change in human activity in buffers, measured as the difference in the mean Human Footprint from 1993 to 2009, was mirrored in PAs (Figure 5). The interpretation of this result, however, requires attention to what the Human Footprint maps represent and how they were produced. Most human pressures included in these maps imply the loss of natural land cover. While mapped built environments, population density, and electrical infrastructure all detect types of human settlements (urban, suburban, and rural) or areas for human activity (buildings, paved areas, and urban parks), crop and pasture lands represent areas subject to intense agriculture (managed monocultures) and presence of livestock, all of which result in the loss of natural habitat. Because the rate of natural land cover loss was much lower than the degree of human pressure inside PAs compared to surrounding lands, it is unlikely that these pressures are the only drivers of the Human Footprint pattern in PAs. Methods used by Venter et al. (2016b) to map modes of human transportation, particularly roads, are likely to have contributed to the observed trend. The Human Footprint data model the direct and indirect impacts of these linear features. The direct effect is considered as the impact on the natural environment from roads themselves (ex. road kills and land cover conversion), while the indirect effect is mapped 15km outward on either side of a road, even in the absence of detectable physical alteration of those environments. These zones adjacent to roads are intended to reflect the impacts of edge effects and human access. This method of mapping the pressure of roads aligns with results describing the preservation of natural land cover inside PA boundaries. If road construction (loss of natural land cover) increased through time in buffer zones, there would be spillover of their mapped indirect effects (no loss of natural land cover) into PAs. These methods are similar to those used to map navigable waterways and may have contributed to the observed HFP pattern in the same way. Important to note, too, is the difference in time periods between our observations of HFP change (1993-2009) and natural land cover change (2000-2015). If losses in natural land cover in PAs had taken place between 1993 and 2000, this could have been detected in the HFP datasets and not in our analysis of natural land cover extent. Nevertheless, while there are limitations to the inferences that can be drawn from Human Footprint trends, it raises an important message: while PAs appear to reduce the direct impacts of human pressures that result in land conversion, the indirect effects of those activities continue to infiltrate PAs, regardless of their management status. Identifying these exact human pressures requires more precise data that measures individual characteristics of human disturbance.

This study has demonstrated that SRS-EBVs are useful tools for measuring important landscape elements to support biodiversity. We emphasize, however, that they do not diminish the need for foundational conservation principles when planning future PA expansion. For example, SRS-EBV measurements show that PAs successfully conserve elements of ecosystem structure and function, most notably natural habitat heterogeneity and existing land covers. As nations worldwide work towards expanding the total coverage of PAs in response to conservation initiatives (SCBD, 2020), PA boundaries will maintain natural land cover variety and reduce anthropogenic land conversion. The goal of these global initiatives, however, is to reduce local extinction rates. Although SRS-EBVs can enable assessment of how PAs maintain environmental characteristics vital to species survival, remote sensing platforms still provide limited insight into direct measures of biological diversity at species or genetic levels (Randin et al., 2020). This gap is filled by ecological theory, such as environment-species richness relationships (Kerr et al., 2007; Algar et al., 2009), that can illustrate how environment and aspects of biological diversity are linked. In addition to increasing the total area of protected land, PA targets also call for PAs to be well-connected, efficiently and equitably managed, and include locations important for biological diversity (CBD, 2010). Systematic conservation practices informed by remotely sensed, essential biodiversity variables demonstrates that PA networks play vital, even unique, roles in meeting local and global conservation objectives.

Conclusion

To curb current trends of biodiversity loss, nations across the world have committed to expanding the global PA network further in the next few decades (SCBD 2020). However, developing the PA network must meet other ecological conditions in addition to having a greater coverage to meet this goal. Using a collection of ecologically relevant satellite remote sensing products, this thesis has highlighted the strengths and weaknesses of the current PA network. While I have shown that PAs maintain elements of ecosystem structure, I have also identified areas of improvement for sustaining ecosystem functions that would benefit from the application of key conservation principles. The protection of natural environments is a critical first step to biodiversity protection that existing PAs achieve. Expanding the PA network in the future must uphold this quality while also making vast improvements to meet additional needs for species. EBVs can be applied as a powerful tool to measure our progress towards building a stronger PA network with supplementation from other data sources. Combining such datasets with the pool of conservation principles and knowledge is promising for the future of PAs and the species that depend on them.

Tables and Figures

Table 1. Essential biodiversity variables (EBVs) and their corresponding candidate satellite remote sensing (SRS) data products. SRS product names and codes, satellite and sensor, spatial resolution (SR), time period, statistics measured, and units are presented. All SRS data products cover a global extent and have an annual temporal resolution.

EBV Class	EBV	SRS Product Name	SRS Product Code	Satellite and sensor	SR (km^2)	Time period	Statistic	Units	Source
Ecosystem function	Primary productivity	Net Primary productivity (NPP)	MOD17A3 v55	Terra/Aqua-MODIS	~1	2000-2015	annual total	g carbon/m2	NTSG
		Gross Primary Productivity (GPP)	MOD17A2 v55	Terra/Aqua-MODIS	~30	2000-2015	annual total	g carbon/m2	NTSG
		Normalized Difference Vegetation Index (NDVI)	VIPPHEN_NDVI v4	Terra-MODIS	~30	1981-2014	annual sum, mean	unitless	LP DAAC
		Enhanced Vegetation Index (EVI)	VIPPHEN_EVI2 v4	Terra-MODIS	~30	1981-2014	annual sum, mean	unitless	LP DAAC
		Fraction of Photosynthetically Active Radiation (fPAR)	MOD15A2H v5	Terra/Aqua-MODIS	~1	2003-2015	annual sum, minimum, variability	unitless	SILVIS Lab
		Leaf Area Index (LAI)	MOD15A2H v5	Terra/Aqua-MODIS	~1	2003-2015	annual sum, minimum, variability	unitless	SILVIS Lab
	Ecosystem disturbances	Fire Duration	MCD64A1 v6	Terra/Aqua-MODIS	~780	2003-2016	annual sum	average number of days all fires in a 0.25-degree cell burned in a given year.	ORNL DAAC
		Fire Ignitions	MCD64A1 v6	Terra/Aqua-MODIS	~780	2003-2016	annual sum	# of fire ignitions in a 0.25-degree cell for a given year.	ORNL DAAC
		Human Footprint Maps	Modelled	Various	~1	1993, 2009	annual mean	unitless	Venter *et al.*, 2016b
Ecosystem structure	Live cover fraction	Land Cover	CCI-LC	Various	~0.3	2000-2015	annual proportion of natural land cover	unitless	CCI-LC project
	Ecosystem distribution	Land Cover	CCI-LC	Various	~0.3	2000-2015	annual land cover heterogeneity	total number of unique land cover types	CCI-LC project

