

# The use of environmental heterogeneity as an indicator of protected area effectiveness in conserving biodiversity

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## Research Article

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# Abstract

Developing innovative monitoring systems for biodiversity outcomes in protected areas (PAs) are important to enable effective adaptive management. Here we show how to quantitatively detect and monitor temporal and spatial patterns in environmental heterogeneity, an important indicator of ecological integrity and biodiversity patterns. We used a 28-year time series (1991 – 2018) generated from freely available Landsat satellite imagery and Roa's quadratic index to calculate trends in heterogeneity for 41 PAs across South Africa. We selected PAs where mega-herbivore assemblages were similar and where management objectives were broadly aligned with South African legislation to protect biodiversity. Heterogeneity decreased in 11 (32%), increased in three (7%), and remained stable in 26 (63%) PAs. In PAs where heterogeneity was decreasing, factors such as fire, precipitation, woody encroachment, and elephants may be contributing to a possible park effect where small, fenced areas are becoming more homogenized. However, our results also indicated that factors such as fire and herbivory as well as the location of roads, waterholes, and camps can be manipulated to increase PA heterogeneity. The framework presented here can be extended to include every PA nationally, or even globally, and the data product fully automated. This presents an opportunity for conservation management to incorporate this important biodiversity indicator in PA monitoring programs as well as other large-scale environmental monitoring initiatives.

## Introduction

Protected areas (PAs) are key to the conservation of biodiversity and provides the foundation for achieving the Sustainable Development Goals (UNEP-WCMC, IUCN & NGS, 2018). They are recognised across multiple international policy processes including the 2030 Agenda for Sustainable Development, the Convention on Biological Diversity (CBD) and the Ramsar Convention. PA coverage is also expected to increase in line with the Aichi Biodiversity Targets and Strategic Plan for Biodiversity and will be central to halting and reversing the ongoing global biodiversity crisis.

However, for PAs to fulfil their intended role they must be effective (Le Saout et al. 2013). PA effectiveness can be assessed in different ways with different approaches emphasising social, environmental, economic, and/or management issues. For example, assessments may focus on the diversity of species, or management adequacy in terms of financial resources or the capacity of staff. However, existing approaches often lack independent quantification (Barnes et al. 2018) and are particularly limited when considering biodiversity outcomes (Stolton et al. 2020). Biodiversity outcomes vary across spatial and temporal scales, not only because of the variability in local ecological factors, but also the political and economic ones affecting PAs (Dos Santos Ribas et al. 2000). This is problematic because PA management must be able to measure their effectiveness in conserving biodiversity in ways that are scientifically sound, practical, cost effective, and comparable over space and time (Parrish et al. 2003). Without objective measurement, it is impossible to claim successes, learn from failures, or inform adaptive management approaches to achieve the desired conservation outcomes.

Environmental heterogeneity is an important indicator of ecological integrity and a key landscape characteristic with strong relevance for biodiversity and its functions (Stein et al. 2014). The variety and geographic layout of habitats affect plant, mammal, and bird diversity, as well as ecosystem function and services (Stein & Kreft, 2015). The literature is replete with studies showing that environmental heterogeneity is strongly linked to species richness at local, regional, and global scales (Tamme et al. 2010; Costanza et al. 2011; Stein et al. 2014, Cramer & Verboom et al. 2017; Udy et al. 2021). Heterogeneity in climate, topography, as well as vegetation composition and structure increase available niches, which allows species to coexist even in restricted geographic space (Beier & de Albuquerque, 2015, but also see Ortega et al. 2018). This positive heterogeneity-diversity relationship predicted by niche theory (Hutchinson 1957, MacArthur & MacArthur 1961) could be used to monitor the effectiveness of PAs in conserving species diversity and ecosystem function. Decreasing heterogeneity within a PA could therefore be an indication that species diversity is also decreasing. Conversely, if heterogeneity is stable in PAs over time, species diversity should theoretically remain unaffected – not considering the influence that selective poaching or translocations may have on community assemblages in PAs (e.g., Ferreira et al. 2015; Cook & Henley 2019). Changes in heterogeneity could also affect ecosystem function by affecting interactions among habitat patches and species across PAs. For example, environmental heterogeneity affects the strength of density-dependent feedbacks on large herbivore population growth and the viability of their populations, which make up a large component of the biomass found in many PAs, specifically in Africa (Sianga et al. 2017). A heterogeneity paradigm therefore offers a powerful framework for PA managers to assess the effectiveness of PAs in conserving biodiversity, given that it emphasises the functioning of ecological systems across a full hierarchy of physical and biological components, processes, and scales in a dynamic space-time mosaic (Pickett et al. 1997; Sinclair & Walker, 2003; Schloss et al. 2011).

However, quantifying and monitoring changes in heterogeneity is challenging. Ways to measure heterogeneity include labour intensive fieldwork that is usually limited to small regions. Given the large size of many PAs, such field measurements of heterogeneity are impractical and too costly to implement widely. Moreover, to detect meaningful trends in heterogeneity, which account for the effect of scale, requires consistent field surveys over multiple years, which is typical of well-funded long-term monitoring programs, but not possible for many underfunded PAs. To overcome these challenges, many broad-scale studies have taken advantage of spatially continuous coverage of remotely sensed data, such as digital elevation models (DEM) or categorical land-cover data, to quantify heterogeneity (Kerr & Packer 1997; Jetz & Rahbek, 2002). In addition, the availability of LiDAR data for some regions have allowed for the monitoring of structural heterogeneity of vegetation (e.g., Asner & Levick, 2012; Davies et al. 2018). However, topography- and land-cover-based measures of heterogeneity have limitations, while the costs involved with acquiring LiDAR data makes it unrealistic to incorporate into long-term monitoring programs that inform PA management. Moreover, land-cover maps derived from remote sensing data can provide information on spatial patterns and temporal dynamics of general habitat types, but their typical categorical format ignores the continuous nature of environmental heterogeneity (Guisan & Thuiller 2005).

Novel approaches, which combine satellite remote sensing technology with information theory, could overcome the challenges associated with measuring and monitoring heterogeneity in PAs over time. Diversity indices such as the Shannon entropy index (Shannon, 1948), Pielou's evenness (Pielou, 1977), and Roa's quadratic entropy diversity index (Rocchini et al. 2017), have been used to calculate environmental heterogeneity across spatial and temporal scales (e.g. Torresani et al. 2019; Doxa & Prastacos, 2020). These indices are based on the continuous variability of pixel values e.g., the original digital numbers of a satellite image (DN) (Rocchini et al. 2017), which represents the strength of the signal (amount of light) that is assigned to each grid cell (pixel). Freely available Landsat Collections data products consist of quantized and calibrated scaled DN representing the multispectral image data. The rationale behind this approach is that spatial variability in the remotely sensed signal relate to environmental variability i.e., different vegetation types, habitats, and/or surfaces (e.g., water, bare ground) will reflect light differently, thereby giving rise to spectral heterogeneity that is indicative of environmental heterogeneity (Rocchini et al. 2010). Detecting heterogeneity through the processing of remotely sensed imagery could allow one to capture changes associated with plant species diversity loss or gain at various spatial and temporal resolutions and extents (Rocchini et al. 2018). This is particularly useful because calculations can be based on satellite imagery that extend back in time, thereby making it suitable to incorporate into PA management. When applied over multiple dates and PAs, such an approach could detect changes in heterogeneity patterns and provide a quantitative measure of the effectiveness of PA management.

In this study, we investigate trends in heterogeneity in South African PAs and propose that remotely sensed environmental heterogeneity can be used to monitor the effectiveness of PAs in conserving biodiversity and ecosystem function. We define environmental heterogeneity as the variation of landscape form (the physical rendition of composition, structure, and function), as represented by spectral variation in satellite images and base this assessment on the Spectral Variation Hypothesis which posits that higher levels of environmental heterogeneity (measured by spectral diversity from remotely sensed images) is related to a higher number of ecological niches for species living therein (Palmer et al. 2002; Rocchini et al. 2004; Torresani et al 2019). In doing so, we have three objectives. First, we use Landsat imagery and Roa's quadratic index to calculate environmental heterogeneity for 41 PAs in South Africa and rank these areas from most to least heterogeneous. Second, we calculate trends in heterogeneity for each of these areas from 1990 – 2018 to determine which of the areas have increasing, decreasing, or stable heterogeneity. Third, we propose incorporating long-term measurements of heterogeneity into adaptive management approaches for biodiversity conservation and provide insight into its application for PA managers. The focus of this contribution is not to assess management effectiveness, but to propose a way of monitoring how effective PAs are in conserving biodiversity.

