



Spatio-temporal variation of vegetation heterogeneity in groundwater dependent ecosystems within arid environments

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ABSTRACT

Climate change, land cover change and the over-abstraction of groundwater threaten the existence of Groundwater-Dependent Ecosystems (GDE), despite these environments being regarded as biodiversity hotspots. The vegetation heterogeneity in GDEs requires routine monitoring in order to conserve and preserve the ecosystem services in these environments. However, in-situ monitoring of vegetation heterogeneity in extensive, or transboundary, groundwater resources remain a challenge. Inherently, the Spectral Variation Hypothesis (SVH) and remotely-sensed data provide a unique way to monitor the response of GDEs to seasonal or intra-annual environmental stressors, which is the key for achieving the national and regional biodiversity targets. This study presents the first attempt at monitoring the intra-annual, spatio-temporal variations in vegetation heterogeneity in the Khakea-Bray Transboundary Aquifer, which is located between Botswana and South Africa, by using the coefficient of variation derived from the Landsat 8 OLI Operational Land Imager (OLI). The coefficient of variation was used to measure spectral heterogeneity, which is a function of environmental heterogeneity. Heterogeneous environments are more diverse, compared to homogeneous environments, and the vegetation heterogeneity can be inferred from the heterogeneity of a landscape. The coefficient of variation was used to calculate the α - and β measures of vegetation heterogeneity (the Shannon-Weiner Index and the Rao's Q, respectively), whilst the monotonic trends in the spatio-temporal variation (January-December) of vegetation heterogeneity were derived by using the Mann-Kendall non-parametric test. Lastly, to explain the spatio-temporal variations of vegetation heterogeneity, a set of environmental variables were used, along with a machine-learning algorithm (random forest). The vegetation heterogeneity was observed to be relatively high during the wet season and low during the dry season, and these changes were mainly driven by landcover- and climate-related variables. More specifically, significant changes in vegetation heterogeneity were observed around natural water pans, along roads and rivers, as well as in cropping areas. Furthermore, these changes were better predicted by the Rao's Q (MAE = 5.81, RMSE = 6.63 and %RMSE = 42.41), than by the Shannon-Weiner Index (MAE = 30.37, RMSE = 33.25 and %RMSE = 63.94). These observations on the drivers and changes in vegetation heterogeneity provide new insights into the possible effects of future landcover changes and climate variability on GDEs. This information is imperative, considering that these environments are biodiversity hotspots that are capable of supporting many livelihoods. More importantly, this work provides a spatially explicit framework on how GDEs can be monitored to achieve Sustainable Development Goal (SDG) Number 15.

1. Introduction

In response to the stimuli caused by various biotic and abiotic factors, vegetation heterogeneity is constantly changing (Collins et al.,

2010; Miranda et al., 2009; Xia et al., 2010; Yan et al., 2015). Understanding some of the drivers of vegetation heterogeneity is imperative for the conservation of ecologically sensitive environments (e.g. Groundwater-Dependent Ecosystems (GDEs)) (Kløve et al., 2011; Kløve

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et al., 2014; Van Engelenburg et al., 2018). Ideally, stable GDEs are expected to be more diverse, compared to degraded GDEs. In the context of vegetation heterogeneity, stable GDEs are characterised by several ecological niches that allow the existence of various species (Barbosa et al., 2001; Fisher et al., 2012). This can be observed in arid environments where areas with a high-water table (e.g., a spring or groundwater seepage) are more ecologically diverse as compared to areas with a low-water table (Mpakairi et al., 2022). Landscape degradation affects the species pool and might affect vegetation communities, even after the restoration of the environment (i.e. the species pool hypothesis) (Eriksson, 1993; Lepš, 2001). The species pool hypothesis stipulates that environmental factors (e.g., climate and soil) drive the species pool in most landscapes and degraded landscapes have a lower species pool (Eriksson, 1993). Consequently, changes in the vegetation heterogeneity within GDEs are driven by various threats. For example, in sub-Saharan Africa, these changes are predominantly driven by groundwater over-abstraction, land-use conversion, climate change and climate variability (Chiloane et al., 2021; Kløve et al., 2014; Orellana et al., 2012). Furthermore, the vegetation heterogeneity in GDEs is also threatened by invasive species (Chiloane et al., 2021) and groundwater pollution (Rohde et al., 2017). To better conserve the biodiversity in GDEs, the spatio-temporal changes in vegetation heterogeneity need to be understood, since vegetation communities respond to environmental threats differently and at different temporal scales. These threats, along with inadequate policies and legislative frameworks, might drive the endemic species within GDEs to extinction (Kløve et al., 2011; Kløve et al., 2014; Kreamer et al., 2014). Therefore, it is important to understand the spatio-temporal variations of vegetation heterogeneity, as well as the drivers of change, in order to inform policy and management programs.

Climate is an important factor that explains the local (i.e. plot-level) and regional (i.e. longitudinal variations) changes in vegetation heterogeneity (Collins et al., 2010; Yan et al., 2015). For example, water availability drives ~40% of the biological processes in most vegetated communities in semi-arid and arid environments (Martiny et al., 2005). Henceforth, increased water availability has the potential to influence the vegetation heterogeneity of GDEs within these environments (Dalu and Wasserman, 2022). However, during the dry season, competitive exclusion might lower the vegetation heterogeneity in GDEs, which favors Groundwater-Dependent Vegetation (GDV) more than non-GDV (Dwire and Mellmann-Brown, 2017). These changes in vegetation heterogeneity may be intense in GDEs without foundational species that are capable of redistributing groundwater to the shallow parts of the soil profile (e.g. the Shepherd's tree *Boscia albitrunca*) (Eamus and Freund, 2006; Humphreys, 2006). The existence of these foundational species makes up most of the GDE biodiversity hotspots, since they facilitate the faunal endemism of regionally-restricted species (Bird et al., 2019; Dalu and Wasserman, 2022). However, when coupled with landcover changes, the biodiversity hotspots in GDEs are susceptible to landscape degradation (e.g. the degraded GDE clusters in California, USA and Central Asia) (Alaibakhsh et al., 2017; Pengra et al., 2007).

Apart from climate, land cover changes also drive the vegetation heterogeneity in most ecosystems, including GDEs (Boulangeat et al., 2014). Urbanization and the need for agricultural land are the predominant drivers of land conversion (Seto et al., 2011; Von Lampe et al., 2014). Like climate, the effects of land cover change on vegetation heterogeneity are varied and depend on the type of land use. For example, land conversion to agriculture has been observed to decrease the vegetation heterogeneity in tropical areas (Newbold et al., 2014), yet the same conversion in arid areas increases the vegetation heterogeneity (Norfolk et al., 2015). The increase in vegetation heterogeneity is expected in arid areas since land conversion can lead to a high species turnover (Graham et al., 2019). The new environment formed after land conversion can become conducive for species on the verge of extirpation and improve their proliferation, as demonstrated in several semi-arid landscapes (Manaye et al., 2019; Van Den Berg and Kellner, 2005; Zhou et al., 2006). It is imperative to understand the influence of

landcover on the spatio-temporal patterns of vegetation heterogeneity in GDEs, since these environments are threatened by the expansion of agricultural land, in order to support the growing human population. Hence, to avert the likely effects of land-use and climate change on the stability of the vegetation heterogeneity of GDEs, a proxy of ecosystem stability can be used to constantly monitor GDEs.