NTSG: Numerical Terradynamic Simulation Group
LP DAAC: Land Processes Distributed Active Archive Center (USGS = US Geological Survey)
SILVIS Lab (University of Wisconsin-Madison): http://silvis.forest.wisc.edu/data/dhis/
ORNL DAAC: Oak Ridge National Laboratory Distributed Active Archive Center (USGS)
CCI-LC: Climate Change Initiative-Land Cover (European Space Agency)

Table 2. Land cover types defined by the Climate Change Initiative - Land Cover Project (CCI-LCP)[a], and their corresponding raster value (CCI Value). CCI values were reclassified into a binary data set, where values of 1 indicate an “apparently natural” land cover type and values of 0 indicate a “built or agricultural” land cover type.

CCI Land Cover Type	CCI Value	Reclassified Value
Cropland, rainfed	10	0
Cropland, irrigated or post-flooding	20	0
Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	30	0
Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)	40	1
Tree cover, broadleaved, evergreen, closed to open (>15%)	50	1
Tree cover, broadleaved, deciduous, closed to open (>15%)	60	1
Tree cover, needleleaved, evergreen, closed to open (>15%)	70	1
Tree cover, needleleaved, deciduous, closed to open (>15%)	80	1
Tree cover, mixed leaf type (broadleaved and needleleaved)	90	1
Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	100	1
Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	110	1
Shrubland	120	1
Grassland	130	1
Lichens and mosses	140	1
Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	150	1
Tree cover, flooded, fresh or brakish water	160	1
Tree cover, flooded, saline water	170	1
Shrub or herbaceous cover, flooded, fresh/saline/brakish water	180	1
Urban areas	190	0
Bare areas	200	1
Water bodies	210	NoData
Permanent snow and ice	220	1

[a](ESA, 2017)

Table 3. Pearson correlation matrices for annual metrics of primary productivity (2003, 2008 and 2014). These metrics include annual EVI and NDVI means and sums, cumulative (c), minimum (m), and seasonal (s) fPAR and LAI, and annual GPP and NPP. These matrices were used to perform principal component analyses for each year.

	EVI mean	EVI sum	fPAR c	fPAR m	fPAR s	GPP	LAI c	LAI m	LAI s	NDVI mean	NDVI sum
						2003					
EVI sum	1.000										
fPAR c	0.931	0.931									
fPAR m	0.869	0.869	0.930								
fPAR s	-0.679	-0.679	-0.691	-0.800							
GPP	0.894	0.894	0.928	0.902	-0.638						
LAI c	0.829	0.829	0.883	0.866	-0.556	0.872					
LAI m	0.758	0.758	0.804	0.869	-0.577	0.824	0.949				
LAI s	-0.670	-0.670	-0.666	-0.784	0.937	-0.640	-0.575	-0.626			
NDVI mean	0.968	0.968	0.954	0.872	-0.683	0.897	0.821	0.732	-0.668		
NDVI sum	0.968	0.968	0.954	0.872	-0.683	0.897	0.821	0.732	-0.668	1.000	
NPP	0.730	0.730	0.776	0.741	-0.526	0.913	0.693	0.648	-0.520	0.757	0.757
						2009					
EVI sum	0.753										
fPAR c	0.884	0.670									
fPAR m	0.817	0.624	0.834								
fPAR s	-0.431	-0.416	-0.493	-0.664							
GPP	0.880	0.658	0.936	0.853	-0.494						
LAI c	0.807	0.597	0.838	0.859	-0.455	0.859					
LAI m	0.725	0.533	0.740	0.853	-0.478	0.795	0.940				
LAI s	-0.491	-0.427	-0.522	-0.672	0.845	-0.539	-0.512	-0.565			
NDVI mean	0.845	0.952	0.797	0.716	-0.453	0.765	0.694	0.603	-0.469		
NDVI sum	0.965	0.724	0.894	0.789	-0.359	0.867	0.796	0.693	-0.430	0.861	
NPP	0.804	0.600	0.857	0.749	-0.419	0.938	0.748	0.667	-0.453	0.812	0.713
						2014					
EVI sum	1.000										
fPAR c	0.929	0.929									
fPAR m	0.854	0.854	0.923								
fPAR s	-0.653	-0.653	-0.675	-0.799							
GPP	0.897	0.897	0.936	0.901	-0.641						
LAI c	0.818	0.818	0.881	0.860	-0.549	0.875					
LAI m	0.743	0.743	0.800	0.869	-0.581	0.820	0.946				
LAI s	-0.629	-0.629	-0.637	-0.770	0.935	-0.634	-0.554	-0.618			
NDVI mean	0.966	0.966	0.947	0.852	-0.659	0.897	0.804	0.712	-0.630		
NDVI sum	0.966	0.966	0.947	0.852	-0.659	0.897	0.804	0.712	-0.630	1.000	
NPP	0.774	0.774	0.815	0.764	-0.556	0.925	0.714	0.654	-0.543	0.800	0.800

Table 4. Terrestrial biomes defined by the World Wildlife Fund – US[a] categorized into regions with (Y) and without (N) regular fire disturbances.

Value	Biome	Fire Regime
1	Tropical & Subtropical Moist Broadleaf Forests	N
2	Tropical & Subtropical Dry Broadleaf Forests	Y
3	Tropical & Subtropical Coniferous Forests	Y
4	Temperate Broadleaf & Mixed Forests	Y
5	Temperate Conifer Forests	Y
6	Boreal Forests/Taiga	Y
7	Tropical & Subtropical Grasslands, Savannas & Shrublands	Y
8	Temperate Grasslands, Savannas & Shrublands	Y
9	Flooded Grasslands & Savannas	Y
10	Montane Grasslands & Shrublands	N
11	Tundra	N
12	Mediterranean Forests, Woodlands & Scrub	Y
13	Deserts & Xeric Shrublands	N
14	Mangroves	N
99	Rock and Ice	N

[a](Olson et al., 2001)

Table 5. Comparison of fit based on Akaike's Information Criterion (AIC) values for generalized linear mixed effects models (GLMMs) and the equivalent spatial GLMM (inclusion of a spatial covariance term) of best fit for temporal and spatial analyses. Moran's I values were calculated to test for spatial autocorrelation (SAC) in model residuals for all GLMMs and are presented below; all tests for SAC were significant ($p < 0.05$), unless indicated otherwise.