## Methods

### Study Area

PAs (n=41) were selected in four regions across South Africa: 1) Eastern Cape (n = 6), 2) KwaZulu-Natal (n = 12), 3) North-West (n = 9), and 4) Kruger (n =14). Given the size and environmental variation associated with the Kruger National Park, we analysed the north, south, and central regions separately and treated these as separate areas in our analysis. The Eastern Cape region is located within the thicket biome. The KwaZulu-Natal and Kruger regions are located in the wet savannahs in the east of the country where rainfall averages approximately 350 – 750 mm, while the North-West region was located in the drier western savannahs where rainfall averages 190 – 350 mm per year (Figure 1).

PAs were private (n =29) and state (n =10) owned and ranged in size from 40 km<sup>2</sup> – 19 485 km<sup>2</sup> (Table 1). We selected areas where mega-herbivore assemblages were similar, for example, every PA in the study harboured elephants. We also focused on areas where management objectives were broadly aligned with South African legislation, where the National Environmental Management: Biodiversity Act (2004) (NEMBA) provides for the management and conservation of South Africa's biodiversity, the protection of species and ecosystems that warrant protection and the fair and equitable sharing of benefits involving indigenous biological resources. In addition, the National Environmental Management Protected Areas Act (2003) (NEMPAA) intend to coordinate the declaration and management of PAs and all biodiversity found in these PAs.

Most PAs included in our assessment were fenced, except for properties adjoining the Kruger National Park (KNP). Fences between the KNP and adjacent properties were dropped in the early 1990's and the area has functioned as a relatively open system, although management practices differ among the different entities. For example, densities of artificial waterholes are higher in some of the adjacent private reserves than in KNP.

### *Data analyses*

All analyses were carried out in R version 3.6.1 (R Development Core Team, 2020) and ArcGIS Pro 2.4.2 in a stepwise manner (Figure 2): (1) acquiring satellite imagery including pre-processing and corrections, (2) calculating indices of heterogeneity for each image, and (3) model trends in heterogeneity across temporal (1990 -2018) and spatial scales (within PAs).

### *Acquiring imagery*

Satellite images were sourced from the United States Geological Survey (USGS) that offers on-demand production of Landsat Surface Reflectance data through EarthExplorer (<https://earthexplorer.usgs.gov/>). The data were located under the Landsat category, Landsat Collection 1 Level-2 (On-Demand) subcategory, with Landsat 8 OLI/TIRS, Landsat 7 ETM+, and Landsat 4-5 TM listed as individual datasets. Images were sourced from all three datasets for the selected PAs. Images representing peak dry season conditions (July and August months) and peak wet season conditions (January and February) were selected for each year from 1990 to 2018.

Once the requested scenes were processed and available for download, the Surface Reflectance products were downloaded in compressed format (tar.gz). In total, 3 022 Landsat images were downloaded and processed. However, we only included dry season images in the analyses, as the amount of cloud cover present in the wet season for most of the selected PAs made calculating meaningful wet season trends in heterogeneity impossible.

### *Calculating heterogeneity*

Most measures of spectral variability are based on information theory, which measures the amount of disorder contained in a system. For example, the Shannon entropy index has been widely used to estimate heterogeneity across local and regional scales (e.g., Albano 2015, Stein & Krefl, 2015). However, Shannon and other similar indices (e.g., Pielou's evenness) only rely on the relative abundance of reflectance values, and therefore does not consider the numerical value of reflectance per se. This means that these indices tend to overestimate heterogeneity (Rocchini et al. 2017).

The Rao's quadratic diversity index (hereafter Rao's Q) considers the numerical values of reflectance by considering the pairwise distance between pixels and has been proposed as a more informative measure of heterogeneity (Rocchini et al. 2017). Given a certain number of reflectance values in a portion of a remotely sensed image (usually a moving window of  $n \times n$  pixels), the metric is defined as the expected difference in reflectance values between two pixels drawn randomly with replacement from the set of pixels:

$$Q = \sum d_{ij} \times p_i \times p_j$$

where  $d_{ij}$  is the spectral distance between pixel  $i$  and  $j$  and  $p_i$  is the relative proportion of pixel  $i$  (i.e., in a window of  $n \times n$  pixels  $p_i = \frac{1}{n^2}$ ). The spectral distance  $d_{ij}$  can be calculated either for a single band or in a multispectral system, thus allowing one to consider more than one band at a time.

We used the spectral Rao function (Rocchini et al. 2017) available in R (R Development Core Team, 2020) to calculate heterogeneity for each PA over a 27-year time period from 1990 – 2018. We calculated Rao's Q on multiple bands for each image using a 3 x 3 moving window, with the resulting value directly related to the variance of reflectance values within the set of pixels that made up each property. In this case, higher heterogeneity values were related to the relative distance of spectral values and to relative evenness in the distribution of such values. Rao's Q were calculated on one cloud free image of the late dry season for each year (July and August) for each PA. We then calculated summary statistics for each PA for each year using ArcGIS Pro version 2.4.2.

### *Trend Analyses*

Trends in heterogeneity (Roa's Q) from 1991 – 2018 were assessed at two scales: within and between PAs. For both scales we used modified Mann-Kendall (MK) trend tests to test whether the time series showed a monotonic (upward or downward) trend. A monotonic upward trend means that heterogeneity consistently increases through time, but the trend may or may not be linear. It is a rank-based test and can hence identify both linear and non-linear trends (Mann, 1945; Kendall, 1975; Gilbert, 1987). The standard Mann-Kendall trend test assumes independence of the observations within the time series. We hence applied modified Mann-Kendall trend tests, which adapts the calculation of the variance of the  $S$  value to make it suitable for auto-correlated datasets and increases the comparability of the trend results between samples with varying numbers of observations. The mathematical details of these modifications can be found in the literature (see Fassnacht et al. 2019).

Trends in heterogeneity for PAs Roa's Q were calculated for every pixel that made up each property for every year from 1990 – 2018. We then used focal statistics in ArcGIS Pro 2.4.2 to calculate the mean and standard deviation for each property for each year. For each of the resultant time-series we used a modified MK trend test for serially correlated data using the Hamed and Rao Variance Correction Approach (Hamed & Rao, 1998) to test whether the time series showed a monotonic trend.

Time series data is often influenced by earlier observations. When data is not random and influenced by autocorrelation, modified Mann-Kendall tests may be used for trend detection studies. Data were initially detrended and the effective sample size was calculated using the ranks of significant serial correlation coefficients, which were then used to correct the inflated (or deflated) variance of the test statistic. A detrended time series was constructed using Sen's slope and the lag-1 autocorrelation coefficient of the ranks of the data. The variance correction approach proposed by Hamed and Rao (1998) uses only significant lags of autocorrelation coefficients. To avoid the detection of false trends, we calculated the Hurst parameter to ensure that long-term persisting trends were detected instead of short-term fluctuation. A statistically significant trend was hence assumed if: 1) the trend was significant according to the Mann-Kendall trend test; 2) the Hurst-coefficient was significantly higher than 0.5, and 3) the bias corrected modified MK-trend test was significant as well.

### *Trends in heterogeneity within PAs*

A modified Mann-Kendall (MK) trend test with continuity correction for raster time-series<sup>7</sup> was then run per-pixel for each of the PAs for the Roa's Q calculated values. The purpose of the MK test was to statistically assess if there is a monotonic upward or downward trend in Roa's Q for each pixel over time. This allowed us to identify specific areas within each PA where heterogeneity increased, decreased, or remained stable. The final map product was then derived by first applying a significance-filter (considering the Hurst parameter and the p-value of the bias corrected MK test) on the Mann-Kendall- $\tau$  product available for each of the PAs. For each of these areas we then counted the number of pixels that did not change or showed either a significant decreasing or increasing monotonic trend.