Field techniques remain the most reliable and accurate techniques for measuring vegetation heterogeneity, regardless of the environment (Beck and Schwanghart, 2010). However, monitoring the spatio-temporal variations of vegetation heterogeneity with field techniques can be laborious and costly in extensive transboundary aquifers (Brown et al., 2007; Chen et al., 2008; Chiloane et al., 2021; John et al., 2008). Fortunately, the Spectral Variation Hypothesis (SVH) and remotely-sensed data can provide a rapid and direct assessment of the vegetation heterogeneity over large and complex landscapes (John et al., 2008; Li et al., 2017; Nakhoul et al., 2020; Woods and Sekhwela, 2003). The working assumption of the SVH is that vegetation heterogeneity can be inferred from the spectral heterogeneity of any landscape, since spectral heterogeneity is a function of environmental heterogeneity (Rocchini et al., 2010). Heterogenous environments are expected to be more diverse, with several ecological niches (i.e. from the different vegetation types), compared to homogenous environments (Rocchini et al., 2004; Rocchini et al., 2017). The SVH has been successfully explored in different environments, including alpine conifers (Torresani et al., 2019) and grasslands (Lopes et al., 2017). Although it does not hold in all environments (Schmidtlein and Fassnacht, 2017), its applicability in arid environments is promising. The SVH can be used to provide estimates of the vegetation heterogeneity in GDEs within arid environments where no prior information exists on the vegetation (e.g., the Khakea-Bray TBA). No a priori information exists on the vegetation heterogeneity or ecological status of the Khakea-Bray TBA and the SVH can provide us with a starting point.

The Khakea-Bray TBA is amongst some of the most under-studied and poorly-managed aquifers in southern Africa, yet it supports many livelihoods and GDEs (Seward and Van Dyk, 2018). The ecological consequences of groundwater draw-down on GDEs within the Khakea-Bray TBA has not received attention, mainly because groundwater use for socio-economic needs largely outweigh ecological integrity (Davies et al., 2013; Ngobe, 2021; Nijsten et al., 2018). This is exacerbated by how livelihoods within the Khakea-Bray TBA are already under threat from the projected increases in temperature which will likely affect agriculture (a vital sector in the region) (Kaya and Koitsiwe, 2016; Oladele, 2011). In 2002, the aquifer was dewatered after groundwater abstraction for irrigation increased to 11.1 Mm³ per annum beyond the average capacity of the aquifer (6.9 Mm³ per annum) (Godfrey and Van Dyk, 2002; Seward and Van Dyk, 2018; Van Dyk, 2005). Although the land use has changed, groundwater remains a key component for supporting key socio-economic needs (Davies et al., 2013; Nijsten et al., 2018). At the same time, the remaining biodiversity in the Khakea-Bray TBA remains threatened from continued groundwater abstraction, land-use conversion and climate change.

Vegetation heterogeneity estimated from environmental heterogeneity using the SVH can be used as an indicator of ecosystem stability. Consequently, the spatio-temporal variations of vegetation heterogeneity can be used to monitor the ecosystem's stability of the Khakea-Bray TBA. The spatio-temporal variation approach allows the monitoring of environmental changes in GDEs and gives a better insight, compared to using the snapshot approach (Solano-Correa et al., 2018). The snapshot approach uses single-date imagery and might not provide the necessary information on the environmental processes before the image was acquired (Solano-Correa et al., 2018). Understanding the intra-annual, or seasonal, variations of vegetation heterogeneity in the Khakea-Bray TBA can also advance its conservation and management, in the face of land-use conversion and climate variability. Therefore, this study presents the first attempt at monitoring and explaining the drivers of the spatio-temporal trends in vegetation heterogeneity in the

Khakea–Bray TBA, by using the SVH and Landsat–8 OLI Operational Line Imager (OLI).

2. Materials and methods

2.1. Study area

The study was conducted in the Khakea–Bray TBA (formerly Pomfret–Vergelegen Transboundary aquifer) which spans across north–western South Africa and south–western Botswana (Fig. 1). Khakea–Bray TBA is supported by the presence of the low–yielding Khakea–Bray dolomitic aquifer measuring approximately $\sim 5\,375.7\text{ km}^2$. Rainfall is the main source of recharge to the Khakea–Bray dolomitic aquifer with geological lineaments, shallow dolomite outcrops, and alluvial channels along the Molopo River serving as recharge areas (Godfrey and Van Dyk, 2002). However, recharge to the Khakea–Bray dolomitic aquifer is limited by low infiltration in the thick Kalahari sands ($>15\text{ m}$) and high rates of evaporation (2050–2250 mm per annum) (Altchenko and Villhoth, 2013; Godfrey and Van Dyk, 2002; Turton et al., 2006).

The Khakea–Bray TBA is characteristic of a semi–arid environment owing to the low annual rainfall (range 107–928 mm) received in the summer months (October–March) (Godfrey and Van Dyk, 2002). The Khakea–Bray TBA is mainly dominated by the Eastern Kalahari Bushveld Bioregion supporting Molopo Bushveld, Mafikeng Bushveld, and Kuruman Mountain Bushveld (Mucina and Rutherford, 2006; Spickett et al., 2011; Van Dyk, 2005). The bushveld is predominantly *Senegalia nigrescens* and *Vachellia grandicornuta* shrubland intermixed with *Scorzonera humilis*, *Eragrostis* spp., *Ziziphus mucronate*, *Leucas martinicensis* and *Lipia javani*. These plant species are facultative phreatophytes (i.e., will use

groundwater when it is available). However, information on the significance or distribution of these vegetation types in the Khakea–Bray TBA remains largely documented.

Agriculture and wildlife ranching are the main land–uses in the Khakea–Bray TBA with irrigated agriculture using the bulk of the groundwater available (Turton et al., 2006). In 2002, the total area under irrigation had increased by 13.95 ha from 100 ha in 1990 (Godfrey and Van Dyk, 2002). The irrigated farmlands used $\sim 11.1\text{ mm}^3$ per annum more than the annual recharge in the area and this caused the dewatering of the Khakea–Bray TBA (Altchenko and Villhoth, 2013, Godfrey and Van Dyk, 2002, Turton et al., 2006). The lack of information on the ecological status of the Khakea–Bray TBA along with the high rates of groundwater abstraction provide basis for the need to monitor the spatio–temporal variation of vegetation heterogeneity.

2.2. Data acquisition and processing

Multi–year Landsat–8 OLI surface reflectance imagery ($n = 535$) was used for this analysis. Landsat–8 OLI was used to maintain image homogenization and to reduce instances of geometric and spectral inconsistencies from using multi–sensor imagery. Surface reflectance data used in this study are provided, corrected for geometric and atmospheric errors. The multi–year images that were used were acquired between January 2016 and December 2020 from the Google Earth Engine (GEE) platform (<https://code.earthengine.google.com>). The Landsat–8 OLI images were converted to monthly time–series composites that were derived from the median spectral reflectance of the multi–spectral bands (i.e., blue, green, red, near–infrared (NIR), and two short–wave infrared). Image compositing allows for the enhancement of spectral reflectance by removing the clouds and shade (Gxokwe et al., 2022). The