EBV		Model	Moran's I	ΔAIC
Temporal				
Mean fPAR	PA	Year:IUCN Group, Biome, Continent, PA ID exponential	0.325 -	-535
	Buffer	Year:IUCN Group, Biome, Continent, PA ID exponential	0.391 -	-8,156
Mean fire duration	PA	Year:IUCN Group:Fire, Biome, Continent, PA ID exponential	0.188 -	-388
	Buffer	Year:IUCN Group:Fire, Biome, PA ID exponential	0.233 -	-639
Mean fire ignitions	PA	Year:IUCN Group:Fire, Biome, Continent, PA ID matern	0.221 -	-447
	Buffer	Year:IUCN Group:Fire, Biome, Year|Continent, PA ID exponential	0.259 -	-758
Natural land cover heterogeneity	PA	Year:IUCN Group Matern[a]	0.122 -	- 38,333
	Buffer	Year:IUCN Group, Year|Biome, Year|Continent, PA ID matern	0.234 -	-407
Proportion of natural land cover	PA	Year:IUCN Group, Year|Biome, Year|Continent, PA ID exponential[b]	0.0403 -	4
	Buffer	Year:IUCN Group, Biome, Continent, PA ID exponential	0.125 -	-646
Spatial				
Mean fPAR		Buffer:IUCN Group, Biome, Continent exponential	0.0671 -	-2.3e7
Proportion of natural land cover		Buffer:IUCN Group, Biome exponential	0.0226 -	-216
Mean fire duration[c]		Buffer:IUCN Group:Fire Buffer:IUCN Group:Fire, Continent	0.00717 -	-1
Mean fire ignitions		Buffer:IUCN Group:Fire, Buffer|Continent matern	0.0497 -	-2.9e12
Mean human footprint		Buffer:IUCN Group, Biome, Continent exponential	0.0667 -	-22
Natural land cover heterogeneity		Buffer:IUCN Group, Biome, Buffer|Continent exponential	0.00951 -	-12

[a]This model was fit using the *spaMM::fitme()* R function (Rousset & Ferdy, 2014), as *glmmTMB* would not produce converging models.
[b]This model had a slightly higher AIC than the corresponding GLMM. However, because significant SAC was detected in the GLMM's residuals, and the GLMM did not have a significantly better fit, I chose to use

the model that includes an exponential spatial covariance term.
[c]The Moran's I value for the spatial model of mean fire duration was not significant ($p > 0.05$). Here, the ΔAIC value represents the comparison of fit between the two best non-spatial GLMMs.

Table 6. Temporal trends of EBVs (i.e. EBV as a function of year) in protected areas (PA) and their corresponding buffer zones (Buffers) for a 13 year period (2003-2015) modeled using GLMMs with spatial autocorrelation covariance terms. Estimated regression parameters, standard errors (SE), z values, P-values, and sample sizes (n) are presented. Significant P-values (<0.05) are bolded.

EBV proxy (n)		Parameter	Estimate	SE	*z* value	*P*-value
Mean FPAR (151,255)	PA	Intercept	-1.736	0.336	-5.764	**0.000**
		Year	0.001	0.000	8.515	**0.000**
		IUCN	0.005	0.020	0.270	0.530
		Year:IUCN	0.000	0.000	-2.069	0.105
	Buffer	Intercept	-1.655	0.595	-3.808	**0.026**
		Year	0.001	0.000	8.238	**0.000**
		IUCN	0.009	0.009	1.205	0.297
		Year:IUCN	-0.001	0.000	-3.639	0.079
Mean fire duration (12,571)	PA	Intercept	-0.140	0.438	-0.319	0.750
		Year	-0.018	0.005	-3.677	**0.000**
		IUCN	0.004	0.125	0.035	0.972
		Fire	0.606	0.360	1.684	0.092
		Year:IUCN	0.002	0.008	0.186	0.853
		Year:Fire	0.010	0.006	1.669	0.095
		IUCN:Fire	-0.139	0.169	-0.824	0.410
		Year:IUCN:Fire	-0.002	0.010	-0.241	0.809
	Buffer	Intercept	-0.338	0.316	-1.070	0.285
		Year	-0.011	0.003	-3.214	**0.001**
		IUCN	0.139	0.082	1.701	0.089
		Fire	0.460	0.218	2.107	**0.035**
		Year:IUCN	-0.005	0.006	-0.923	0.356
		Year:Fire	0.004	0.004	0.961	0.337
		IUCN:Fire	-0.243	0.111	-2.190	**0.029**
		Year:IUCN:Fire	0.003	0.007	0.464	0.643
Mean fire ignitions (12,597)	PA	Intercept	-1.213	0.504	-2.406	**0.016**
		Year	-0.018	0.004	-4.377	**0.000**
		IUCN	0.220	0.152	1.450	0.147
		Fire	0.351	0.502	0.700	0.484
		Year:IUCN	-0.022	0.007	-3.052	**0.002**
		Year:Fire	0.023	0.005	4.902	**0.000**
		IUCN:Fire	-0.136	0.207	-0.658	0.510
		Year:IUCN:Fire	0.016	0.008	1.904	0.057
	Buffer	Intercept	-0.945	0.438	-2.156	**0.031**
		Year	-0.025	0.014	-1.812	0.070
		IUCN	0.188	0.099	1.888	0.059
		Fire	0.339	0.374	0.905	0.365

		Year:IUCN	-0.002	0.005	-0.373	0.709
		Year:Fire	0.016	0.004	3.932	**0.000**
		IUCN:Fire	-0.338	0.136	-2.485	**0.013**
		Year:IUCN:Fire	0.007	0.006	1.157	0.247
Proportion of natural land cover (79,638)	PA	Intercept	3.465	0.400	8.733	**0.000**
		Year	0.000	0.001	-0.197	0.846
		IUCN	-0.586	0.134	-4.393	**0.001**
		Year:IUCN	-0.001	0.000	-1.429	0.168
	Buffer	Intercept	1.559	0.396	3.968	**0.000**
		Year	-0.001	0.000	-14.980	**0.000**
		IUCN	-0.295	0.111	-2.646	**0.009**
		Year:IUCN	-0.001	0.000	-3.954	**0.000**
Natural land cover heterogeneity (154,986)	PA[a]	Intercept	15.416	1.709	11.870	**0.000**
		Year	0.002	0.004	0.600	0.548
		IUCN	0.492	0.388	1.266	0.206
		Year:IUCN	0.002	0.008	0.203	0.839
	Buffer	Intercept	2.359	0.093	25.640	**0.000**
		Year	0.000	0.000	0.906	0.349
		IUCN	0.953	0.171	5.569	**0.000**
		Year:IUCN	0.000	0.000	-5.474	**0.000**

[a]The *spaMM::fitme()* R function (Rousset & Ferdy, 2014) was used to model these data as *glmmTMB* would not produce converging models. As a result, the z-values presented here are t-values produced by the *spaMM::fitme()* model.