## **Results**

Roa's Q values for PAs ranged from 148.33 to 449.63 (mean = 284.47; median = 270.92; SD = 62.85). The PAs with the lowest Roa's Q values were Atherstone Nature Reserve, Pongola Game Reserve, and Madikwe Game Reserve, while the highest values were recorded for Songimvelo Game Reserve, Ithala Game Reserve, and Kariega Game Reserve. There were no clear regional patterns in Roa's Q values i.e., low, or high Roa's Q values did not cluster within specific regions (Figure 3).

### *Trends in heterogeneity for PA's*

Mann-Kendall trend tests indicated that nearly two-thirds 63% (26 out of 41) of PAs showed no trend in heterogeneity over time, 32% (11 out of 41) decreased, and 7% (3 out of 41) increased. There were no significant differences in the mean Roa's Q values and properties for which heterogeneity increased, decreased, or remained stable (Kruskal-Wallis test;  $P = 0.89$ ). In other words, properties that were generally homogenous were not more likely to show decreasing trends in heterogeneity, or properties that were generally heterogeneous were not more likely to show increasing trends in heterogeneity.

However, there appeared to be regional patterns underlying trends in heterogeneity – for example, in the dry thicket biome of the Eastern Cape, heterogeneity decreased for most of the PAs included in the analyses (four out of six PAs: Addo Elephant Park, Amakhala Private Game Reserve, Kwandwe Private Game Reserve, and Shamwari Private Game Reserve), while in the Greater Kruger region none of the PAs showed a decrease in heterogeneity. Moreover, when grouped per region, PAs with low Roa's Q values were more likely to show a decreasing trend in heterogeneity – this was the case for the Eastern Cape, North-west, and KwaZulu-Natal regions.

Of the three properties that showed significant increases in heterogeneity, two were in the Greater Kruger region (Kapama and Balule Game Reserves), while one (Mabula Private Game Reserve) was located in the North-west region.

### *Trends in heterogeneity within PAs*

Changes at the pixel level within properties can be interpreted in two ways. First, we can evaluate the proportion of pixels that increased, decreased, or remained stable over time. For 36% (15 out of 42) of the PAs the majority of pixels showed a decrease in heterogeneity, while the rest (64%) increased. The PAs where most pixels decreased were again predominant in the Eastern Cape thicket region, where the majority of pixels decreased for five out of six PAs. Secondly, to guide management actions, it is important to consider the spatial arrangement of pixels within each PA. This gives an indication of the locations within each PA where changes in heterogeneity occurred. For example, pixels that showed increases in heterogeneity might be found next to a road or other disturbed areas. Conversely, pixels that showed no significant change might indicate areas not easily accessible to people or mega herbivores such as elephants, for example steep slopes. The maps included in this contribution (Supporting Information S1) gives context to increasing, decreasing, and stable pixels and must inform inferences made on the effects of these.

## Discussion

Ensuring the sustainability of PAs requires information on the effectiveness of management decisions at large spatial scales (Leverington et al. 2010; Rodrigues & Cazalis, 2020). However, few PAs have established systems to evaluate management effectiveness or to determine whether they are achieving their aims such as conserving biodiversity (Hockings et al. 2000; Parirish et al. 2003). For example, in South African state PAs the Management Effectiveness Tracking Tool (METT) is used to evaluate management effectiveness. The tool monitors if management actions take place, but do not report on the effect(s) of these i.e. the METT would check if a planned block burn took place, but does not measure the biodiversity outcomes of the block burn. Moreover, most monitoring programs are opportunistic rather than strategic, mostly because it is unclear what should be monitored, where, and why (Dale and Beyeler 2001). This is particularly important given the effect of the COVID-19 pandemic on PA funding and planning for biodiversity conservation in a post-COVID-19 economy (Sandbrook et al. 2020). Here, we propose a cost-effective and standardised way for PA managers to monitor changes in heterogeneity directly and across scales. By monitoring heterogeneity, park managers can answer logical questions concerning environmental change that could affect species diversity and ecosystem function. For example, long-term trends in heterogeneity might reveal differences among PAs that can be linked to management practices, such as the opening and closing of waterholes or changes in fire regimes. Moreover, drawing from the maps for each PA, managers may be able to identify possible “hotspots” and focus research into the empirical effects of changes in heterogeneity, for example associated changes in species diversity and potential ecosystem regime shifts. Such maps may also prove useful to detect changes in vegetation structure and composition, which could lead to an alteration in the provision of ecosystem services or indicate local extinction events.

Monitoring heterogeneity within numerous PAs may appear to be a daunting task. However, it does not involve conservation planners, expert knowledge, or the investment of additional field resources – the heterogeneity product for each PA can be regularly updated by replacing the acquisition dates in the associated R scripts and re-running the remaining code-parts (Supporting Information S2 and S3). The approach is generic and applicable to different datasets at all scales (local, regional, national) and at different resolutions. This framework now exists for the 41 areas included in this analyses but can be extended to include every PA nationally, or even globally, and the data product fully automated. For this study, we used the Mann-Kendall test to determine significant trends in heterogeneity, however other models can also be fitted to the time series. For example, piece-wise regression can be used to detect breakpoints in the time series, which could signify the impact of management interventions. Importantly, we do not advocate that this monitoring approach replace current monitoring programs – rather that it can add value and further support the monitoring of PA effectiveness in achieving desirable conservation outcomes.

Are PAs in South Africa successful in maintaining heterogeneity? Generally, yes. For the majority (63%) of PAs included in this analysis, heterogeneity did not change significantly during the last 28 years. This does not mean that heterogeneity remained unchanged across the entire PA, but rather that the mean

heterogeneity for these PAs remained unchanged (within each PA there were areas where heterogeneity increased, decreased or remained stable). PAs where heterogeneity remained stable were found across the country, but noticeably, almost all of the PAs in the subtropical low veld Kruger region were stable. Many of these PAs are part of an open system with the Kruger National Park, South Africa's largest conservation area. Here fences were removed in the early 1990's and since then the area has functioned as a relatively open system, although management practices do differ among the different entities. The management philosophy of South African National Parks (SANParks) is centred on maintaining heterogeneity, where the restoration of ecological processes should result in the formation of more heterogeneous landscapes. Our results suggest that in the KNP, trends in heterogeneity since 1990 were stable across the three different regions of the park: north, central, and south, which indicate that management actions are having the desired effect of maintaining heterogeneity. Moreover, in the south and central regions, heterogeneity increased for the majority of pixels, which is a further positive development from a management perspective. However, in the north, the majority of pixels decreased, although the general trend was stable. This may indicate a possible shift towards a more homogenous landscape, possibly in response to changes in elephant space use (MacFadyen et al. 2019), rainfall (Smit et al. 2013), or frequent fires (Ribeiro et al. 2019). The maps presented here could aid managers in identifying where these vulnerable areas are, as well as determine and mitigate the potential drivers of decreasing heterogeneity.

There was pronounced spatial variation in heterogeneity within PAs. Specifically, the proportion of pixels that increased, decreased, or remained stable were never more than half of the total number of pixels. This suggests that the overall landscape complexity associated with PAs, where underlying physical landscape templates (e.g., topography, soils, watershed areas) interact with dynamic landscape processes and stochastic disturbance events generate a 'heterogeneity mosaic', irrespective of management actions or regional factors (e.g. rainfall) (see MacFadyen et al. 2016). This can be exploited by managers by stratifying PA monitoring and research planning using these maps as blueprints. For example, it might be easier and more cost effective to maintain heterogeneity in more complex landscapes than artificially increasing heterogeneity in more simple areas. This is important, particularly given that heterogeneity is noticeably higher along roads, fences, infrastructure, and waterholes, and shows that a significant increase in heterogeneity over time is not always caused by natural phenomena. Local factors (e.g., roads, waterholes, or herbivory) can therefore be manipulated to some extent to alter heterogeneity at fine scales. However, deciding where to do this is crucial for PA management as such an increase in heterogeneity might have the opposite effect of boosting ecological integrity by increasing edge effects, eliminating the seasonal ranges of animals, and destroying habitats.