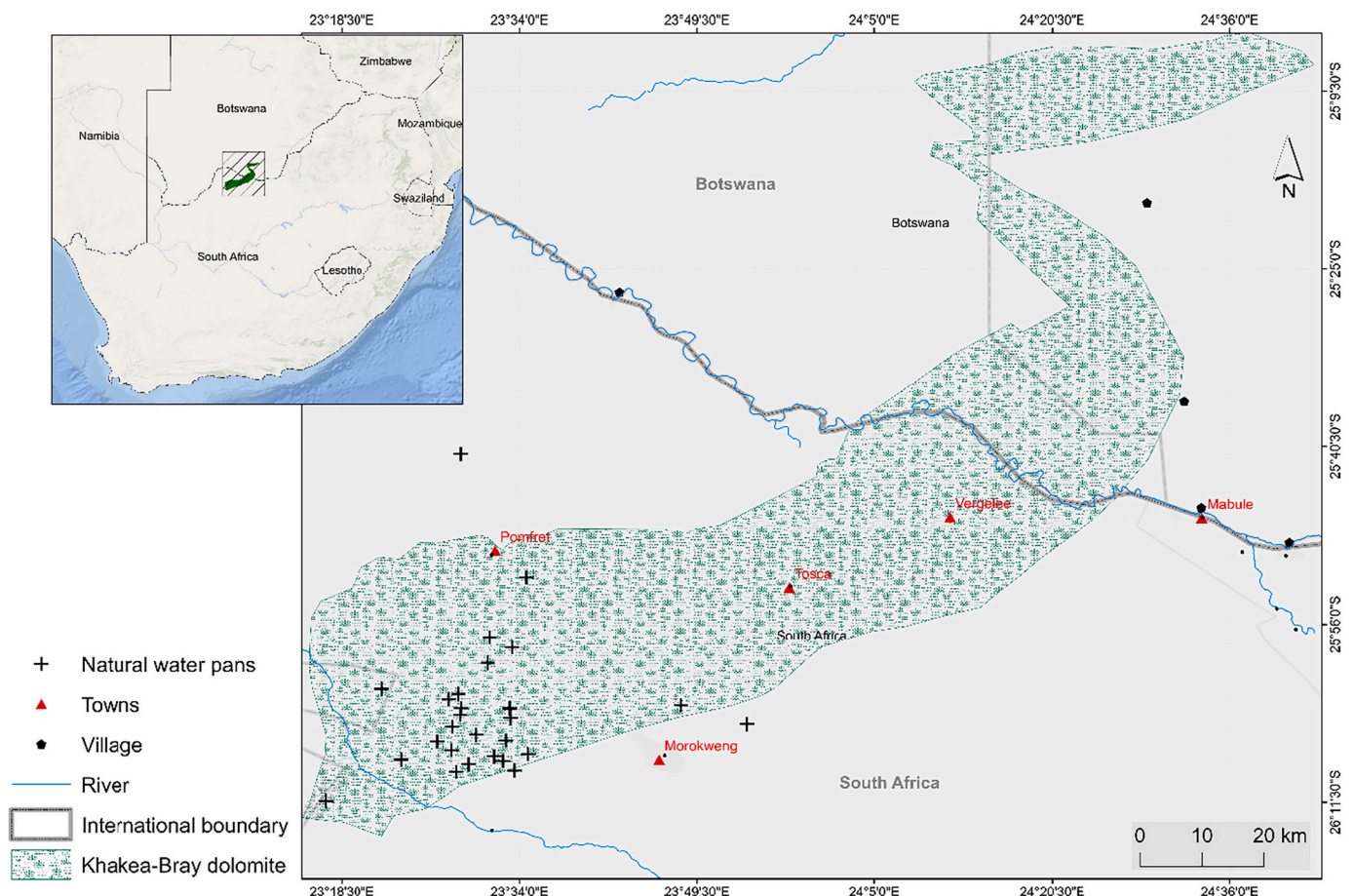


Fig. 1. Location of the Khakea–Bray Transboundary Aquifer in southern Africa. The map was created in ArcMap 10.8 (Esri, 2020).

2016–2020 study period was selected, since the study region has been experiencing severe droughts, including the 2015/2016 El Niño and the ongoing 2018–2021 southern Africa drought (Blamey et al., 2018; Marumbwa et al., 2021). The ongoing drought allows for the enhanced identification of Groundwater-Dependent Vegetation (GDV), since there is minimal surface water available for the non-GDVs.

Since the study focused on monitoring the spatio-temporal variations of vegetation heterogeneity, the built-up water and remnant cloud pixels were masked from the analysis. Cloud pixels were masked by using the QA band (QA60) with in-built functions in GEE, while the Normalized Difference Built-up Index (NDBI) and Modified Normalized Difference Water Index (MNDWI) were used to mask the built-up and water pixels respectively. The NDBI and MNDWI indices were selected over other indices, based on their frequent use in water and built-up mapping (Bhatti and Tripathi, 2014; Jiang et al., 2012; Xu, 2008). The NDBI values greater than 0 and MNDWI values greater than 1 were considered to be built up and water pixels, respectively. The MNDWI can be calculated as follows:

$$MNDWI = \frac{Green - SWIR}{Green + SWIR} \quad (1)$$

and NDBI as:

$$NDBI = \frac{SWIR - NIR}{SWIR + NIR} \quad (2)$$

Where Green, NIR and SWIR are reflectance in the green, shortwave infrared, and near-infrared spectral regions, respectively.

From the masked imagery, the Coefficient of Variation (CV) was calculated to measure the spectral variation of all the images. More specifically, the CV was used because it has been shown to perform better ($r^2 > 0.5$) than other measures for estimating vegetation heterogeneity with remote sensing imagery (Madonsela et al., 2017; Madonsela et al., 2021). The CV was calculated using Eq. 3 below:

$$\text{Coefficient of variation (CV)} = \frac{\text{Standard deviation of all the bands}}{\text{mean of all the bands}} \quad (3)$$

2.3. Environmental variables

Climate and landcover variables were used to explain the drivers of vegetation heterogeneity in the Khakea–Bray TBA. The climate data included the mean temperature, the minimum temperature, the maximum temperature, the annual precipitation, the potential evapotranspiration and the wet day frequency. The climate data were provided monthly (January 2016 – December 2020), with a spatial resolution of 0.5° (Harris et al., 2020). The precipitation data were summed to derive annual totals, and for the other climate variables, the annual averages were used. The climate data were then averaged to derive the mean values for the 2016–2020 period. The climate data were accessed from the Climatic Research Unit gridded Time Series (CRU TS) v. 4.05 and downloaded from <https://crudata.uea.ac.uk/cru/data/hrg/>. In addition to the climate data, land cover data from the European Space Agency (ESA)–Climate Change Initiative (CCI) available from <http://2016africallandcover20m.esrin.esa.int/> was used. The landcover data have several landcover classes, including tree cover, shrub cover, grassland, cropland, aquatic vegetation or regularly flooded, lichens mosses / sparse vegetation, bare land, built-up land, snow and/or ice and open water areas. The Khakea–Bray is characteristic of shrubland savannah (i.e. bushveld) and the landcover data included this vegetation class (i.e. shrub cover). These data were provided at 20 m and were derived from Sentinel–MSI imagery (Alkhalil et al., 2020). The landcover and climate variables were included, based on their generalized interaction with groundwater and plant growth (Brolsma et al., 2010; Eamus et al., 2006; Zhu et al., 2015).

2.4. Vegetation heterogeneity from remote sensing images

To measure the spatio-temporal variation of vegetation heterogeneity in the Khakea–Bray TBA, the study utilized α - and β -diversity measures, namely, the Shannon–Weiner Index and the Rao's Q, respectively. The Shannon–Weiner Index calculates vegetation heterogeneity by considering the abundance and richness of spectral values for the entire image (Rocchini et al., 2017) and it can be calculated by using Eq. 4.4 below:

$$H' = - \sum_{i=1}^S p_i \ln p_i \quad (4)$$

Where S is the image extent or plot area, and p_i is the proportion of pixel i to S.

Although the Shannon–Weiner Index is a commonly-used measure; it has been observed to saturate over areas with high vegetation heterogeneity and it is affected by subtle changes in the pairwise pixel values (Rocchini et al., 2017), which is the reason why the Rao's Q was also included. In remote sensing, the Rao's Q calculates vegetation heterogeneity from the pairwise spectral distance between the spectral values of pixel i and j (Khare et al., 2021; Torresani et al., 2021). The measure also incorporates the abundance and proportion of pixels i and j. Rao's Q is calculated as follows:

$$Q_{rs} = \sum_{i=1}^{F-1} \sum_{j=i+1}^F d_{ij} p_i p_j \quad (5)$$

Where Q_{rs} represents the Rao Q applied to the remote sensing image and d_{ij} is the distance between i th and j th pixel ($d_{ij} = d_{ji}$ and $d_{ii} = 0$). The selected image extent or plot area is F, with p_i and p_j being the proportion of pixel i and j to F, respectively.