Table 7. Spatial trends of EBVs (i.e. EBV change in protected areas as a function of EBV change in their corresponding buffers) modeled using GLMMs with spatial autocorrelation covariance terms, unless specified otherwise. EBV change was calculated as the difference between the first and last year of observation for each variable's unique time period (Table 1). Estimated regression parameters, standard errors (SE), z values, P-values, and sample sizes (n) are presented. Significant P-values (<0.05) are bolded.

EBV proxy (n)	Parameter	Estimate	SE	*z* value	*P*-value
Mean FPAR (11,635)	Intercept	0.001	0.001	0.810	0.438
	Buffer	0.833	0.023	35.828	**0.000**
	IUCN	0.001	0.001	1.569	0.059
	Buffer:IUCN	0.008	0.044	0.169	0.528
Mean fire duration (967)	Intercept	-0.510	0.395	-1.290	0.197
	Buffer	0.944	0.093	10.099	**0.000**
	IUCN	0.315	0.649	0.485	0.627
	Fire	-0.468	0.533	-0.878	0.380
	Buffer:IUCN	-0.001	0.149	-0.009	0.993
	Buffer:Fire	-0.257	0.111	-2.316	**0.021**
	IUCN:Fire	0.350	0.917	0.381	0.703
	Buffer:IUCN:Fire	0.183	0.184	0.998	0.319
Mean fire ignitions (969)	Intercept	0.129	0.571	0.225	0.822
	Buffer	0.956	0.146	6.546	**0.000**
	IUCN	-0.011	0.196	-0.056	0.956
	Fire	0.951	0.562	1.693	0.090
	Buffer:IUCN	-0.265	0.087	-3.051	**0.002**
	Buffer:Fire	-0.089	0.081	-1.102	0.271
	IUCN:Fire	-0.465	0.656	-0.710	0.478
	Buffer:IUCN:Fire	0.450	0.120	3.757	**0.000**
Mean human footprint (11,910)	Intercept	-0.327	0.174	-1.877	0.062
	Buffer	0.892	0.027	32.599	**0.000**
	IUCN	-0.009	0.090	-0.102	0.619
	Buffer:IUCN	0.048	0.048	0.988	0.344
Proportion of natural land cover (6,126)	Intercept	0.001	0.001	0.880	0.379
	Buffer	0.286	0.045	6.552	**0.000**
	IUCN	0.000	0.001	-0.020	0.980
	Buffer:IUCN	0.181	0.082	2.138	0.084
Natural land cover heterogeneity (11,922)	Intercept	-1.782	0.203	-9.177	**0.000**
	Buffer	0.299	0.199	1.597	0.178
	IUCN	0.065	0.183	0.312	0.723
	Buffer:IUCN	-0.151	0.319	-0.527	0.526