Although heterogeneity remained stable for most of the PAs considered in our analysis, there were also 11 (32%) PAs where heterogeneity decreased significantly during the last three decades. Closer inspection revealed that heterogeneity also decreased for the majority of pixels in 10 of these 11 PAs. These trends are worrying as a decrease in heterogeneity may indicate a decrease in species richness and the viability of animal populations that occur here (e.g., McCleery et al. 2018). Unravelling the drivers of changes in heterogeneity are beyond the scope of this contribution, yet we know that in African savannahs fire,

rainfall, and herbivores play key roles in shaping vegetation communities (Sinclair & Walker 2003). To maintain heterogeneity, animals must utilise distinct wet and dry season ranges, fires should occur sporadically and unpredictably, and woody encroachment must be inhibited by local variations in rainfall, soil type, grazing pressure, and even the impact of people (Wang et al. 2013; Smit et al. 2013; Van Langevelde et al. 2017). However, in fenced reserves with ecologically arbitrary boundaries and set management regimes these processes may be fundamentally altered, which could reduce heterogeneity. For example, in some PAs, the widespread provision of artificial waterholes may degrade functional wet and dry season resources by homogenising animal distribution patterns. Moreover, uniform fire regimes can result in more homogenous vegetation structures where small trees and shrubs expand at the expense of taller savannah woodlands (van Wilgen et al. 2003), while CO<sub>2</sub> levels may be driving woody encroachment (Stevens et al. 2016). We may therefore be recording a type of 'park effect' where herbivory, fire, and a combination of rainfall and increasing CO<sub>2</sub> levels may be contributing to the homogenization of these PAs (see also Guldemon & van Aarde, 2010). This should be of particular concern to PA management. The approach presented here can be used as an early warning system to identify PAs where homogenization is occurring and alter management actions to halt this.

We must, however, also consider possible caveats associated with our approach. First, the Mann-Kendall-trend test must be interpreted as a measure of consistency of the trend and not the intensity of the trend. A maximum Mann-Kendall value can be reached with a small difference in absolute values (e.g., heterogeneity), if the change was constant over time. If the focus is on measuring the intensity of the trend, other analyses such as Structural Equation Models (SEMs) may be more informative. Secondly, ecological components and processes have an underlying spatial structure that is locally heterogeneous, for example topography, soil type, and watershed areas contribute to the overall complexity of the landscape (MacFadyen et al. 2016). For example, the two PAs with the highest mean Roa Q values were Songimvelo and Itala Game Reserve, which have high levels of topographical variability. Interpretations of heterogeneity should be cognisant of this – however, because we were interested in changes in heterogeneity over time, we assumed that these stable physical elements did not change over a 28-year period, and that the changes that were detected were linked to changes in vegetation as reflected by the spectral variation in the remote sensing product. Third, we did not include heterogeneity values for the years 2008 – 2012, because of the scan line correction error of Landsat 7. Although these regularities are subtle, they are still visible in the product and likely would have affected our calculations of heterogeneity. Nonetheless, we are confident that leaving out these values would not affect the overall trends reported here, given the length of the time series and the application of the Mann-Kendall-trend tests.

## Conclusion

Environmental heterogeneity is a well-known determinant of biodiversity for a variety of attributes and taxa and, as we show here, could effectively be used to evaluate temporal and spatial changes across landscapes. This approach presents an opportunity for conservation management to incorporate this

important biodiversity indicator into PA monitoring to evaluate PA effectiveness as well as inform local, regional, and even national ecological monitoring initiatives.

## Declarations

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### AUTHORS CONTRIBUTIONS

AP, MM, JS, JK, HM, and PO conceived the ideas and designed the methodology, AP and MM collected the data, AP analysed the data, PO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## References

1. Albano, C. M. (2015). Identification of geophysically diverse locations that may facilitate species' persistence and adaptation to climate change in the southwestern United States. *Landscape Ecology*, 30(6), 1023-1037.
2. Asner, G. P., & Levick, S. R. (2012). Landscape-scale effects of herbivores on treefall in African savannas. *Ecology letters*, 15(11), 1211-1217.
3. Bar-Massada, A., & Wood, E. M. (2014). The richness–heterogeneity relationship differs between heterogeneity measures within and among habitats. *Ecography*, 37(6), 528-535.
4. Barnes, M. D., Glew, L., Wyborn, C., & Craigie, I. D. (2018). Prevent perverse outcomes from global protected area policy. *Nature Ecology & Evolution*, 2(5), 759-762.
5. Beier, P., & de Albuquerque, F. S. (2015). Environmental diversity as a surrogate for species representation. *Conservation Biology*, 29(5), 1401-1410.
6. Cook, R. M., & Henley, M. D. (2019). The management dilemma: Removing elephants to save large trees. *Koedoe: African Protected Area Conservation and Science*, 61(1), 1-12.
7. Costanza, R., Kubiszewski, I., Ervin, D., Bluffstone, R., Boyd, J., Brown, D., ... & Yeakley, A. (2011). Valuing ecological systems and services. *F1000 biology reports*, 3.
8. Cramer, M. D., & Verboom, G. A. (2017). Measures of biologically relevant environmental heterogeneity improve prediction of regional plant species richness. *Journal of Biogeography*, 44(3), 579-591.
9. Dale, V. H., & Beyeler, S. C. (2001). Challenges in the development and use of ecological indicators. *Ecological indicators*, 1(1), 3-10.
10. Davies, A. B., Gaylard, A., & Asner, G. P. (2018). Megafaunal effects on vegetation structure throughout a densely wooded African landscape. *Ecological Applications*, 28(2), 398-408.

11. Dos Santos Ribas, L. G., Pressey, R. L., Loyola, R., & Bini, L. M. (2020). A global comparative analysis of impact evaluation methods in estimating the effectiveness of protected areas. *Biological Conservation*, 246, 108595.
12. Doxa, A., & Prastacos, P. (2020). Using Rao's quadratic entropy to define environmental heterogeneity priority areas in the European Mediterranean biome. *Biological Conservation*, 241, 108366. doi:<https://doi.org/10.1016/j.biocon.2019.108366>
13. Doxa, A., & Prastacos, P. (2020). Using Rao's quadratic entropy to define environmental heterogeneity priority areas in the European Mediterranean biome. *Biological Conservation*, 241, 108366.
14. Fassnacht, F. E., Schiller, C., Kattenborn, T., Zhao, X., & Qu, J. (2019). A Landsat-based vegetation trend product of the Tibetan Plateau for the time-period 1990–2018. *Scientific data*, 6(1), 1-11.
15. Ferreira, S. M., Greaver, C., Knight, G. A., Knight, M. H., Smit, I. P., & Pienaar, D. (2015). Disruption of rhino demography by poachers may lead to population declines in Kruger National Park, South Africa. *PLoS One*, 10(6), e0127783.
16. Gilbert, R. O. (1987). *Statistical methods for environmental pollution monitoring*. John Wiley & Sons.
17. Guisan A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993-1009.
18. Guldemond, R.A.R & van Aarde, R.J. (2010) The influence of tree canopies and elephants on sub-canopy vegetation in savannah. *African Journal of Ecology*, 48, 180-189.
19. Hamed, K. H., & Rao, A. R. (1998). A modified Mann-Kendall trend test for autocorrelated data. *Journal of hydrology*, 204(1-4), 182-196.
20. Hockings, M., Stolton, S. & Dudley, N. (2000) *Evaluating effectiveness: a framework for assessing the management of protected areas* (No. 6). IUCN.
21. Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.
22. Jetz, W., & Rahbek, C. (2002). Geographic range size and determinants of avian species richness. *Science*, 297(5586), 1548-1551.
23. Kendall, M. G., *Rank Correlation Methods*, Charles Griffin, London, 1975.
24. Kerr, J. T., & Packer, L. (1997). Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 385(6613), 252-254.
25. Kerr, J. T., Southwood, T. R. E., & Cihlar, J. (2001). Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences*, 98(20), 11365-11370.
26. Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T. M. & Rodrigues, A. S. (2013). Protected areas and effective biodiversity conservation. *Science*, 342(6160), 803-805.
27. Leverington, F., Costa, K. L., Pavese, H., Lisle, A., & Hockings, M. (2010). A global analysis of protected area management effectiveness. *Environmental management*, 46(5), 685-698.
28. MacArthur, R.H. & MacArthur, J.W. (1961) On bird species diversity. *Ecology*, **42**, 594–598.