The coefficient of variation that was calculated from the pre-processed images was used to calculate the Rao's Q and Shannon–Weiner index in R (Team, 2020), using the spectralrao function provided in Rocchini et al. (2017) and Rocchini et al. (2019). A 3×3 - pixel moving window was used when computing the vegetation heterogeneity.

2.5. Spatio-temporal variation analysis

To measure the monthly spatio-temporal variations of the vegetation heterogeneity in the Khakea–Bray, the Mann–Kendall non-parametric test was used. This test measures the monotonic trends in time-series data and has been used in most studies, owing to its robustness (Libiseller and Grimvall, 2002; Shadmani et al., 2012). In this study, the Mann–Kendall test was used to detect trends in the seasonal vegetation heterogeneity from the Rao's Q and the Shannon–Weiner data. The p-value and S-values from the Mann–Kendall test were used to evaluate the significance of the trend and the rate of change in the vegetation heterogeneity within the Khakea–Bray TBA, respectively. The significance was tested with an alpha value of 0.05 (i.e., $p < 0.05$ confidence interval).

2.6. Drivers of vegetation heterogeneity spatio-temporal variation

To determine the drivers in the spatio-temporal variation of vegetation heterogeneity, the variable importance function in the random forest algorithm was used, which uses classification and regression trees to build a highly-predictive ensemble model (Breiman, 2001; Mpakairi and Muvengwi, 2019). The random forest algorithm was used, as it is insensitive to the data structure, it is highly predictive and it does not overfit (Breiman, 2001; Liaw and Wiener, 2002). This model was executed in R, using the caret and randomForest package (Breiman, 2001; Kuhn, 2009; Liaw and Wiener, 2002). To build the random forest model, data from the Mann–Kendall test were used, which showed the spatio-temporal variations of vegetation heterogeneity along with

climate and land cover variables. The data used to build the model were derived from areas where the spatio-temporal changes in vegetation heterogeneity were significant (i.e., $p < 0.05$). Seventy-five percent of the data was used for model training and the remaining 25% was used for model evaluation. To evaluate the accuracy of the model, the Mean Absolute Error (MAE), the Root Mean Square Error (RMSE) and the percentage RMSE (% RMSE) were used. The MAE, RMSE and % RMSE measure the agreement between the actual and predicted values of the model and can be used to compare the predictive errors of different models (Piepho, 2019; Zhang, 2017). A model with a lower RMSE and MAE is considered to be highly predictive, when compared to a model with a higher RMSE and MAE (Chai and Draxler, 2014). In addition, a model with a low % RMSE means that the model has less residual variance than a model with a high % RMSE (Lin et al., 2016).

To measure the variable contribution, the Increased Impurity Index (IncNodePurity) was utilized, following Mpakairi and Muvengwi (2019), Pal (2005) and Svetnik et al. (2003). IncNodePurity measures how a variable decreases the Residual Sum of Squares (RSS) at each node for all the regression trees in a model (Pal, 2005; Svetnik et al., 2003). The variable with the highest IncNodePurity explained the changes in vegetation heterogeneity more than the other variables. All the methods used are summarized in Fig. 2.

3. Results

3.1. Spatio-temporal variation of vegetation heterogeneity

Our results showed that the vegetation heterogeneity was high

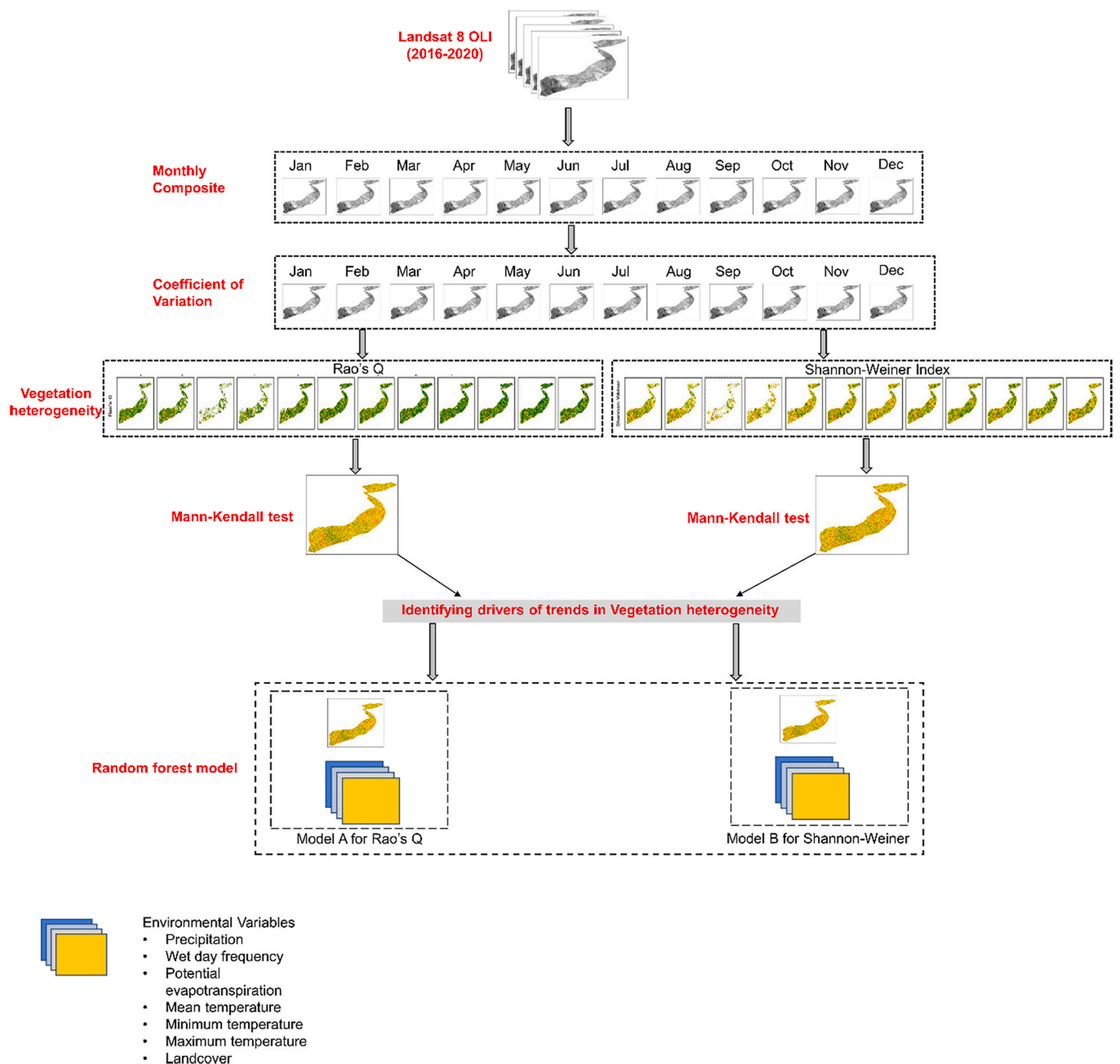


Fig. 2. Summarized flowchart showing the steps undertaken to detect the trends in vegetation heterogeneity and to identify the drivers of the changes in vegetation heterogeneity.

during the wet season and low during the dry season. Peak vegetation heterogeneity was observed in April and the lowest vegetation heterogeneity was observed in September (Fig. 3), and it also peaked in the middle of winter (July) before summer. These changes were more noticeable when using the Shannon–Weiner Index, rather than the Rao’s Q (Fig. 4 and Fig. 5). However, the changes in vegetation heterogeneity from the Shannon–Weiner Index were more generalized, when compared to those from the Rao’s Q, which showed more pronounced changes in the vegetation heterogeneity (Fig. 6).