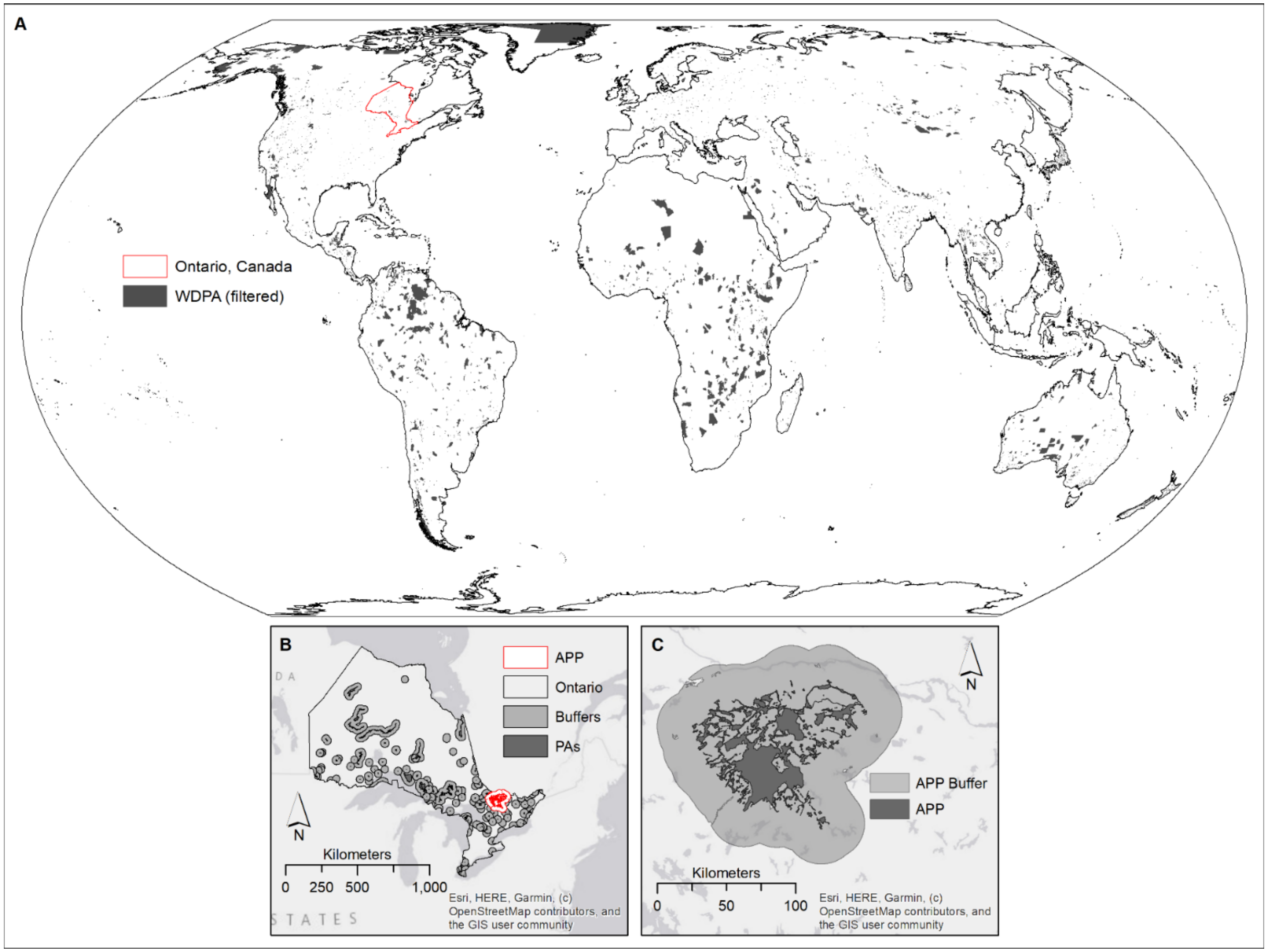

Figure 1. (A) The World Database on Protected Areas (WDPA) was filtered by the following criteria: a protected area (PA) must be terrestrial, assigned an IUCN category ranging from Ia to VI (Dudley, 2008) and established by the year 2000, inclusively. PAs represented by their centroids or surrounded by water (islands) in the WDPA were excluded. (B) An example of 25km buffers drawn around PAs in Ontario, Canada. Buffers of this distance were drawn around all PAs in the filtered WDPA. A close up of one PA, Algonquin Provincial Park (APP), and its 25km buffer is presented (C).

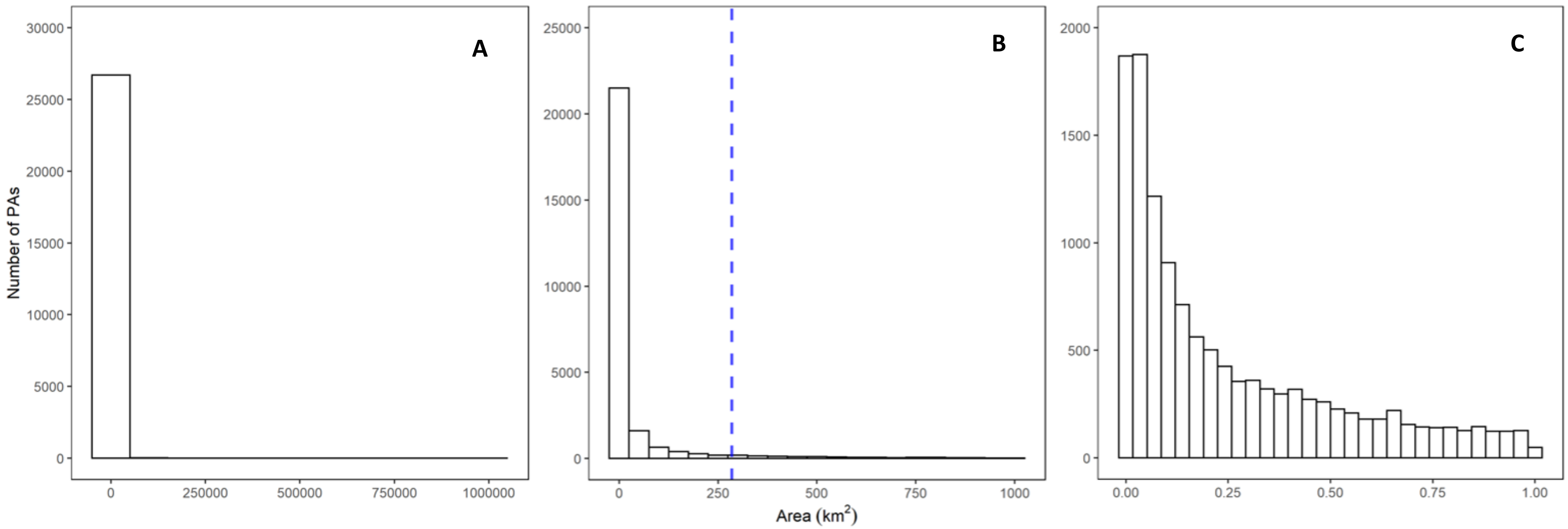

Figure 2. The distribution of protected area (PA) sizes (km^2) in the complete filtered WDPA (A; n= 26,708). To visualize the distribution of small PAs more clearly, the same histograms are presented for PAs in the filtered WDPA with (B) an area less than or equal to 1000km^2 (n=25,749) and (C) an area less than or equal to 1km^2 (n=12,547). The mean size of all PAs in the filtered WDPA (~285 km^2) is plotted as a dashed blue line (B).

