LETTER • OPEN ACCESS

Seeing roots from space: aboveground fingerprints of root depth in vegetation sensitivity to climate in dry biomes

To cite this article: Nicola Kühn *et al* 2022 *Environ. Res. Lett.* **17** 114062

View the article online for updates and enhancements.

ENVIRONMENTAL RESEARCH
LETTERS

CrossMark

LETTER

Seeing roots from space: aboveground fingerprints of root depth in vegetation sensitivity to climate in dry biomes

Nicola Kühn[1,2,*] ⦿, Marcus P Spiegel[1] ⦿, Carolina Tovar[2] ⦿, Katherine J Willis[3] ⦿ and Marc Macias-Fauria[1] ⦿

[1] School of Geography and the Environment, University of Oxford, Oxford, United Kingdom
[2] Royal Botanic Gardens, Kew, Jodrell Laboratory, Richmond, United Kingdom
[3] Department of Biology, University of Oxford, Oxford, United Kingdom
* Author to whom any correspondence should be addressed.

E-mail: n.kuhn@kew.org

Abstract

With predicted climate change, drylands are set to get warmer and drier, increasing water stress for the vegetation in these regions. Plant sensitivity to drier periods and drought events will largely depend on trait strategies to access and store water, often linked to the root system. However, understanding the role of below-ground traits in enhancing ecological resilience to these climate changes remains poorly understood. We present the results of a study in southern Africa where we analysed the relationship between root depth and the vegetation sensitivity index (VSI) (after Seddon and Macias-Fauria *et al* 2016 *Nature* **531** 229–32). VSI demonstrates remotely-sensed aboveground vegetation responses to climate variability; thus our study compares aboveground vegetation responses to belowground root traits. Results showed a significant negative relationship between root depth and vegetation sensitivity. Deeper roots provided greater resistance to climate variability as shown by lower sensitivity and higher temporal autocorrelation in vegetation greenness (as measured by the enhanced vegetation index). Additionally, we demonstrated a link between deeper roots and depth to groundwater, further suggesting that it is the ability of deeper roots to enable access to groundwater that provides ecological resistance to climate variability. Our results therefore provide important empirical evidence that the ability to access deeper water resources during times of lower water availability through deeper roots, is a key trait for dryland vegetation in the face of future climate change. We also show that belowground traits in drylands leave a fingerprint on aboveground, remotely-sensed plant–climate interactions, an important finding to aid in scaling up data-scarce belowground research.

1. Introduction

Plant traits play a fundamental role in mediating vegetation responses to climate change. Recent work has demonstrated that belowground traits (e.g. rooting depth, resprouting ability, belowground storage) might be at least as important as aboveground traits in promoting plant fitness and performance in the face of climate change (Kühn *et al* 2021), enabling plants in dryland biomes to cope with climate and associated environmental changes. The relationship between belowground plant traits and climatic/environmental factors is thus potentially important for determining plant resilience to future change. However, in comparison to other traits, roots are rarely studied due to difficulties in field extraction (Laliberté 2017). Preliminary hypotheses backed up by root research based on a limited global dataset ($n = 475$) predict that deeper roots will be more prevalent in arid and semi-arid systems than in humid ones, and more prevalent in certain growth forms (trees from savanna/thorn scrub, or seasonally dry forests) (Schenk and Jackson 2002, Schenk 2005).

Recent collation of existing data in online trait databases (GRooT, FRED, TRY, BIEN) (Enquist *et al* 2009, Kattge *et al* 2011, 2020, Iversen *et al* 2017, Guerrero-Ramírez *et al* 2021) and the advancement of remote root measuring techniques (i.e. isotope

analysis and remote sensing techniques) have supported these hypotheses over large spatial scales. Fan *et al* (2017) for example, showed that groundwater plays a key role in driving root depth patterns at both the landscape and global scale. Similarly, deep roots have also been found to strongly correlate with the ability to access deep soil water (Fort *et al* 2017, Liu *et al* 2021). For example, a recent study in sub-tropical coniferous shrubs showed that during dry seasons the majority of water uptake occurred in deep soil layers (Jiang *et al* 2020). Ability to access water from the deeper groundwater table, additional to the rooting zone of soil (Leenaars *et al* 2018) through deeper rooting depth (Weigelt *et al* 2021), may therefore be an important trait from local (Kühn *et al* 2022) to global scales (Laughlin *et al* 2021) in times of drought.

Previous studies on groundwater-dependent ecosystems support the suggestion that certain species are reliant on this deeper groundwater (so called phreatophytes) (Naumburg *et al* 2005, Eamus *et al* 2015) especially in drier intervals (Gou and Miller 2014). However, the hypothesis of deeper roots mediating plant sensitivity to hydroclimate variability via groundwater access has not yet been widely demonstrated. Furthermore, there is little understanding of whether this relationship is consistent across functionally different biomes within drylands.

In this study we analysed the relationship between root characteristics and above-ground patterns of vegetation sensitivity to climate variability. The vegetation sensitivity index (VSI; Seddon *et al* 2016) quantifies the relationship between anomalies in monthly vegetation greenness (as measured by the enhanced vegetation index (EVI)) and climate anomalies. In the VSI's multiple regression approach, the month-to-month temporal autocorrelation in EVI (EVI_{t-1}) represents the potential influence of lagged effects on vegetation, which have been found to be key to explain vegetation productivity in drylands (Liu *et al* 2018). Greater magnitude in EVI_{t-1} indicates that EVI anomalies are more strongly linked to the previous month's EVI anomaly than the current climate. Seddon *et al* (2016) generated a coarse (5 km), spatially-continuous global map of vegetation sensitivity considering the period 2000–2013. Within this global analysis, southern Africa showed strong variation in vegetation sensitivity to climate variability, with large areas showing high sensitivity to water availability and high temporal autocorrelation in EVI. This makes the region a suitable case study to test if water-related traits such as root depth play a role in determining vegetation sensitivity to climate change as observed by the aboveground VSI patterns. Further, this offers the opportunity to analyse whether belowground traits can be estimated by analysing the variability in EVI of aboveground vegetation.