The results of the Mann–Kendall test for the monthly Shannon–Weiner Index and the Rao’s Q showed that the vegetation heterogeneity changed significantly around natural water pans, along roads and rivers, and in most farming areas. More specifically, a significant decrease in vegetation heterogeneity was observed along the roads and a significant increase was observed in the cropping areas, around natural water pans and along rivers (Fig. 6).

3.2. Drivers of variation in vegetation heterogeneity

Our random forest models, using the Shannon–Weiner Index (MAE = 30.37, RMSE = 33.25 and %RMSE = 63.94) and the Rao’s Q (MAE = 5.81, RMSE = 6.63 and %RMSE = 42.41), were able to show the environmental drivers and explain the changes in vegetation heterogeneity. The random forest model, using the Rao’s Q, performed better than the model using the Shannon–Weiner Index, since the %RMSE, RMSE and MAE from the Shannon–Weiner Index model were higher. Although the models performed differently, the effect of the environmental drivers on the changes in vegetation heterogeneity were relatively similar.

Overall, the changes in vegetation heterogeneity were predominantly driven by land cover, precipitation, the mean temperature and the wet day frequency (Fig. 7). On the other hand, the maximum temperature, the minimum temperature and the potential evapotranspiration contributed least to the changes in the vegetation heterogeneity. For land cover, the changes in vegetation heterogeneity were more noticeable in areas with water, cropland, shrubland and bare land cover (Fig. 8). In addition, a low wet day frequency (< 4 days/year) facilitated the changes in vegetation heterogeneity more than a high wet day frequency (Fig. 9). However, changes in the vegetation heterogeneity varied according to the precipitation amount. Changes in the vegetation heterogeneity were observed in areas with high rainfall (> 380 mm/year), low rainfall (< 300 mm/year), or with relatively high mean temperatures (20.9–21.2 °C).

4. Discussion

It is imperative to understand the spatio–temporal variations of vegetative heterogeneity for the conservation of the ecological integrity of GDEs within arid environments. Therefore, this study sought to detect the spatio–temporal variations of vegetative heterogeneity in the Kha-kea–Bray TBA by using remote sensing measures. Overall, the results showed how land cover and climate explain the intra–annual and seasonal changes in vegetation heterogeneity.

4.1. Response of vegetation heterogeneity to environmental variables

Our observation on the response of vegetative heterogeneity to seasonality can be associated with the phenological patterns of vegetation and the relationship between climate and vegetation (Adole et al., 2016; Wessels et al., 2011). The primary productivity of plants has been observed to peak during the wet season and to decrease during the dry season, owing to limited water and nutrient availability (Byrne et al., 2013; Prev y and Seastedt, 2014). These seasonal changes in productivity affect vegetative heterogeneity and have been observed in most environments, including arid areas (Aronson and Shmida, 1992; February et al., 2007; Kushwaha and Nandy, 2012). These patterns are important for arid environments in the context of climate change, since precipitation and temperature seasonality are expected to increase (Scholes, 2020). The projected increase in precipitation and temperature seasonality means that seasons will most likely be extreme, and this might affect the ability of plants to tolerate extreme seasons (Scholes, 2020; Zeppel et al., 2014). The effect of climate seasonality on vegetative heterogeneity is also supported by our observations from the random forest model, which showed that changes in the vegetative heterogeneity responded more to the precipitation and mean temperature. This is also supported by how temperature and water availability are driving variables behind the longitudinal variations in vegetative heterogeneity (Collins et al., 2010; Yan et al., 2015).

In arid areas, precipitation is more impactful than temperature, since subtle changes in precipitation have the potential to alter the structure and composition of the species therein (Byrne et al., 2013; Prev y and Seastedt, 2014). However, the negative feedback between wet day frequency and changes in vegetative heterogeneity plausibly means that most of the species within the arid Kha-kea–Bray TBA have adapted to water stress, and increased precipitation might cause soil flooding. Soil flooding can suffocate the plant roots, and the reduced soil aeration will result in the death of the aboveground vegetation (Adler and Levine,

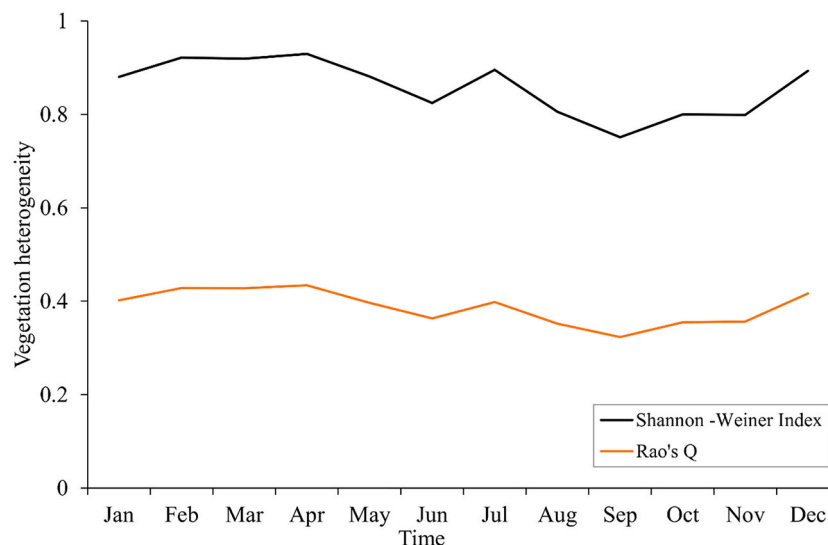


Fig. 3. Monthly average of vegetation heterogeneity measured by the Shannon–Weiner Index and the Rao’s Q.