29. MacFadyen, S., Hui, C., Verburg, P. H., & Van Teeffelen, A. J. (2019). Spatiotemporal distribution dynamics of elephants in response to density, rainfall, rivers and fire in Kruger National Park, South Africa. *Diversity and Distributions*, 25(6), 880-894.
30. MacFadyen, S., Hui, C., Verburg, P. H., & Van Teeffelen, A. J. (2016). Quantifying spatiotemporal drivers of environmental heterogeneity in Kruger National Park, South Africa. *Landscape Ecology*, 31(9), 2013-2029.
31. MacFadyen, S., Hui, C., Verburg, P.H. & Van Teeffelen, A.J.A. (2016) Quantifying spatiotemporal drivers of environmental heterogeneity in Kruger National Park, South Africa. *Landscape Ecology*, 31, 2013-2029.
32. Mann, H. B. (1945). Nonparametric tests against trend. *Econometrica: Journal of the econometric society*, 245-259.
33. McCleery, R., Monadjem, A., Baiser, B., Fletcher Jr, R., Vickers, K., & Kruger, L. (2018). Animal diversity declines with broad-scale homogenization of canopy cover in African savannas. *Biological Conservation*, 226, 54-62.
34. Naughton-Treves, L., Holland, M. B., & Brandon, K. (2005). The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annu. Rev. Environ. Resour.*, 30, 219-252.
35. Palmer, M. W., Earls, P. G., Hoagland, B. W., White, P. S., & Wohlgemuth, T. (2002). Quantitative tools for perfecting species lists. *Environmetrics: The official journal of the International Environmetrics Society*, 13(2), 121-137.
36. Palmer, M.W., Earls, P., Hoagland, B.W., White, P.S. & Wohlgemuth, T. (2002) Quantitative tools for predicting species lists. *Environmetrics* 13, 121-137.
37. Parrish, J. D., Braun, D. P., & Unnasch, R. S. (2003). Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioScience*, 53(9), 851-860.
38. Pickett, S. T., Shachak, M., Ostfeld, R. S., & Likens, G. E. (1997). Toward a comprehensive conservation theory. In *The Ecological Basis of Conservation* (pp. 384-399). Springer, Boston, MA.
39. Pielou, E. C. (1977). *Mathematical ecology* (No. 574.50151 P613 1977). Wiley.
40. R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
41. Ribeiro, N., Ruecker, G., Govender, N., Macandza, V., Pais, A., Machava, D., & Bandeira, R. (2019). The influence of fire frequency on the structure and botanical composition of savanna ecosystems. *Ecology and evolution*, 9(14), 8253-8264.
42. Rocchini D, Bacaro, G., Chirici, G. et al. (2018) Remotely sensed spatial heterogeneity as an exploratory tool for taxonomic and functional diversity study. *Ecological Indicators*, 85, 983-990.
43. Rocchini, D., Bacaro, G., Chirici, G., Da Re, D., Feilhauer, H., Foody, G. M., & Rugani, B. (2018). Remotely sensed spatial heterogeneity as an exploratory tool for taxonomic and functional diversity study. *Ecological indicators*, 85, 983-990.

44. Rocchini, D., Balkenhol, N., Carter, G. A., Foody, G. M., Gillespie, T. W., He, K. S., ... & Neteler, M. (2010). Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. *Ecological Informatics*, 5(5), 318-329.
45. Rocchini, D., Balkenhol, N., Carter, G.A. et al. (2010) Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. *Ecology Information*, 5, 318-329.
46. Rocchini, D., Chiarucci, A., & Loiselle, S. A. (2004). Testing the spectral variation hypothesis by using satellite multispectral images. *Acta Oecologica*, 26(2), 117-120.
47. Rocchini, D., Marcantonio, M., & Ricotta, C. (2017). Measuring Rao's Q diversity index from remote sensing: An open source solution. *Ecological indicators*, 72, 234-238.
48. Rodrigues, A. S., & Cazalis, V. (2020). The multifaceted challenge of evaluating protected area effectiveness. *Nature Communications*, 11(1), 1-4.
49. Sandbrook, C., Gómez-Baggethun, E. & Adams, W.M. (2020) Biodiversity conservation in a post-COVID-19 economy. *Oryx*, <https://doi.org/10.1017/S0030605320001039>
50. Shannon C. (1948) A mathematical theory of communication. *Bell System Technical Journal*, 27, 379-423.
51. Sianga, Keoikantse, van Telgen, Mario, Vrooman, Jip, Fynn, Richard W.S., & van Langevelde, Frank. (2017). Spatial refuges buffer landscapes against homogenisation and degradation by large herbivore populations and facilitate vegetation heterogeneity. *Koedoe*, 59(2), 1-13.
52. Sinclair, A. R., & Walker, B. (2003). *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press.
53. Smit, I. P., Smit, C. F., Govender, N., Linde, M. V. D., & MacFadyen, S. (2013). Rainfall, geology and landscape position generate large-scale spatiotemporal fire pattern heterogeneity in an African savanna. *Ecography*, 36(4), 447-459.
54. Stein, A., & Kreft, H. (2015). Terminology and quantification of environmental heterogeneity in species-richness research. *Biological Reviews*, 90(3), 815-836.
55. Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology letters*, 17(7), 866-880.
56. Stevens, N., Erasmus, B. F. N., Archibald, S., & Bond, W. J. (2016). Woody encroachment over 70 years in South African savannahs: overgrazing, global change or extinction aftershock? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1703), 20150437.
57. Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R., & Pärtel, M. (2010). Environmental heterogeneity, species diversity and co-existence at different spatial scales. *Journal of Vegetation Science*, 21(4), 796-801.
58. Torresani, M., Rocchini, D., Sonnenschein, R., Zebisch, M., Marcantonio, M., Ricotta, C., & Tonon, G. (2019). Estimating tree species diversity from space in an alpine conifer forest: The Rao's Q diversity index meets the spectral variation hypothesis. *Ecological Informatics*, 52, 26-34.

59. Udy, K., Fritsch, M., Meyer, K. M., Grass, I., Hanß, S., Hartig, F., ... & Wiegand, K. (2021). Environmental heterogeneity predicts global species richness patterns better than area. *Global Ecology and Biogeography*, 30(4), 842-851.
60. UNEP-WCMC, IUCN and NGS (2018). Protected Planet Report 2018. UNEP-WCMC, IUCN and NGS: Cambridge UK; Gland, Switzerland; and Washington, D.C., USA.
61. Van Wilgen, B. W., Govender, N., Biggs, H. C., Ntsala, D., & Funda, X. N. (2004). Response of savanna fire regimes to changing fire-management policies in a large African national park. *Conservation Biology*, 18(6), 1533-1540.