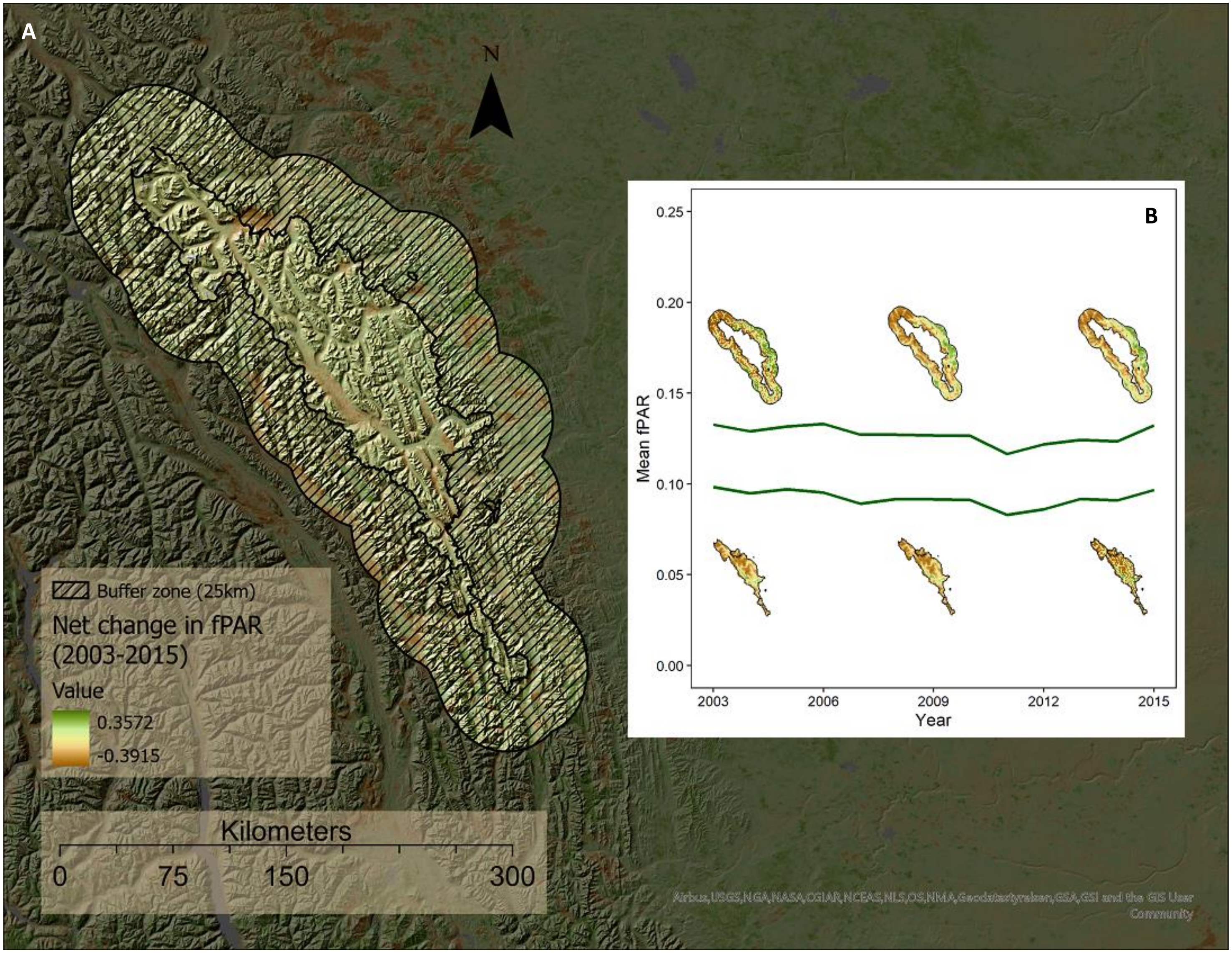

Figure 3. Global trends in mean fraction of photosynthetically active radiation (fPAR) are represented here by Banff (IUCN category II) and Height of the Rockies (IUCN category Ib) national parks located in Alberta, Canada. Mean fPAR remained stable through time both within the protected areas and their buffer zones (B). Net change in mean fPAR in both parks was also about the same as that in their buffers (A).

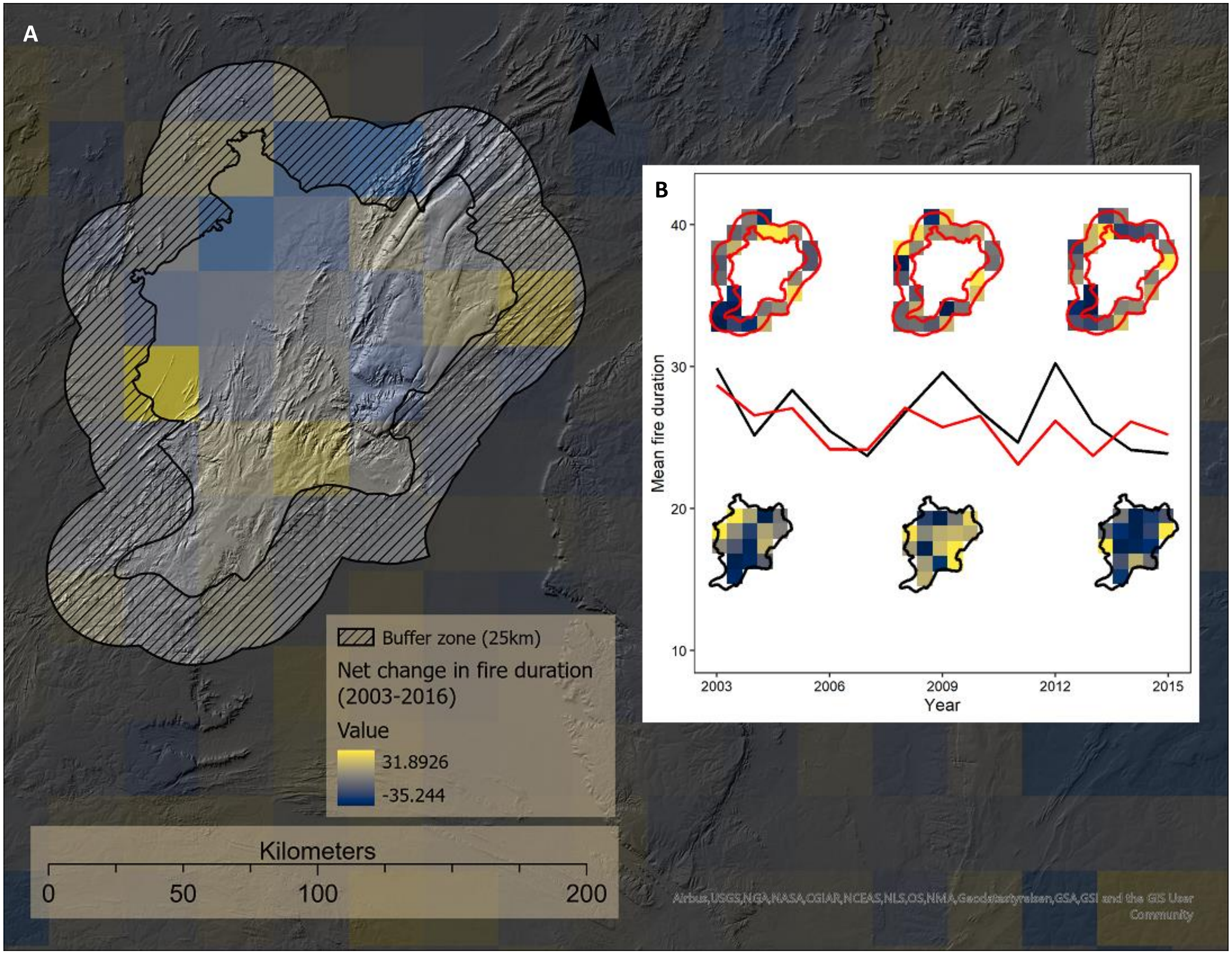

Figure 4. Global trends of mean fire duration are exemplified here by Upemba National Park (IUCN category II) located in the Democratic Republic of Congo. Mean fire duration was approximately unchanged in protected areas (PAs) and buffer zones through time (B), and the net change in mean fire duration from 2003-2016 was roughly the same between PAs and buffers (A).