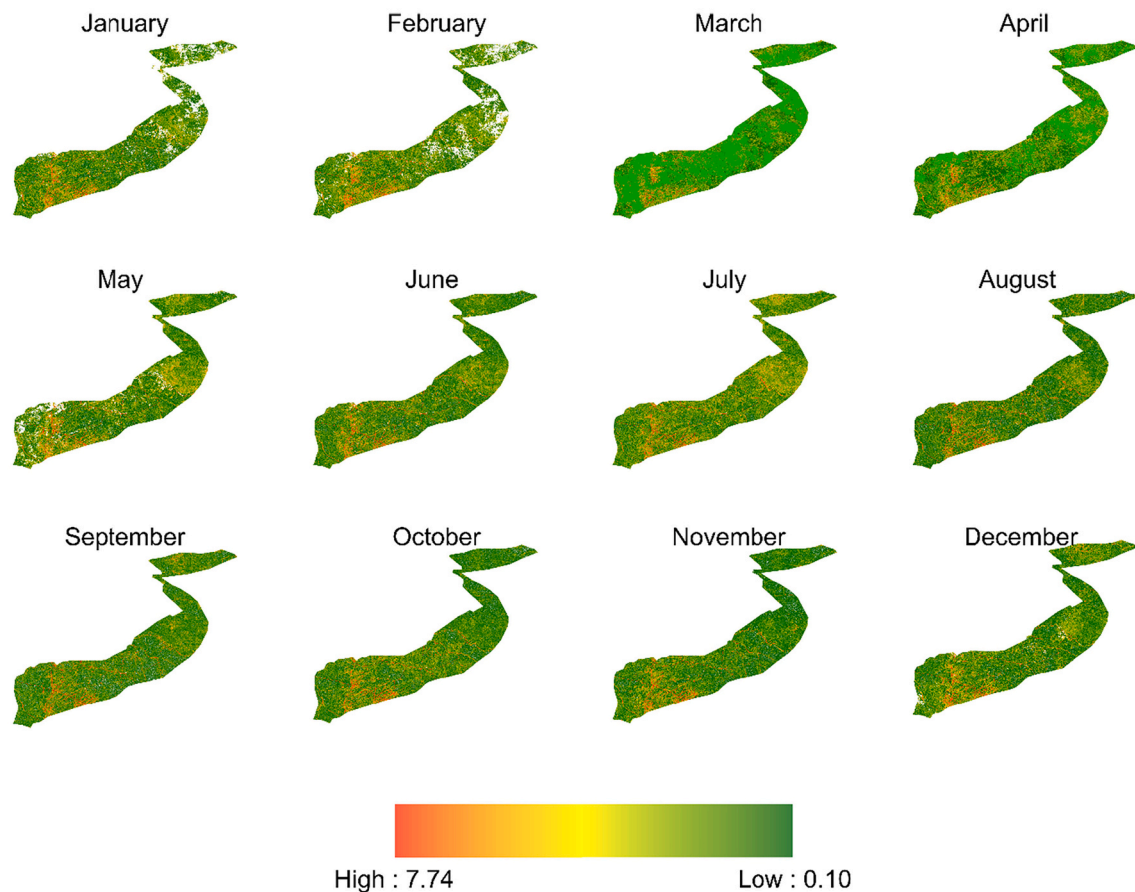


Fig. 4. Five-year (2016–2020) monthly changes in vegetation heterogeneity, as calculated by the Rao's Q.

2007; Cleland et al., 2013). This is supported by the species pool hypothesis in that, increased wetness will only support species that are capable of surviving the increased availability of water (Grace, 2001). Therefore, species that are not adapted to the increased water availability will likely die.

The counter-intuitive observation on the negative interaction between changes in vegetative heterogeneity and the increasing wet day frequency is corroborated by previous studies (Adler and Levine, 2007; Swemmer et al., 2007; Yan et al., 2015). For instance, Adler and Levine (2007) observed that increasing precipitation did not affect the species richness in areas with annual plants within the Colorado prairies. These findings were also similar to observations by Cleland et al. (2013), who found that the regional species richness of grasslands was not influenced by annual precipitation; instead, annual precipitation influenced plot-level richness. These observations are relevant to the Khakea-Bray TBA, since it is extensive and covers several landcover types.

4.2. Spatio-temporal dynamics of vegetation heterogeneity in the Khakea-Bray TBA

Our findings on how the vegetative heterogeneity changes around natural water pans, along roads and rivers, and in most farming areas, were supported by the results of the variable importance analysis, which showed that landcover (water, cropland, shrubland and bare land cover) explained most of the changes in the vegetative heterogeneity. The onset of the farming season and the harvesting period in farming areas may explain the changes in spectral heterogeneity vis-à-vis vegetation heterogeneity (Eilu et al., 2003; Kindt et al., 2004); for example, the land-use change from cattle ranching to crop farming before the growing season, and back to cattle ranching after the rainy season (Dahlberg, 2000; Ramberg et al., 2006). These changes in land use are essential for

supporting cattle ranching, which is mostly practised in the Khakea-Bray TBA, and they therefore explain the trends in the vegetative heterogeneity in the farming areas. On the other hand, the seasonality of precipitation and groundwater availability could be driving the increases in vegetation heterogeneity around natural water pans and along rivers (Buchsbbaum et al., 2006; Utete et al., 2018). The groundwater level is usually high, with the obligatory and facultative phreatophytes present, around natural water pans and along rivers (Hoyos, 2016). Facultative phreatophytes will most likely remain present during the wet season, but in the dry season, the lowering of the groundwater level may affect them and lead to wilting or stunted growth (Buchsbbaum et al., 2006; Ward et al., 2013). At a later stage, the improved groundwater availability from groundwater recharge might improve plant growth and the development of obligatory and facultative phreatophytes (Thomas, 2014; Torres-García et al., 2021).

These dynamics of groundwater availability may explain the changes in vegetation heterogeneity around natural water pans and along rivers. In addition, the changes around natural water pans could be related to the piosphere effect, because water resources benefit livestock more during the dry season and less during the wet season (Andrew, 1988; Carbonell et al., 2021; Shezi et al., 2021). The aggregation of livestock and grazing around natural water pans creates a utilization gradient (Andrew, 1988; Shezi et al., 2021). Our observations on how the vegetation heterogeneity changes around natural water pans, along roads and rivers, and in most farming areas, have been observed before in different environments (Junk et al., 2006; Li et al., 2014; López-Gómez et al., 2008; Msiteli-Shumba et al., 2017; Wei and Jiang, 2012).

4.3. Model comparison and implications on future work

The Rao's Q performed better than the Shannon-Weiner Index, since

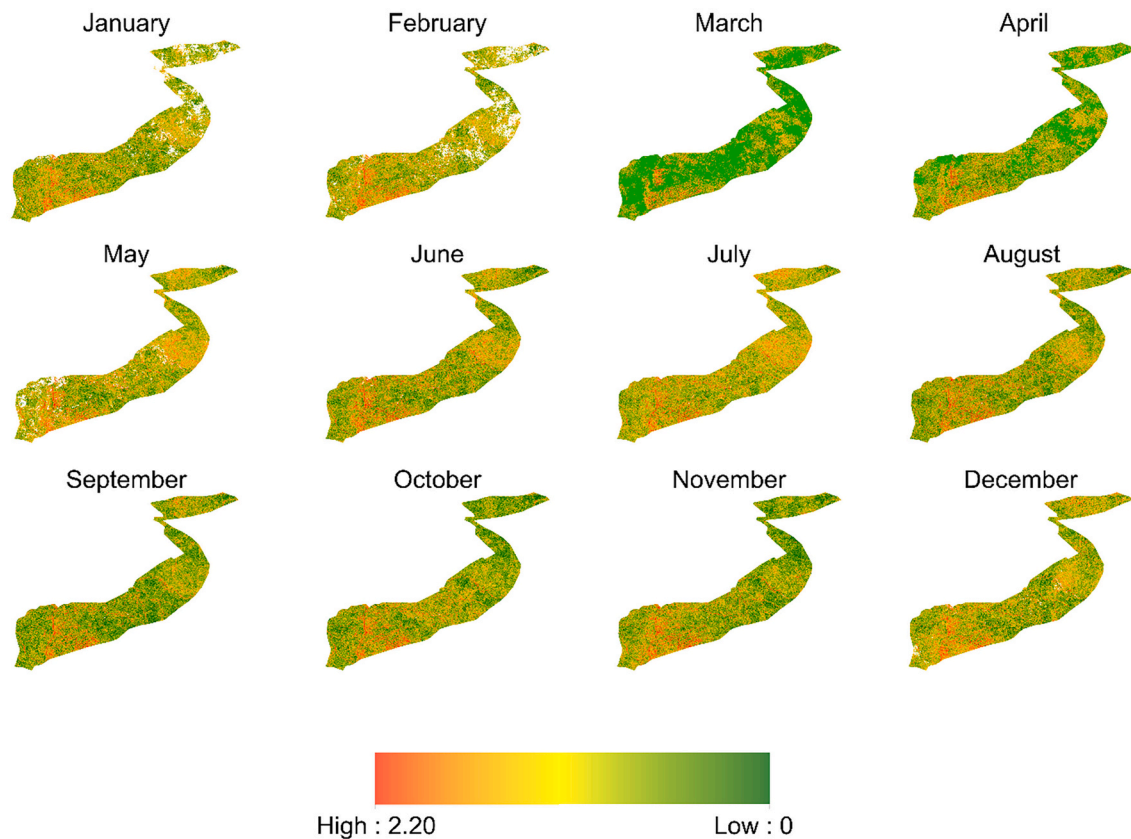


Fig. 5. Five-year (2016–2020) monthly changes in vegetation heterogeneity, as calculated by the Shannon–Weiner Index.