We recomputed the VSI at a finer spatial resolution (1 km) and analysed the relationship between root depth and sensitivity to climate variability for the 20 year period comprising 2000–2019 in the biodiverse dryland biomes of southern Africa to test the following hypotheses:

(a) Deeper roots are found in areas with lower VSI (thus deeper roots result in greater ecological resistance to drought events).

(b) Deeper roots are also found in areas that demonstrate greater temporal autocorrelation in EVI (EVI_{t-1}) (thus suggesting previous state, mediated by belowground traits, are more important in determining EVI anomalies than month-to-month climate variability).

(c) The relationships apparent in (a) and (b) are regulated by overall growth form and vegetation characteristics captured by biome type.

(d) We expect a positive relationship between root depth and groundwater depth and a negative relationship between root depth and soil water holding capacity, in agreement with the proposed mechanism that deeper roots enables access to deeper groundwater resources.
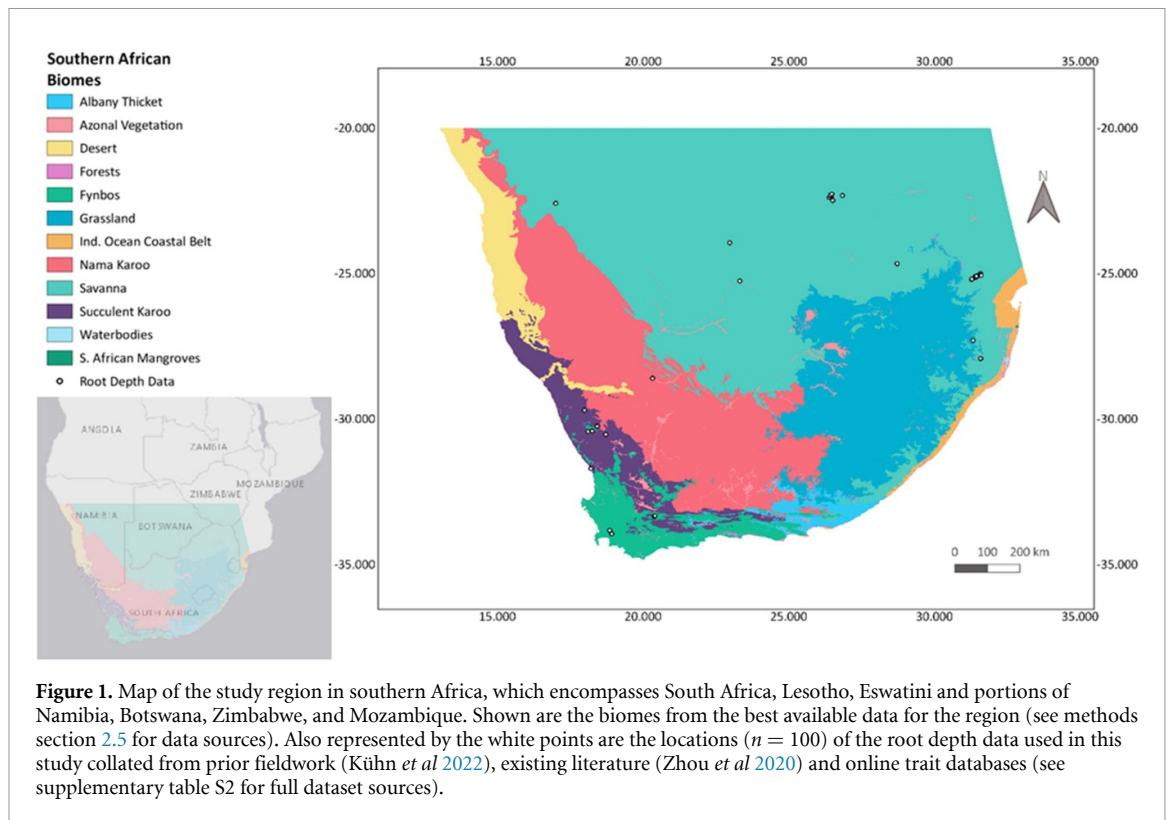
2. Methods

2.1. Study site and climate

We conducted our analysis in southern Africa, including all land area between 20° S and 40° S and 11° E and 35° E. This area encompasses 11 biomes, with varying vegetation types and growth forms (figure 1 and see supplementary table S1).

Most of southern Africa experiences a colder dry season (April–October) and a warmer wet season (November–March). However, in the south-western tip of the region (covering Fynbos and Succulent Karoo biomes), the seasons are reversed, with dry summers and wet winters produced by mid-latitude cyclones. Observed past climate change in southern Africa indicates warming of 0.4 °C per decade between 1961 and 2014, making it one of the regions experiencing the greatest warming in Africa (Davis and Vincent 2017). This warming has resulted in greater evapotranspiration. Further, the region has shown declining trends in rainfall, resulting in an aridification trend that is predicted to continue, with increased frequency and intensity of droughts implying even greater future water stress across the region (Davis and Vincent 2017, Naik and Abiodun 2019).

2.2. Trait data

Root depth data and their geographical coordinates from the study area in southern Africa were collated from existing datasets from published literature and online trait databases, resulting in 88 records. These data are collected using a range of methods including root excavations, isotopic analysis, and borehole inspections. In addition, 12 more records were randomly subset (see methods section 2.6) from root depth data collected via excavation by a prior study (Kühn *et al* 2022) ($n = 124$). In total, 100 records of

Figure 1. Map of the study region in southern Africa, which encompasses South Africa, Lesotho, Eswatini and portions of Namibia, Botswana, Zimbabwe, and Mozambique. Shown are the biomes from the best available data for the region (see methods section 2.5 for data sources). Also represented by the white points are the locations ($n = 100$) of the root depth data used in this study collated from prior fieldwork (Kühn *et al* 2022), existing literature (Zhou *et al* 2020) and online trait databases (see supplementary table S2 for full dataset sources).

root depth across biomes and growth forms were collated from existing datasets (see supplementary table S2). These covered six out of the 11 biomes in the study region, with the most data points in Savanna ($n = 67$) and Fynbos ($n = 22$) and fewer in Succulent Karoo (5), Nama Karoo (3), Azonal Vegetation ($n = 2$), Grassland ($n = 1$). Four growth forms were considered: trees ($n = 64$); shrubs ($n = 30$); graminoids ($n = 4$); and non-graminoid herbaceous plants ($n = 2$).