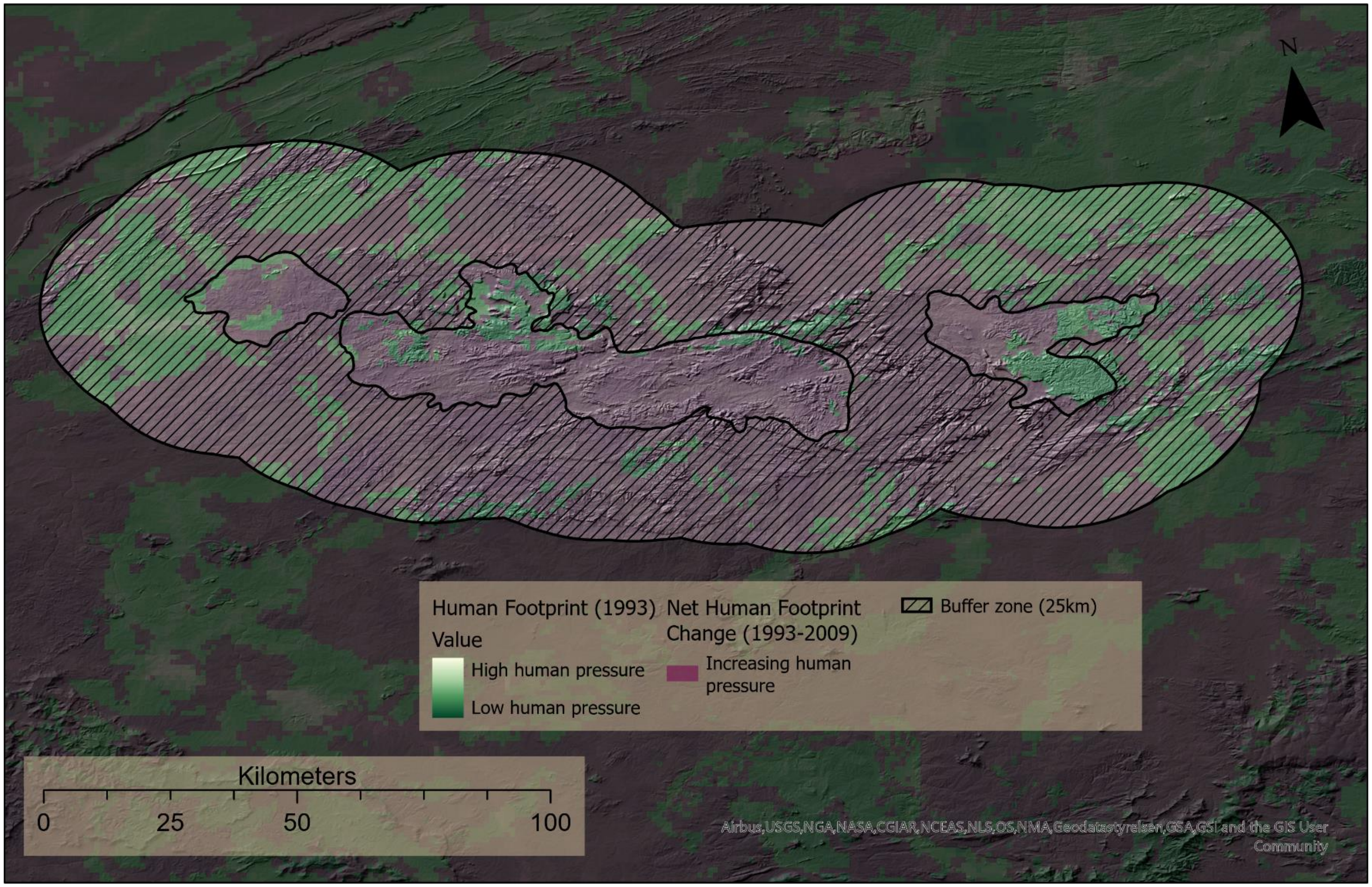

Figure 5. Increased human pressure between 1993 and 2009 (i.e. net change > 0 in the Human Footprint Index; Venter et al., 2016a) detected in three neighbouring protected areas and their buffer zones located at the Chhattisgarh-Madhya Pradesh border in India. Sanjay Dubri Sanctuary (right) and Tamor Pingla Sanctuary (left) are IUCN category IV PAs, while Sanjay National Park (center) is an IUCN category II PA.