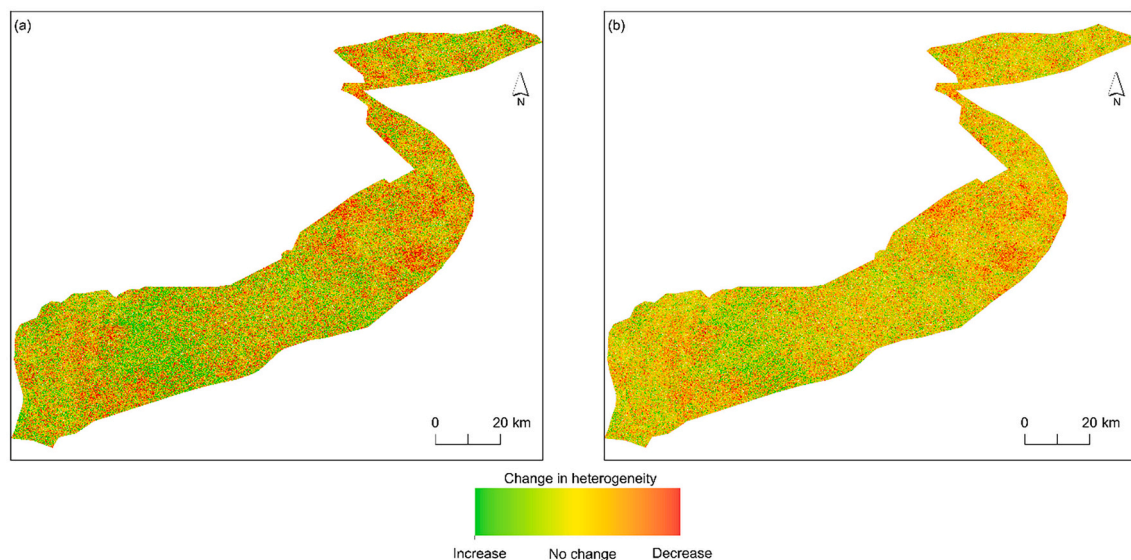


Fig. 6. Spatio-temporal trends of vegetation heterogeneity as measured by (a) the Shannon–Weiner Index and (b) the Rao’s Q, using the Mann–Kendall test.

it allows the monitoring of vegetation heterogeneity across landscapes by incorporating the spectral distance (Khare et al., 2019; Rocchini et al., 2018). The Rao’s Q can estimate vegetation heterogeneity at a community level, rather than at a plot or pixel-level, as with the Shannon–Weiner Index (Hernández-Stefanoni et al., 2012; Rocchini et al., 2018). These characteristics are ideal, since the Khakea–Bray TBA is an extensive landscape with several vegetation communities, and the Shannon–Weiner Index would be oversaturated from the high vegetation heterogeneity (Khare et al., 2019; Rocchini et al., 2017). However,

monthly changes in vegetation heterogeneity were more noticeable with the Shannon–Weiner Index, since it can detect subtle changes in vegetation heterogeneity, compared to the Rao’s Q (Féret and De Boissieu, 2020; Rocchini et al., 2018).

Vegetation growth and development are in sync with the precipitation and land cover patterns in most environments (Jamieson et al., 2012; Jolly and Running, 2004; Prasad et al., 2007). Understanding the spatio-temporal variations of vegetation heterogeneity from the interaction of the vegetation, land use and climate patterns can assist in the

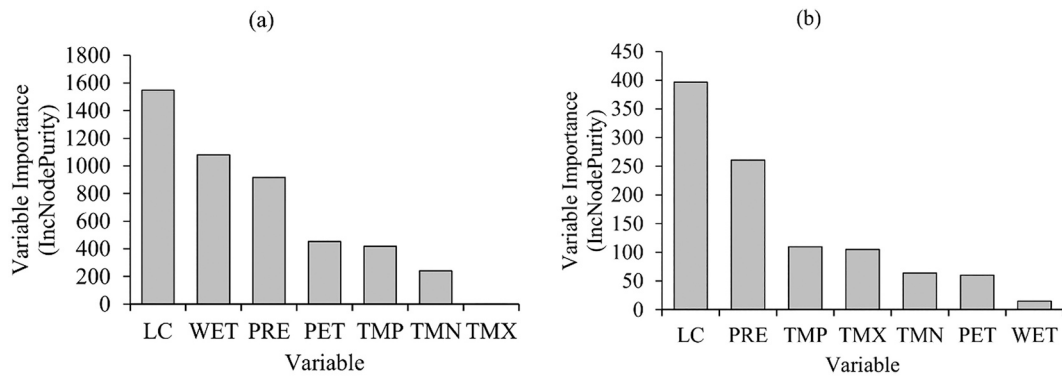


Fig. 7. Variable contribution to the spatio-temporal changes in vegetation heterogeneity from (a) the Shannon–Weiner and (b) the Rao’s Q random forest models. Where PRE refers to precipitation, WET represents wet day frequency, PET represents the potential evapotranspiration, TMN represents the minimum temperature, TMP is the mean temperature, TMX represents the maximum temperature and LC represents the landcover.