2.3. Climate and vegetation data
Climate data used in this study were obtained from the satellite Moderate Resolution Imaging Spectroradiometer (MODIS) 8 day composite ratio of actual vs potential evapotranspiration (Running *et al* 2019). These were obtained at a 0.5 km resolution over 2000–2019, along with MODIS daily cloudiness (Vermote and Wolfe 2020) at 1 km resolution over 2000–2019, which was calculated following the methodology outlined by Wilson and Jetz (2016). In addition, we obtained Climatologies at high resolution for the earth's land surface areas, CHELSA monthly timeseries of maximum temperature at 1 km resolution (period 2000–2019) (Karger 2018, Karger *et al* 2017), as well as data from the MODIS monthly EVI (Didan 2015) at 1 km resolution over the period 2000–2019. All outputs were then calculated using layers at a spatial resolution of 1 km.

2.4. Vegetation sensitivity to climate variability and temporal autocorrelation in EVI
The VSI was calculated at a spatial resolution of 1 km over the time period 2000–2019, using the

methodology developed by Seddon *et al* (2016). This involved modelling the relationship between monthly anomalies in EVI and monthly anomalies in climate variables (evapotranspiration, cloudiness, temperature), together with the EVI anomaly of the previous month for the whole period. The details of the algorithm are described in the supplementary material and in Seddon *et al* (2016). Higher values of VSI indicate greater sensitivity to month-to-month climate variability. As part of the multiple regression approach to estimate VSI, the temporal autocorrelation in the EVI of the previous month is estimated (hereafter temporal autocorrelation in EVI (EVI_{t-1})). This represents the contribution of the previous month's state to the anomalies in the EVI. Higher values of EVI_{t-1} indicate greater association of past EVI with current EVI anomalies.

2.5. Comparison of all VSI data across biomes
Biome maps from The Vegetation Map (SANBI 2018), the Atlas of Namibia Project (Directorate of Environmental Affairs Ministry of Environment and Tourism 2002), and World Wildlife Fund (WWF) Ecoregions maps (Olson *et al* 2001) were merged and rasterised using the 'raster' package in R (Hijmans 2012). Mean and median VSI and EVI_{t-1} values were calculated for each biome to facilitate comparison of their central tendencies. One-way analysis of variance (ANOVA) and Tukey honestly significant difference (HSD) tests (with a 95% confidence interval) were performed on a 10% random subsample of pixels for each biome to compare whether VSI and EVI_{t-1} differed across biomes.

2.6. Statistically exploring the relationship between VSI and EVI_{t-1} vs root depth

We tested the relationship between VSI and EVI_{t-1} (response variables) vs root depth, biome and growth form using generalised least squares models. This approach was used to account for heteroskedasticity and correlation between residuals. VSI and EVI_{t-1} values were extracted for each of the 1 km pixels where root depth data were present ($n = 100$ in total).

These relationships can be summarised by the following functions:

$$
\begin{aligned}
\text{VSI} = {}& \alpha_{\text{VSI}} + \beta_{\log(\text{root depth})-\text{VSI}} \times \log(\text{root depth}) \\
& + \beta_{\text{biome}-\text{VSI}} \times \text{Biome} + \beta_{\text{growth form}-\text{VSI}} \\
& \times \text{growth form} + \varepsilon
\end{aligned}
$$

$$
\begin{aligned}
\text{EVI}_{t-1} = {}& \alpha_{\text{EVI}_{t-1}} + \beta_{\log(\text{root depth})-\text{EVI}_{t-1}} \\
& \times \log(\text{root depth}) + \beta_{\text{biome}-\text{EVI}_{t-1}} \\
& \times \text{Biome} + \beta_{\text{growth form}-\text{EVI}_{t-1}} \\
& \times \text{growth form} + \varepsilon
\end{aligned}
$$

where α is the estimated random intercept and β is the estimated regression coefficient associated with each of the explanatory variables, given by the subscript. The α and β parameters are estimated separately in two models, one with VSI and the other with EVI_{t-1} as the response variable, again indicated by the subscripts. The error terms are captured by ε, and all model assumptions were verified using diagnostic plots (supplementary figure S1). Models were run both with the full set of root depth data as well as without an extreme value of root depth found to be deeper than modelled depth to groundwater (section 2.7) to ensure the results were robust to uncertainty in the root depth measurements (supplementary table S3).

This analysis assumes that the rooting depth value is representative of the 1 km^2 pixel in which it was collected. This assumption is supported by the fact that rooting depths were collected from dominant vegetation in the landscape (Higgins *et al* 1987, Obakeng 2007, Zhou *et al* 2020). Of the 100 root depths collected, 21% were outside the time period of our remote sensing data (2000–2019). We chose to retain these points in our analysis as we assume that areas where vegetation had deep roots in the earlier time periods of collected data (pre-2000) are likely to have deep roots now.

2.7. Depth to groundwater and root zone plant-available water holding capacity

To determine whether access to deeper groundwater (beyond shallow rooting zone water) via deeper roots was a potential mechanism underlying the relationships found between root depth and VSI, we regressed root depth against modelled groundwater depth (at 5 km resolution) (MacDonald *et al* 2012)

and root zone plant-available water holding capacity (at 1 km resolution) (Leenaars *et al* 2018) (see supplementary material for further details). Depth to groundwater used in this analysis is defined as the maximum depth from the ground surface to the phreatic water table. Further, VSI was regressed against these metrics in order to compare published climate responses obtained using hydrological modelling to connect climate drivers to belowground water resources (Gao *et al* 2014, de Boer-euser *et al* 2019, Bouaziz *et al* 2022) against our approach of connecting aboveground climate-mediated vegetation responses to belowground traits.