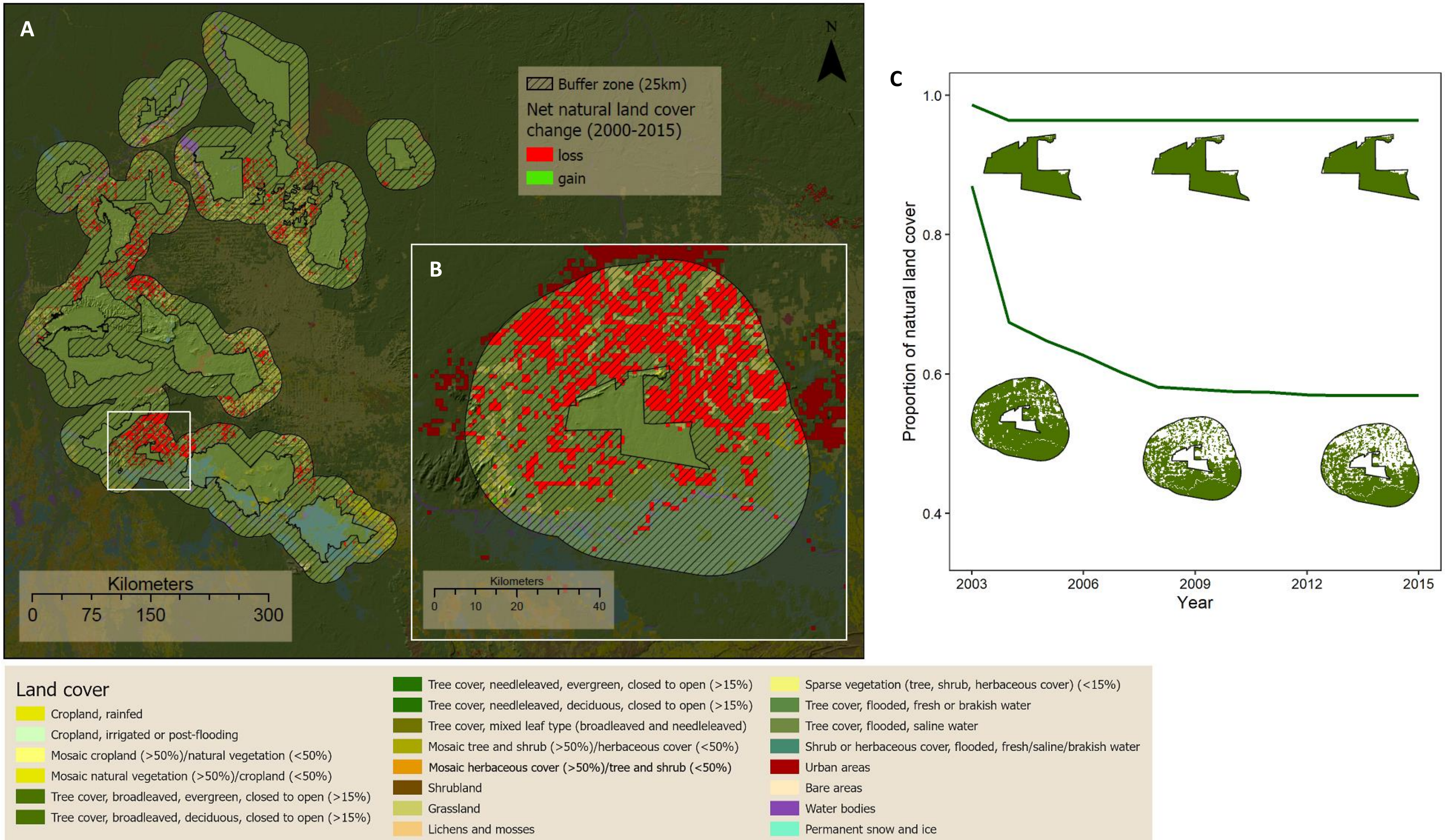

Figure 6. The efficacy of the global protected area (PA) network at preventing habitat loss inside of its boundaries is demonstrated by this cluster of PAs located at the Brazil-Bolivia border in South America (A). The Serra dos Reis State Park (IUCN category II) was particularly effective at maintaining habitat within its boundaries over the 2000-2015 period despite extensive habitat loss in the surrounding area (B, C).

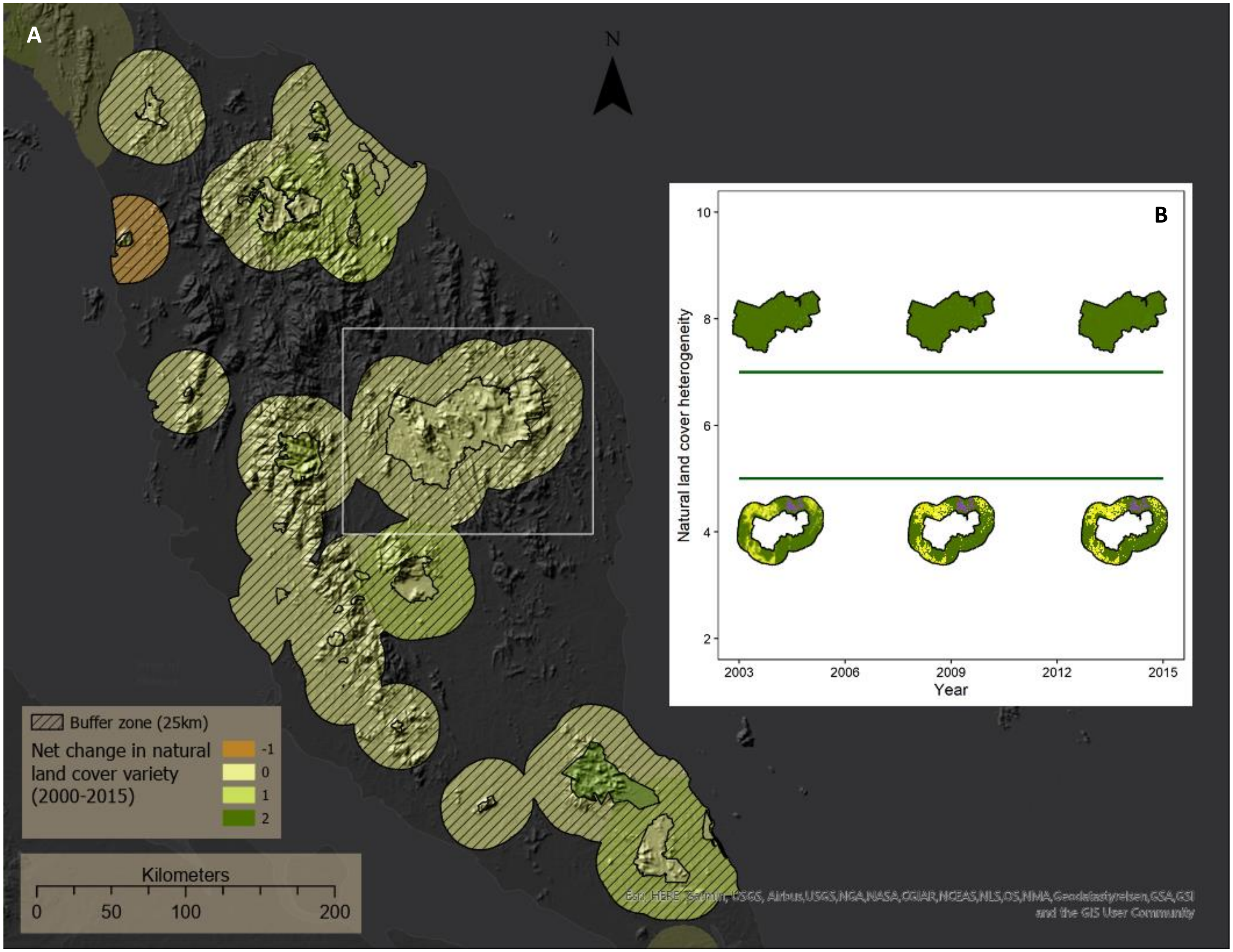

Figure 7. Habitat heterogeneity (measured as natural land cover variety) was approximately stable through time in protected areas (PAs) and buffer zones from 2003-2015. This pattern is exemplified by the PA Taman Negara National Park (IUCN category II), located in Pahang, Malaysia (B). Change in habitat heterogeneity between 2000 and 2015 in buffer zones did not significantly impact the likelihood of a similar change in corresponding PAs (A).

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