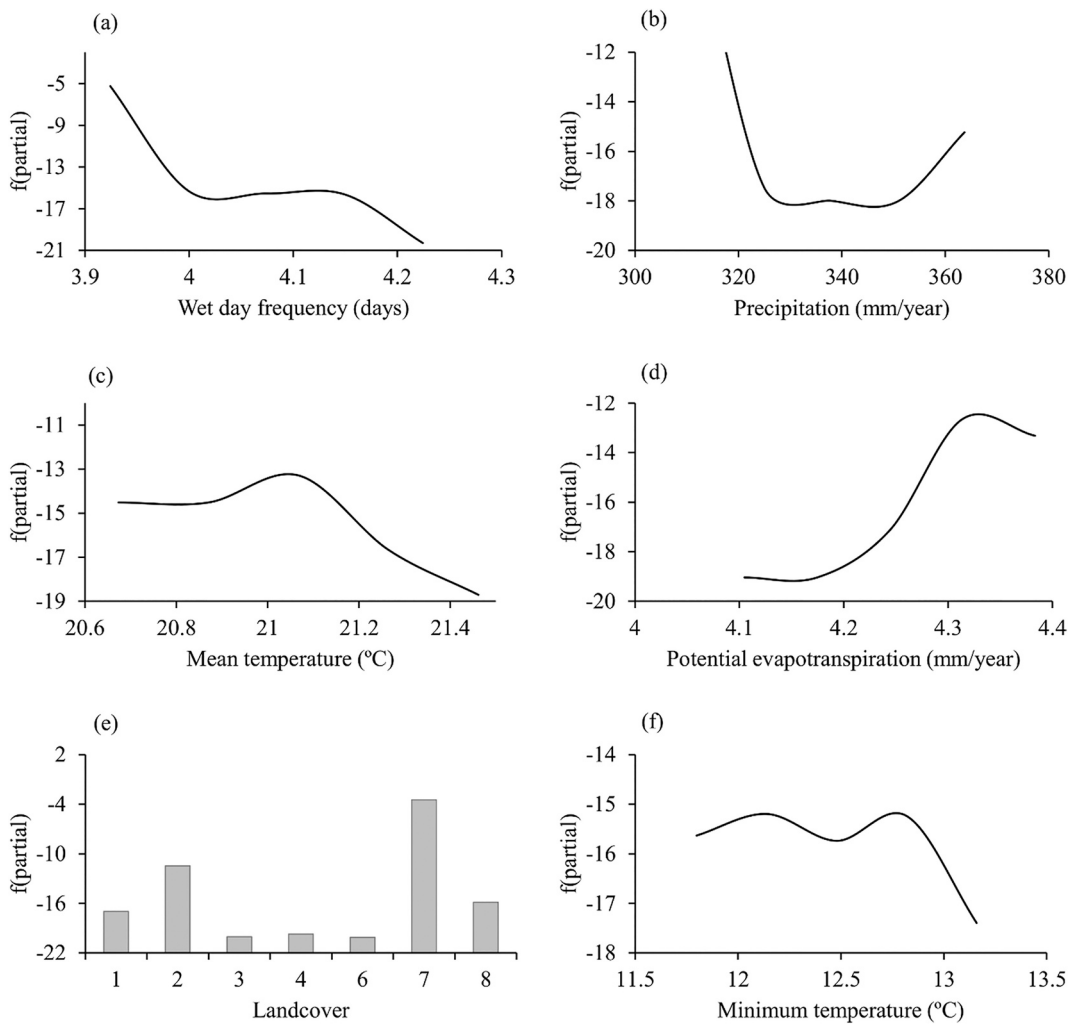


Fig. 8. Partial dependence plots from the Shannon–Weiner random forest model showing the response in the spatio-temporal variation of vegetation heterogeneity to (a) wet day frequency, (b) precipitation, (c) mean temperature, (d) potential evapotranspiration, (e) land cover (1 = Tree cover, 2 = Shrubland, 3 = Grassland, 4 = Cropland, 6 = Sparse vegetation, 7 = Bare land, 8 = Built-up areas) and (f) minimum temperature. The maximum temperature had zero contribution to the model, hence there was no partial dependence curve for this variable.

plausible prediction of the effects of climate change and land cover on GDEs (Dwire et al., 2018; Van Engelenburg et al., 2018; Xu and Su, 2019). The results of this study are robust, since they converge and support each other. The principle of converging evidence postulates that when the results converge, then the conclusions of these results are

robust (Kuo et al., 2019). However, data on the groundwater level in the Khakea–Bray TBA were not available and future studies should include this variable, when identifying the drivers of change in vegetation heterogeneity. Regardless of these setbacks, our results have merit, and future studies could focus on the effects of climate change and

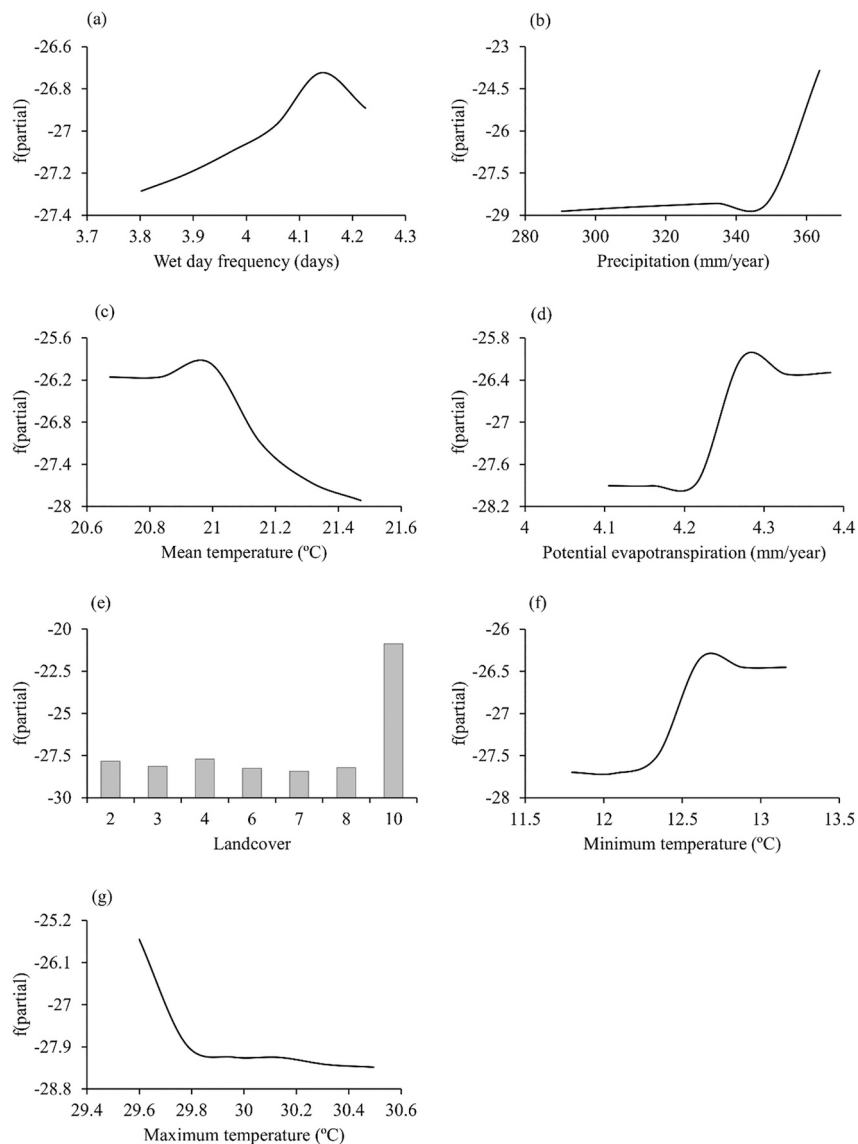


Fig. 9. Partial dependence plots from the Rao's Q random forest model showing the response in the spatio-temporal variation of vegetation heterogeneity to (a) wet day frequency, (b) precipitation, (c) mean temperature, (d) potential evapotranspiration, (e) land cover (2 = Shrubland, 3 = Grassland, 4 = Cropland, 6 = Sparse vegetation, 7 = Bare land, 8 = Built-up areas and 10 = Open Water), (f) minimum temperature and (g) maximum temperature.

variability, as well as land use, on the vegetation heterogeneity in GDEs. Future studies can also focus on the species rarity from spectral uniqueness since this could assist in the management of keystone species within arid environments.

5. Conclusions

GDEs are sensitive environments and protect keystone species and regionally restricted species. Land-use, climate variability and change are expected to intensify the aridity of southern Africa, which will most likely affect the GDEs in these countries, since they are already at risk from other compounding factors, such as groundwater draw-down and unsustainable groundwater abstraction. Currently, there is a dearth of literature on the ecological or economic significance of the Khakea-Bray TBA, despite the fact that its GDEs are under threat from climate change and unsustainable groundwater extraction and despite their relevance for sustaining livelihoods and biodiversity (Seward and Van Dyk, 2018; Van Dyk, 2005). Hence, this study presents the first attempt at monitoring the spatio-temporal variations of vegetation heterogeneity, as well as the drivers of these variations, in the Khakea-Bray TBA. The

results will provide resource managers and ecologists with a priori information on the role of land cover and climate change in influencing the changes in vegetation heterogeneity. The methods used in this study are robust and can be used to monitor other GDEs in similar environments.

Data availability statement

Data used in this research is freely available online and upon request from the corresponding author.

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CRediT authorship contribution statement

Kudzai S. Mpakairi: Conceptualization, Formal analysis,

Methodology, Writing – original draft, Writing – review & editing. **Timothy Dube**: Conceptualization, Supervision, Writing – review & editing. **Farai Dondofema**: Supervision, Software, Validation. **Tatenda Dalu**: Conceptualization, Supervision, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that there exists no competing financial interests or personal relationships that could have appeared to influence the work reported in this study.

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