2.8. Savanna biome root depth prediction

To further explore the biome with the most comprehensive root depth data, we used a linear model to test the relationship between VSI and root depth in the Savanna biome ($n = 63$):

$$
\begin{aligned}
\text{VSI}_{\text{savanna}} = {}& \alpha_{\text{VSI}_{(\text{savanna})}} + \beta_{\log(\text{root depth})-\text{VSI}_{(\text{savanna})}} \\
& \times \log(\text{root depth})_{\text{savanna}} + \varepsilon.
\end{aligned}
$$

A further motivation for this step was that if the above regression on VSI-only works, it has the potential to produce a spatially comprehensive map of predicted root depth over the savanna for the region. We cross-evaluated the model to ensure its generalisability by randomly partitioning the data into a training and a test set in a 70:30 ratio over 1000 iterations. After checking for model robustness, the relationship was then inverted, treating root depth as the response variable, which enabled us to predict root depth using the spatially continuous map of VSI. We ran the model and the root prediction map for trees only, as most of the data (94%) was for trees. To ensure that there was no bias in the prediction for high or low root depth values, we compared observed vs predicted values of tree root depth for the region. To assess the applicability of our model for the range of tree cover of this study region, we also compared tree cover density of the study region vs our empirical root data using MOD44B version 6 vegetation continuous fields yearly product (DiMiceli *et al* 2015), where we used the per cent tree cover in each pixel in 2020. The final spatial prediction of root depth was limited to pixels whose VSI values were within the range of values in pixels covering our calibration root depth observation dataset.

3. Results

3.1. Vegetation sensitivity varies across biomes

Vegetation sensitivity differed across southern Africa (figure 2(a)) and significantly among biomes (supplementary figure S2(a), table S4) ($F = 14\,033$, $\text{Df} = 11$, $p < 2 \times 10^{-16}$; one-way ANOVA): all biomes were significantly different in their mean VSI values from
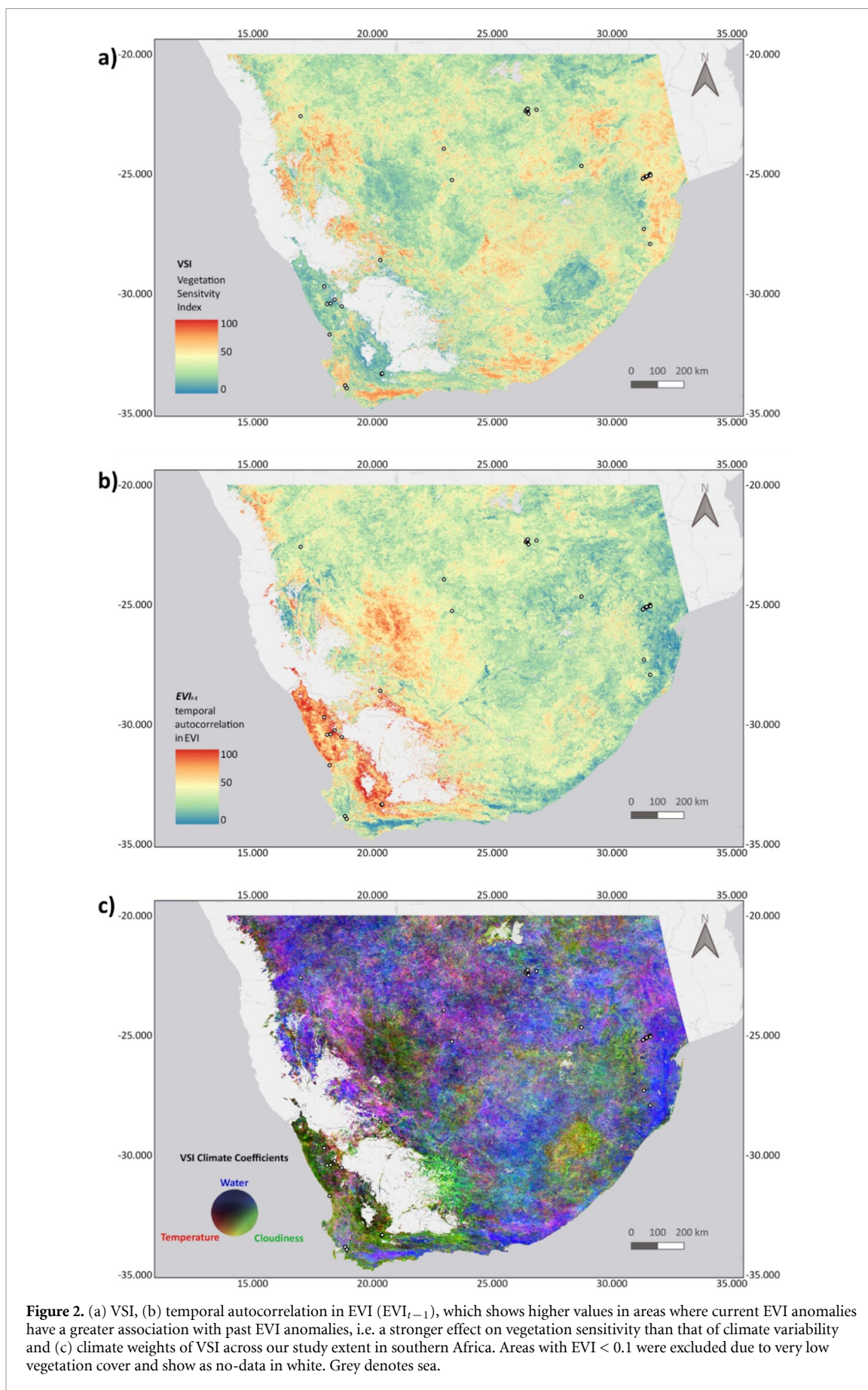
Figure 2. (a) VSI, (b) temporal autocorrelation in EVI (EVI$_{t-1}$), which shows higher values in areas where current EVI anomalies have a greater association with past EVI anomalies, i.e. a stronger effect on vegetation sensitivity than that of climate variability and (c) climate weights of VSI across our study extent in southern Africa. Areas with EVI < 0.1 were excluded due to very low vegetation cover and show as no-data in white. Grey denotes sea.