## Tables

**Table 1.** The South African PAs included in the analysis.

	Protected Area	Region	Area (km <sup>2</sup> )	State/Private
1	Addo Elephant Park (Main Camp)	Eastern Cape	230	State
2	Amakhala Private Game Reserve	Eastern Cape	60	Private
3	Amakhosi Safari Lodge	KwaZulu	45	Private
4	Atherstone Nature Reserve	North-west	227	State
5	Balule Game Reserve	Greater Kruger	416	Private
6	Bonamanzi Game Reserve	KwaZulu	40	Private
7	Central KNP	Greater Kruger	-	State
8	Greater KuduLand Safaris	Greater Kruger	160	Private
9	Greater Makalali Private Game Reserve	Greater Kruger	340	Private
10	Hluhluwe-Imfolozi Park	KwaZulu	960	State
11	Itala Nature Reserve	KwaZulu	300	State
12	Kapama Game Reserve	Greater Kruger	130	Private
13	Kariega Game Reserve	Eastern Cape	75	Private
14	Klaserie Private Nature Reserve	Greater Kruger	590	Private
15	Kwandwe Private Game Reserve	Eastern Cape	190	Private
16	KwaZulu Private Game Reserve	KwaZulu	45	Private
17	Mabalingwe Nature Reserve	North-west	89	Private
18	Mabula Game Reserve	North-west	85	Private
19	Madikwe Game Reserve	North-west	660	Private
20	Manyeleti Game Reserve	Greater Kruger	173	Private
21	Manyoni Private Game Reserve	KwaZulu	225	Private
22	Mapungubwe National Park	North-west	360	State
23	Marakele National Park	North-west	640	State
24	Mthethomusha Nature Reserve	Greater Kruger	75	Private
25	Munyawana Game Reserve	KwaZulu	230	Private
26	Nambiti Private Game Reserve	KwaZulu	98	Private
27	Northern KNP	Greater Kruger	-	State

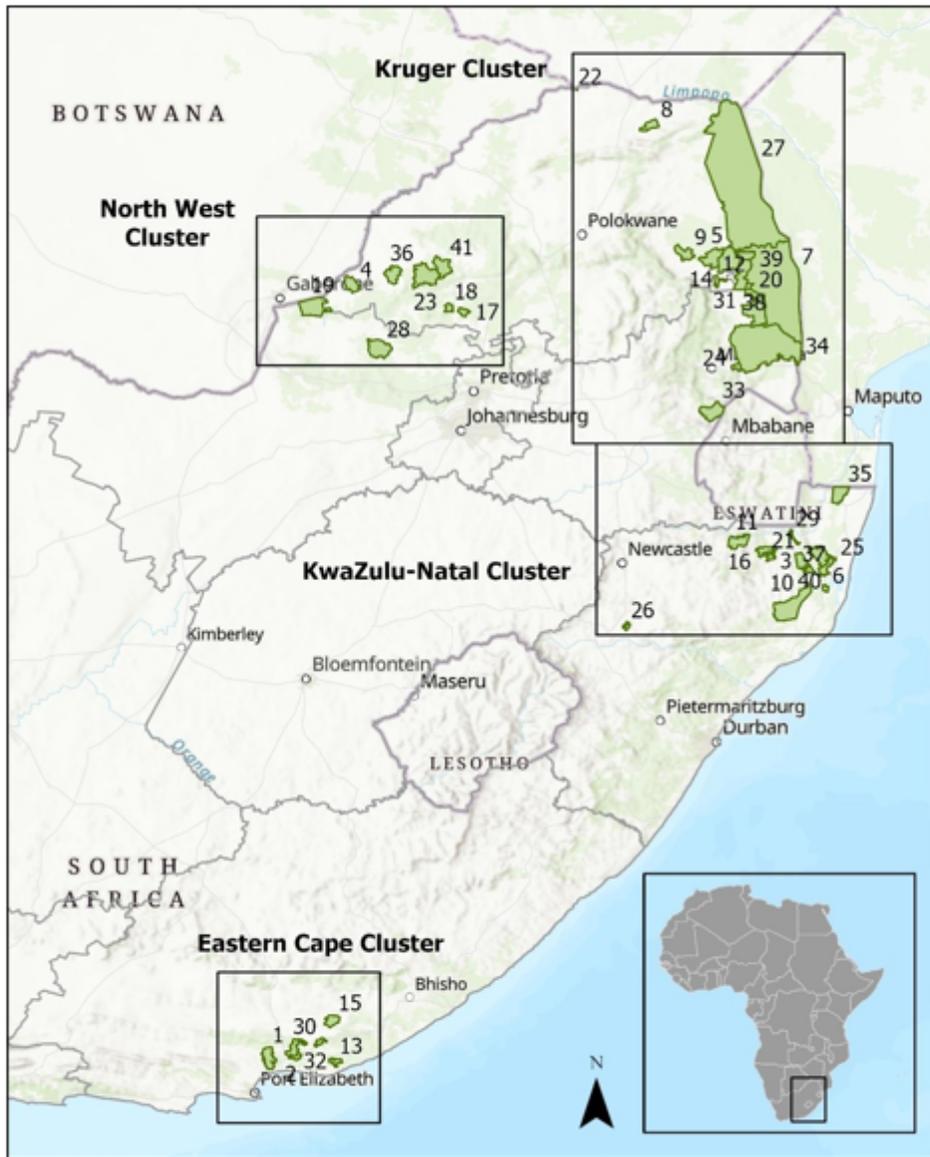
28	Pilanesberg Game Reserve	North-west	490	State
29	Pongola Game Reserve	KwaZulu	50	Private
30	Pumba Private Game Reserve	Eastern Cape	65	Private
31	Sabie Sands Private Nature Reserve	Greater Kruger	596	Private
32	Shamwari Private Game Reserve	Eastern Cape	187	Private
33	Songimvelo Game Reserve	Greater Kruger	232	State
34	Southern KNP	Greater Kruger	-	State
35	Tembe Elephant Park	KwaZulu	300	Private
36	Thaba Tholo Game Farm	North-west	300	Private
37	Thanda Private Game Reserve	KwaZulu	140	Private
38	Timbavati Game Reserve	Greater Kruger	502	Private
39	Umbabat Game Reserve	Greater Kruger	185	Private
40	uMkuzi Game Reserve	KwaZulu	400	State
41	Welgevonden Game Reserve	North-west	340	Private

**Table 2.** Results from the MK Tau analysis to test for significant trends in Rao's Q values for the 41 PA's included in the analysis. N indicates the length of the time series i.e. the number of years (and satellite images) analysed for each PA. \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001.

Property	N	Property-scale		Pixel-scale (%)		
		P-value	MK Tau	Stable	Increase	Decrease
Addo Elephant Park (Main Camp)	24	0.000*	-0.370	35.88	24.90	39.22
Amakhala Private Game Reserve	20	0.000*	-0.326	28.60	33.69	37.71
Amakhosi Safari Lodge	20	0.206	-0.211	29.48	35.54	34.98
Atherstone Nature Reserve	23	0.003*	-0.447	38.45	24.02	37.53
Balule Game Reserve	20	0.048*	0.326	14.87	58.74	26.40
Bonamanzi Game Reserve	22	0.284	-0.169	24.40	41.61	34.00
Central KNP	23	0.233	-0.123	18.25	43.74	38.01
Greater KuduLand Safaris	25	0.154	-0.207	22.15	40.36	37.49
Greater Makalali Private Game Reserve	21	0.325	0.105	16.86	46.02	37.12
Hluhluwe-Imfolozi Park	22	0.159	-0.221	20.18	45.33	34.49
Itala Nature Reserve	20	0.018*	-0.389	27.42	40.53	32.05
Kapama Game Reserve	22	0.000*	0.550	31.97	49.20	18.83
Kariega Game Reserve	20	0.707	0.032	33.10	43.50	23.40
Klaserie Private Nature Reserve	24	0.123	0.319	17.51	58.45	24.04
Kwandwe Private Game Reserve	20	0.006*	-0.453	32.96	26.02	41.02
KwaZulu Private Game Reserve	20	0.025*	-0.368	28.28	35.35	36.37
Mabalingwe Nature Reserve	25	0.870	-0.027	23.18	43.43	33.38
Mabula Game Reserve	23	0.045*	0.304	30.54	45.00	24.46
Madikwe Game Reserve	22	0.018*	-0.221	27.09	32.09	40.82
Manyeleti Game Reserve	23	0.882	-0.020	17.51	44.71	37.78
Manyoni Private Game Reserve	21	0.017*	-0.381	27.28	25.26	47.46
Mapungubwe National Park	23	0.008*	-0.399	25.29	30.24	44.47
Marakele National Park	23	0.679	-0.091	17.73	51.92	30.34
Mthethomusha Nature Reserve	23	0.113	-0.241	16.72	53.78	29.50
Munyawana Game Reserve	21	0.928	0.019	20.16	48.28	31.56
Nambiti Private Game Reserve	21	0.566	-0.095	24.19	35.82	39.99