Table 1. Generalised least squares model parameter estimates, standard error, confidence interval, test statistic (*t*-value), *p*-value (bold values indicate significance at p<0.05) and R^2 for VSI and EVI_{t-1} models. Although growth form alone is deemed non-significant, it is nonetheless required in the best model.

Parameters	VSI					EVI_{t-1}				
	Parameter estimates	Std. error	CI	Test statistic	*p*	Parameter estimates	Std. error	CI	Test statistic	*p*
α (intercept)	21.87	3.75	14.52–29.22	5.83	**<0.001**	70.34	8.38	53.91–86.77	8.39	**<0.001**
$\beta_{\log(\text{root depth})}$	−2.45	0.45	−3.33−−1.57	−5.45	**<0.001**	2.93	1.00	0.97–4.90	2.92	**0.004**
β_{biome} [Savanna]	18.09	4.26	9.73–26.45	4.24	**<0.001**	−73.83	9.53	−92.51−−55.16	−7.75	**<0.001**
β_{biome} [Fynbos]	7.62	3.01	1.71–13.52	2.53	**0.013**	−37.86	6.73	−51.06−−24.66	−5.62	**<0.001**
β_{biome} [Nama-Karoo]	22.13	4.41	13.50–30.77	5.02	**<0.001**	−77.90	9.85	−97.21−−58.60	−7.91	**<0.001**
β_{biome} [Grassland]	13.62	7.37	−0.83–28.06	1.85	0.068	−63.55	16.47	−95.83−−31.27	−3.86	**<0.001**
β_{biome} [Azonal Vegetation]	11.91	4.95	2.21–21.61	2.41	**0.018**	−47.87	11.06	−69.55−−26.18	−4.33	**<0.001**
$\beta_{\text{growth form}}$ [herb]	−1.08	5.16	−11.18–9.03	−0.21	0.835	−6.93	11.52	−29.51–15.66	−0.60	0.549
$\beta_{\text{growth form}}$ [shrub]	4.11	3.29	−2.34–10.55	1.25	0.215	8.58	7.35	−5.82–22.98	1.17	0.246
$\beta_{\text{growth form}}$ [tree]	7.56	4.45	−1.16–16.29	1.70	0.093	11.98	9.95	−7.51–31.48	1.21	0.231
Observations			100					100		
R^2			0.607					0.665		

one another (except Desert, which was not significantly different from Nama Karoo nor from Indian Ocean Coastal Belt) (supplementary figure S2(a) for results from Tukey's HSD test for multiple comparisons). Notably, the Succulent Karoo biome showed the lowest sensitivity.

Month-to-month temporal autocorrelation in EVI (EVI_{t-1}) also differed significantly among biomes (figure 2(b), see supplementary figure S2(b)) ($F = 105\,588$, Df = 10, $p < 2 \times 10^{-16}$; one-way ANOVA): all biomes were significantly different from one another in their EVI_{t-1} (supplementary figure S2(b) for results from Tukey's HSD test for multiple comparisons) and showed even more inter-biome contrast than with VSI, with the drier biomes (Succulent Karoo, Desert, Fynbos and Nama Karoo) having greater EVI_{t-1} values, thus showing a higher role of lagged effects on EVI anomalies and a lower response to the climate conditions of the concurrent month than wetter biomes (e.g. Indian Ocean Coastal Belt, Forests and Albany Thicket biomes). Water availability is the key climate driver of the VSI patterns in most of our study area, except in parts of the Grassland biome (including the Lesotho Highlands), which show temperature and cloudiness as key explanatory variables (figure 2(c)). The drier portions of the Savanna, Succulent Karoo, Fynbos, Nama Karoo and Desert biomes (with enough vegetation cover to produce VSI values—see supplementary material) show a mixed signal, with no overall dominant climate variable driving VSI (figure 2(c)).

3.2. Vegetation sensitivity vs root depth
Results from the generalised least squares model indicate that in the best model (table 1) root depth, in combination with biome and growth form, significantly explain vegetation sensitivity across southern Africa ($R^2 = 0.607$, $p < 0.001$). This model shows a negative linear relationship between VSI and root depth (i.e. deeper roots are found in areas with

lower climate sensitivity) (VSI range 9.43–43.85). Models using other variable combinations show higher Akaike information criterion (AIC) than the model shown in table 1 (see model comparisons in supplementary table S5). Results also indicate a positive linear relationship between root depth and temporal autocorrelation in EVI (EVI_{t-1}) (i.e. deeper roots are associated with areas with higher past EVI and less associated with month-to-month climate variability) ($R^2 = 0.665$, $p < 0.001$) (table 1 and see model comparisons supplementary table S6) (EVI_{t-1} range 8.96–97.02). Additional models run with the criterion of excluding rooting depth outliers that are greater than modelled depth to groundwater have negligible differences and thus indicate robustness of original models that include extreme rooting depths (see supplementary material table S3). Graphical representation of linear relationships between VSI and EVI_{t-1} and root depth individually for biomes and growth forms reflect the relationships identified by this model and are presented in supplementary figures S3 and S4.

3.3. Depth to groundwater and root zone plant-available water holding capacity
Results indicate that as the depth to groundwater increases, root depth increases (figures 3(a) and S5(a)) and vegetation sensitivity to climate variability declines (figure S6(a)). Further, as the water holding capacity of the rooting zone for plants increases, root depth declines (figures 3(b) and S5(b)) and vegetation sensitivity to climate variability increases (figure S6(b)). These results are mostly driven by the very consistent relationships found in the savanna.

3.4. Root depth in savanna
In the Savanna biome of southern Africa, tree root depth alone can significantly explain VSI (and EVI_{t-1}) ($R^2 = 0.418$, $p < 0.001$; table 2). Cross-evaluation of our model indicates consistent correlation statistics (table S7). Further, the data used for
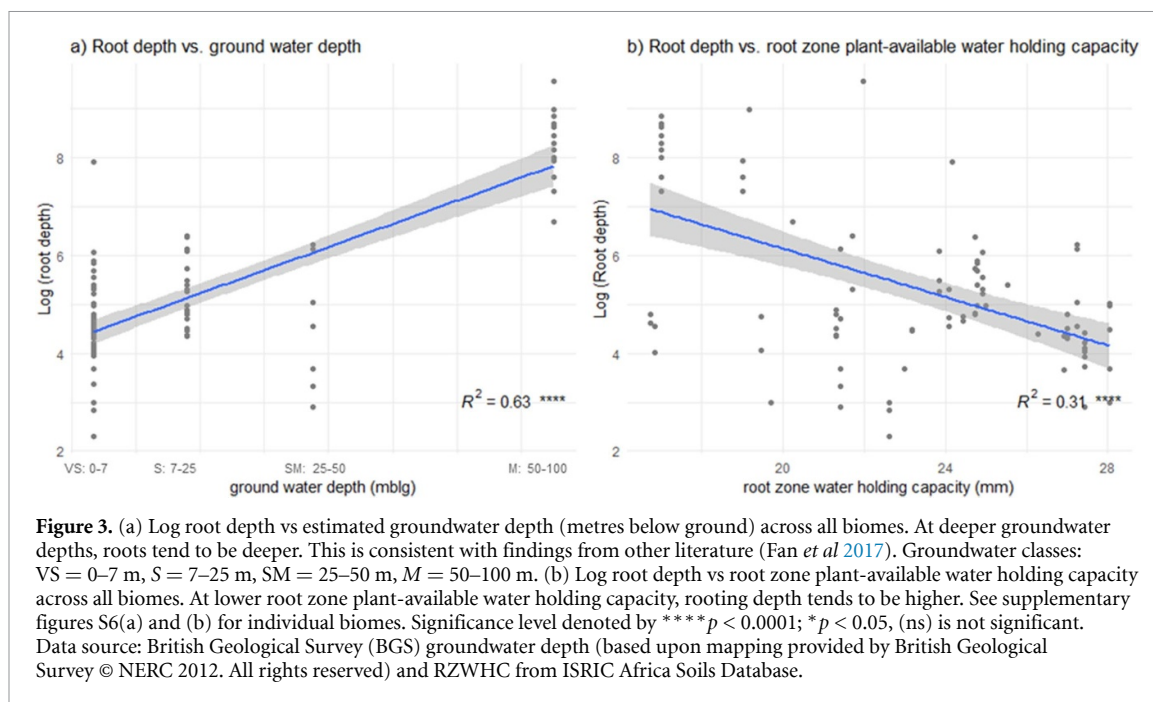
Figure 3. (a) Log root depth vs estimated groundwater depth (metres below ground) across all biomes. At deeper groundwater depths, roots tend to be deeper. This is consistent with findings from other literature (Fan *et al* 2017). Groundwater classes: VS = 0–7 m, S = 7–25 m, SM = 25–50 m, M = 50–100 m. (b) Log root depth vs root zone plant-available water holding capacity across all biomes. At lower root zone plant-available water holding capacity, rooting depth tends to be higher. See supplementary figures S6(a) and (b) for individual biomes. Significance level denoted by $****p < 0.0001$; $*p < 0.05$, (ns) is not significant. Data source: British Geological Survey (BGS) groundwater depth (based upon mapping provided by British Geological Survey © NERC 2012. All rights reserved) and RZWHC from ISRIC Africa Soils Database.

Table 2. Generalised linear model parameter estimates, standard error, confidence interval, test statistic (*t*-value), *p*-value (bold values indicates significance at p<0.05) and R^2 for VSI model for the Savanna biome.

Parameters	VSI$_{savanna}$				
	Parameter estimates	Std. error	CI	Test statistic	*p*
α (intercept)	48.43	2.41	$43.71 - 53.15$	20.11	**<0.001**
$\beta_{\log(\text{root depth})}$	-2.60	0.39	$-3.37 - -1.83$	-6.61	**<0.001**
Observations			63		
R^2			0.418		

the model span the range of tree coverage of the entire biome extent (figure S7), suggesting that this model can be used at a biome level since it will only predict tree root depths for areas where tree density is within the range of the calibration dataset. The spatial prediction of tree root depth in the Savanna biome (figure 4) indicates the shallowest roots (<0.7 m) in the eastern extent (e.g. Kruger National Park, SA) and deeper roots in the southern-central (e.g. Southern Kalahari Desert) and across the northern extents of the mapped region, where roots range between 2–5 m, and up to 15 m. We restricted our prediction using the model to a range of VSI values fully encompassed by that of the calibration dataset: within this range of VSI values, the model predicted extreme root depths of up to 67 m.

4. Discussion

4.1. Vegetation sensitivity and temporal autocorrelation in EVI varies across biomes

Biomes in the study region show significantly different vegetation sensitivity to climate variability (VSI) and temporal autocorrelation in EVI (EVI$_{t-1}$) from one another, reflecting the varying ability of species, plant functional types and ecosystems to

respond to climate variability in drylands. In the four driest biomes in the study region—Desert, Succulent Karoo, Nama Karoo and Fynbos (10–80, 20–290, 100–520 and 200–800 mm total annual precipitation respectively, supplementary table S1), we observe the highest influence of lagged effects (EVI$_{t-1}$) and thus a weaker relation of EVI anomalies to month-to-month climate variability. In the wetter, more forested biomes, we observe the lowest influence of the temporal autocorrelation in EVI and the highest influence of month-to-month climate variability. The best explanation for the lack of association between EVI anomalies and month-to-month climate variability is that vegetation in the driest biomes tends to have traits that allow for buffering short-term (monthly) climate variability (e.g. drought and high evaporative demands), through facilitating access to groundwater reserves.