Northern KNP	21	0.349	-0.152	22.16	35.12	42.72
Pilanesberg Game Reserve	23	0.267	-0.170	16.40	41.76	41.84
Pongola Game Reserve	22	0.002*	-0.481	34.28	18.25	47.47
Pumba Private Game Reserve	20	0.056	-0.316	31.47	31.71	36.81
Sabie Sands Private Nature Reserve	23	0.792	-0.043	18.83	45.21	35.96
Shamwari Private Game Reserve	20	0.018*	-0.389	32.64	27.88	39.48
Songimvelo Game Reserve	22	0.159	-0.221	17.98	46.07	35.94
Southern KNP	22	0.866	-0.030	15.14	53.39	31.48
Tembe Elephant Park	20	0.381	0.147	30.94	47.08	21.97
Thaba Tholo Game Farm	23	0.673	-0.067	25.16	37.02	37.82
Thanda Private Game Reserve	22	0.009*	-0.403	29.25	31.17	39.58
Timbavati Game Reserve	23	0.335	0.162	15.14	49.98	34.89
Umbabat Game Reserve	23	0.751	-0.051	20.24	47.63	32.14
uMkuzi Game Reserve	20	0.417	-0.137	25.72	41.85	32.43
Welgevonden Game Reserve	23	0.187	-0.202	17.85	52.84	29.31

## Figures



### Protected Areas included in the analysis

1. Addo Elephant Park (Main Camp)
2. Amakhala Private Game Reserve
3. Amakhosi Safari Lodge
4. Atherstone Nature Reserve
5. Balule Game Reserve
6. Bonamanzi Game Reserve
7. Central Kruger National Park
8. Greater KuduLand Safari
9. Greater Makalali Private Game Reserve
10. Hluhluwe-Imfolozi Park
11. Itala Nature Reserve
12. Kapama Game Reserve
13. Kariega Game Reserve
14. Klaserie Private Nature Reserve
15. Kwandwe Private Game Reserve
16. KwaZulu Private Game Reserve
17. Mabalingwe Nature Reserve
18. Mabula Game Reserve
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36. Thaba Tholo Game Farm
37. Thanda Private Game Reserve
38. Timbavati Game Reserve
39. Umbabat Game Reserve
40. uMkuzi Game Reserve
41. Welgevonden Game Reserve

Esri, HERE, Garmin, FAO, NOAA, USGS, Esri, USGS

Figure 1

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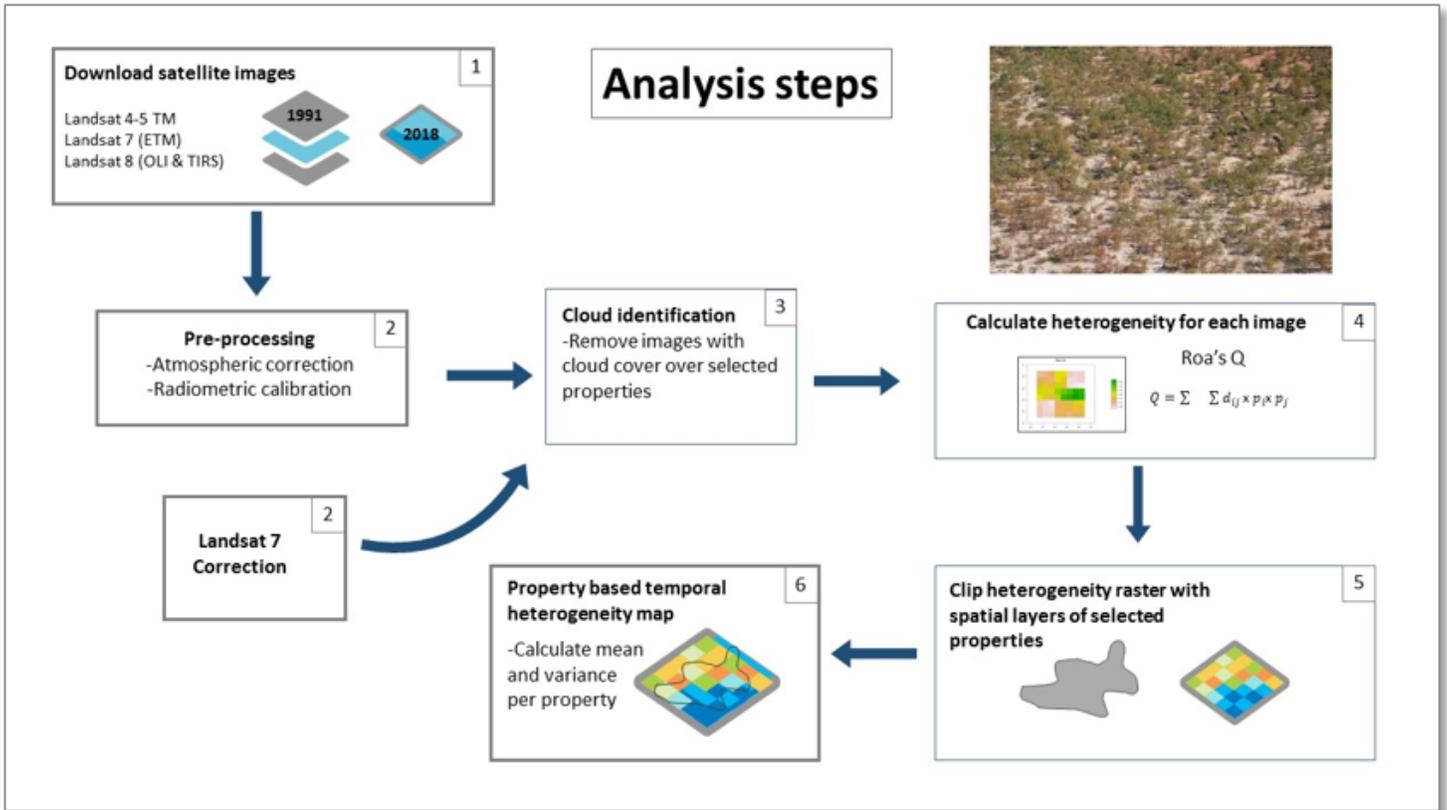