4.2. Vegetation sensitivity can be explained by root depth

Our model results provide evidence in favour of the hypothesis that the observed variation in remotely-sensed aboveground sensitivity to climate variability can, to a significant extent, be explained by root depth (hypothesis i) in water-limited environments. Within
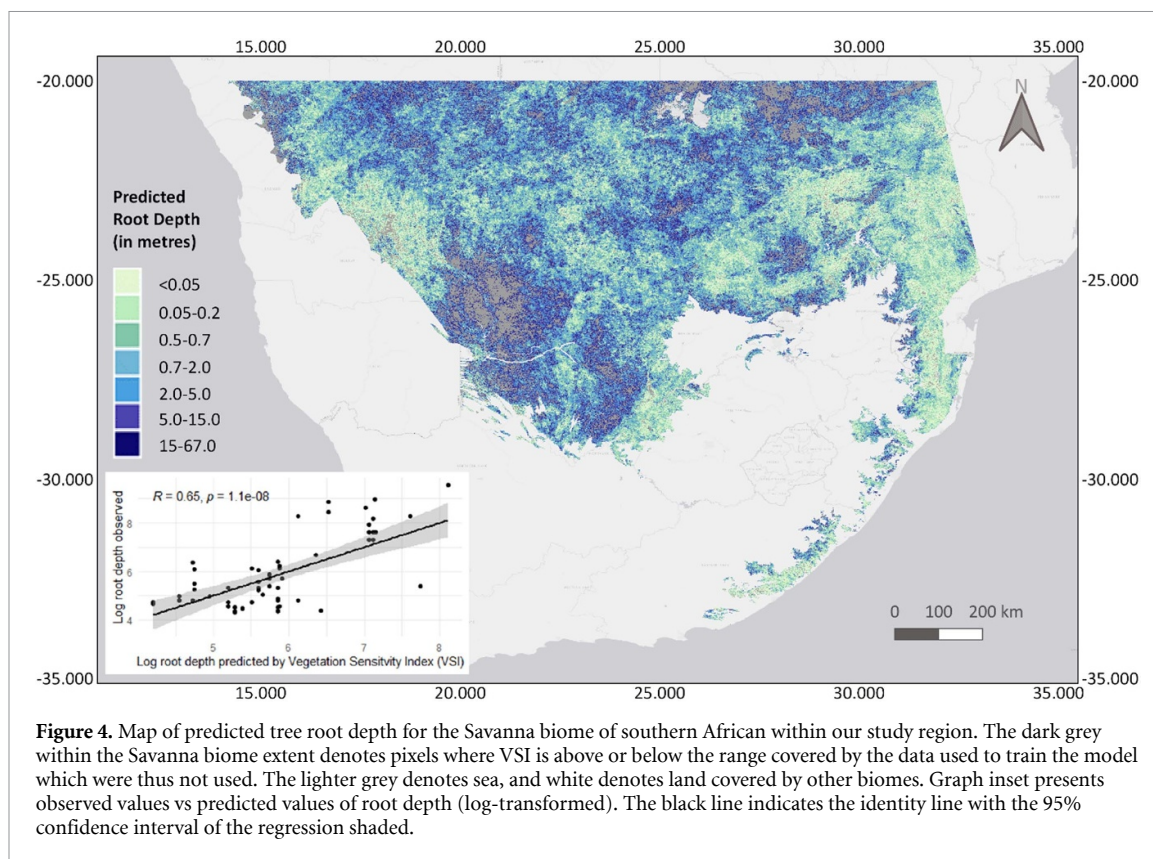
Figure 4. Map of predicted tree root depth for the Savanna biome of southern African within our study region. The dark grey within the Savanna biome extent denotes pixels where VSI is above or below the range covered by the data used to train the model which were thus not used. The lighter grey denotes sea, and white denotes land covered by other biomes. Graph inset presents observed values vs predicted values of root depth (log-transformed). The black line indicates the identity line with the 95% confidence interval of the regression shaded.

the limited empirical root depth data available, this hypothesis is shown to be consistent across the studied biomes and growth forms of southern Africa. This finding suggests that plants with deeper roots might be able to tap into deeper water resources, reducing sensitivity to month-to-month climate variability. This is also supported by the association between higher temporal autocorrelation in EVI (EVI_{t-1}) and deeper roots where deep rooted plants are likely more dependent on groundwater and less responsive to daily variability in surface water availability (hypothesis ii). Our findings are very much in line with those from a study in the Kgalagadi Transfrontier Park in Botswana where it was observed that *Vachellia erioloba* and *Vachellia haematoxylon*, (previously *Acacia*, known to root very deeply), did not show significant canopy dieback in times of drought even though they are facultatively deciduous species (Shadwell and February 2017). The authors suggested this is because these species could continue to obtain water for photosynthesis by tapping deeper water resources. The regions known for these deep-rooted *Vachellia* species coincide with the areas in our study with lower vegetation sensitivity and the deepest roots in our dataset (e.g. *V. erioloba* and *Senegalia flecki* in the Botswanan Kalahari; Obakeng 2007). This link is worth exploring, especially considering research demonstrated by Stevens *et al* (2016) in semi-arid South African Savannas, where deciduousness has water cues as opposed to the globally more common temperature and light cues.

Relationships between vegetation sensitivity and root depth display the same trends across the biomes with sufficient data (i.e. Savanna, Fynbos and Succulent Karoo, figures S3(a) and (b)), but the range of sensitivity values vary. This suggests that while similar plant rooting strategies exist, biome and growth form may also play an important role in the way this is then manifested in terms of response, in agreement with our hypothesis iii. The best model for this relationship indicates that growth form does not statistically contribute to the relationship, however the overall model does improve with its inclusion. This variable is therefore an ecologically informed inclusion in the model. It should also be noted that herbaceous and graminoid growth forms require further study as our results for these growth forms individually were inconclusive due to limited data.