Figure 2

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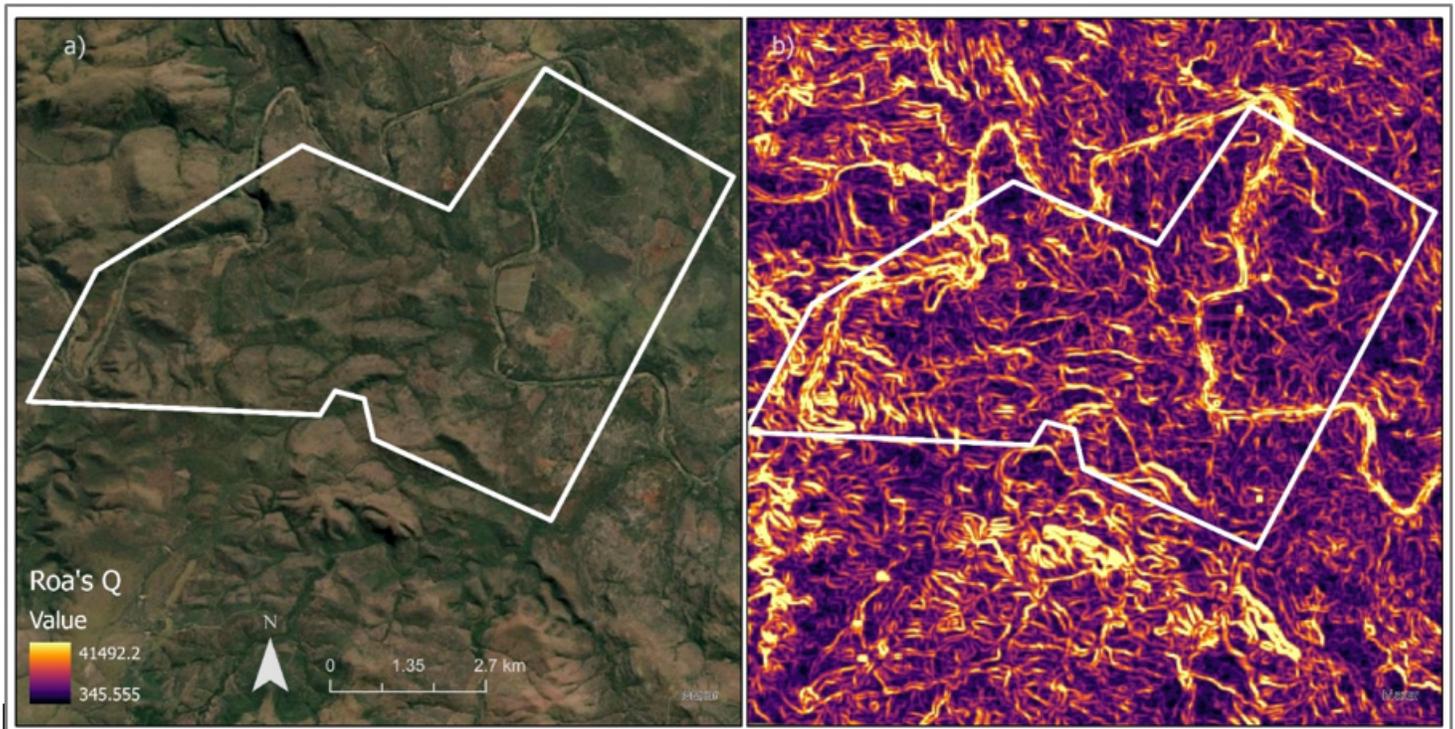


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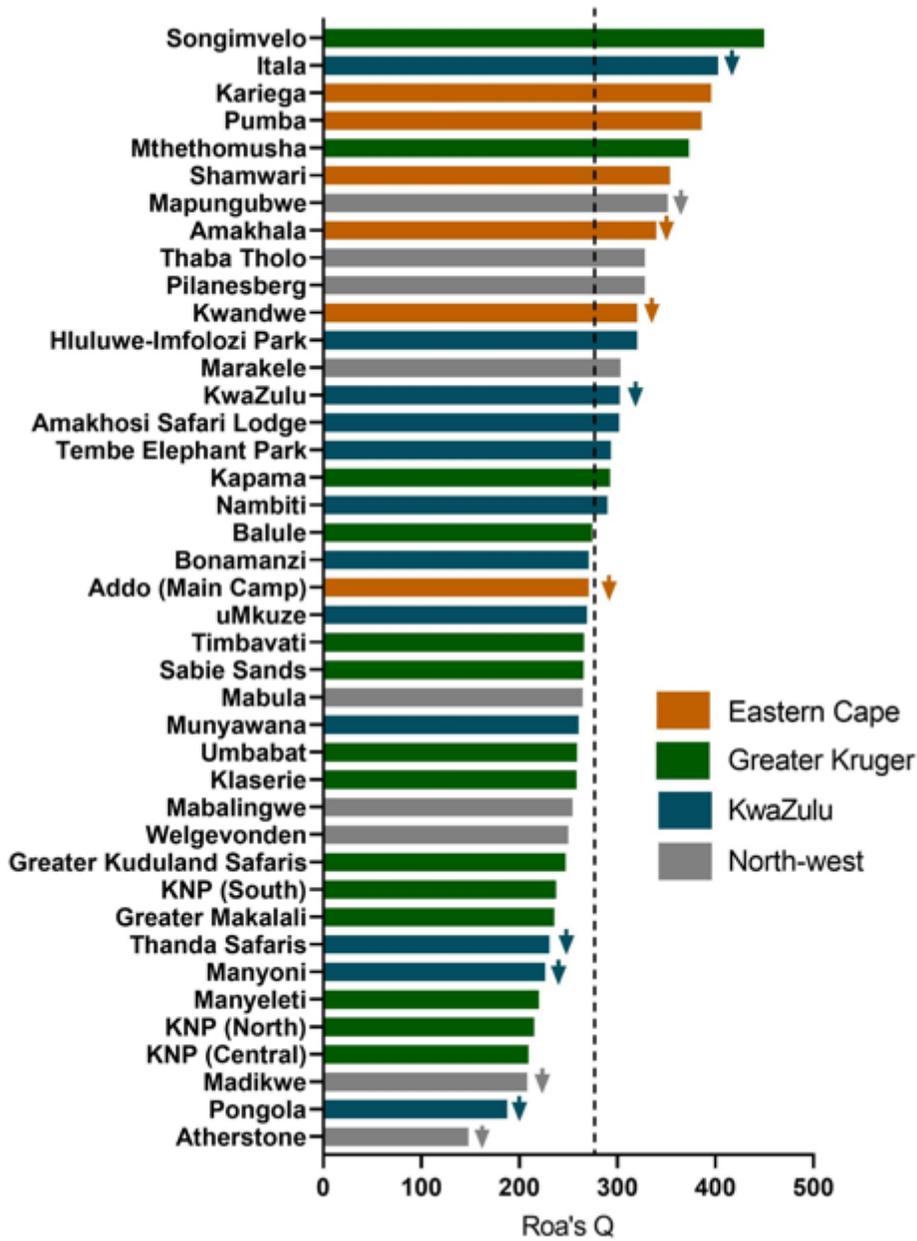


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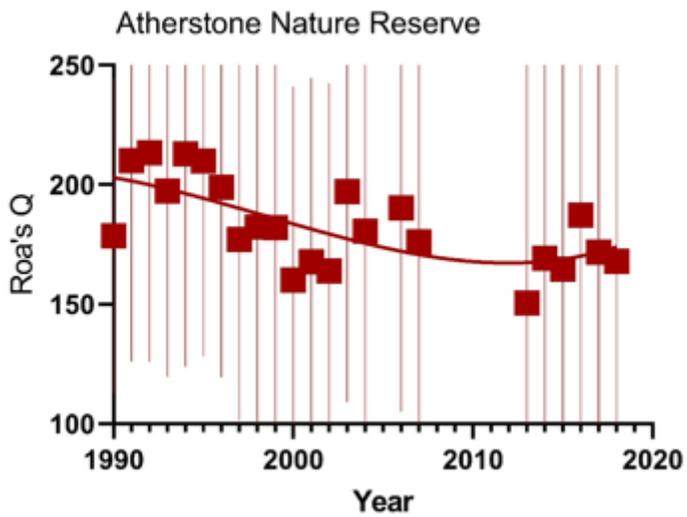
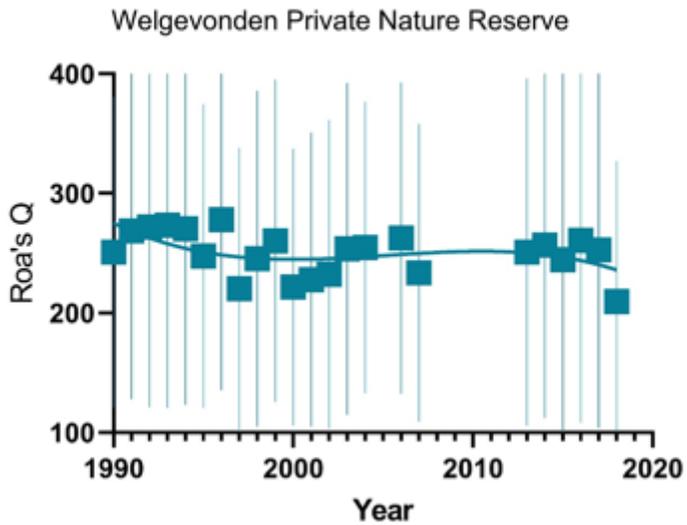


Figure 5

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## Supplementary Files

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- [S2CalculatingRoa'sQ.docx](#)
- [S3RscriptMannKendallTrendtests.docx](#)