For the individual Savanna tree model, the strong relationship between root depth and the aboveground response to both month-to-month climate variability and previous EVI (VSI and EVI_{t-1}) indicates that root depth is likely to play a key role in buffering sensitivity to future climate change. It is therefore important to understand which regions have deep roots that offer this enhanced resistance to climatic variability, and which ones may be more vulnerable to short-term climate anomalies. The ability to predict root depth as we have shown in the Savanna biome of southern Africa (figure 4) represents a step forward in this direction and could inform future natural resource management strategies of

groundwater reserve management and conservation strategies under changing climates. Our model predicted root depths of up to 67 m in Savanna regions that correspond to the dry limits of the study extent including the Kalahari Desert (figure 4), where there is likely very low vegetation productivity. The trees that do grow in these regions represent a priority for field validations and for the study of the mechanisms of surviving drier limits of this biome, including tree access to deep water resources via very deep roots.

The environmental correlates associated with the VSI data (figure 2(c)) predictably indicate that across most of southern Africa the primary driver of climate sensitivity is water availability. However, areas with lower sensitivity, which correspond to the driest biomes (e.g. Desert, Succulent Karoo, Fynbos and Nama Karoo), do not indicate sensitivity to current water availability as defined in the VSI (Seddon *et al* 2016) (figure 2(c)) and show a mixed signal with no overall dominant variable driving VSI. This is likely due to underlying drought adaptations, such as deeper roots shown in this study, but may also include succulent water storage in the Desert, Succulent and Nama Karoo and more efficient water use in the Fynbos (Skelton 2014, Skelton *et al* 2015) through isohydry for example (West *et al* 2012).

The positive correlation between root depth and depth to groundwater (figures 3(a) and S5(a)) agrees with global trends (Fan *et al* 2017). The negative relationship between root depth and root zone water holding capacity (figures 3(b) and S5(b)) is in line with observed effective rooting depth in temperate biomes (see Speich *et al* (2018), who also find nonconformity of Mediterranean ecosystems which could relate to the patterns we observe in Fynbos (figure S5)) and offers another line of evidence that deeper and shallower rooted plants differ greatly in where they are accessing water from. Both confirm our hypothesis iv. These relationships, taken alongside the negative relationship between VSI and groundwater depth and the positive relationship between VSI and root zone water holding capacity (figures S6(a) and (b)), support the hypothesis that plants with deeper roots that can access deeper groundwater resources (beyond the shallower rootable depth (Leenaars *et al* 2018)) to cope with drier periods, are less sensitive to climate variability. Our findings align with previous work in semiarid regions of California showing that groundwater dependent vegetation is unaffected by periods of lower rainfall (Elmore *et al* 2003). Relatedly, previous studies also suggest that precipitation reliant vegetation e.g. non-native cheat grass in the Great Basin, USA, shows higher variability than native shrubs and grasses that typically have deeper roots and depend on groundwater (Bradley and Mustard 2005).

Due to the difficulties in field collection, root depth data in this study are limited in size and spread. Furthermore, some of the available data are pre-2000

so they may not fully represent current traits, for e.g. if non-native species have invaded an area. To deal with this as far as possible, we checked the validity of these data by consulting original literature and correlating root depth against modelled groundwater depth data. These checks supported our findings and led us to conclude that the root depth data are reliable and representative of the vegetation in their associated remote sensing pixels.

4.3. Implications

The results of our study hold important implications for the understanding of vegetation resistance and eventual resilience to current and future climate change. Applications of this knowledge may prove key for dryland biodiversity conservation under future climate change by providing information about which biomes, growth forms, belowground trait strategies and indeed species may be more vulnerable in a drier future, as determined by the ability to access groundwater resources with deeper roots. This knowledge can further inform conservation management strategies under climate change, where for example, restoration of dry regions may select for species that have traits such as the ability to root deeply, to improve the future adaptability of these systems.

These applications can be extended to agricultural systems in Africa, where along with aridification, irrigation of crops is very limited. Our findings support calls for a shifted focus in drylands to crops with resilient traits (Satori *et al* 2021), such as enhanced root investment, which preliminary findings suggest could be favoured under future climates (Manners *et al* 2021). Additional benefits of this approach could exist for crops where yield is gained from belowground plant parts, which might be less affected by short-term drought than aboveground plant parts.

In those biomes that do not have species that have evolved deeper roots as an adaptation to drier periods or do not have the ability to plastically alter root depth (or other traits), plants may not be able to tolerate future drier climatic conditions. This could result in mass plant mortality during drier times or drought periods, and/or gradual shifts in species compositions where some species can tolerate drier conditions and will replace those that cannot. This will also in part depend on the rate of groundwater reduction, and whether this will exceed potential root growth (Naumburg *et al* 2005).

In those biomes already using deeper roots to deal with water stress, inevitable decline in groundwater resources due to climate change and human extraction (Liu 2011, Mamuye and Kebebewu 2018, Chiloane *et al* 2021) may present a challenge to these plants' survival. Previous studies have shown that in areas with groundwater extraction, groundwater dependent plants had a reduced capacity to cope with drought than those where groundwater extraction is

not present (Stromberg *et al* 1996, Elmore *et al* 2003, 2006). Groundwater pumping can thus switch a system from one buffered from drought to being sensitive to drought (Elmore *et al* 2003). Related to this, deeper-rooted species have been suggested to play a key role in maintaining groundwater resources themselves (e.g. facilitating surface water penetration to deeper soils or redistribution of water in soils via hydraulic lift) (le Maitre *et al* 1999). If these species are no longer able to survive in drier times due to groundwater decline, and are subsequently lost to these systems, groundwater reserves may be impacted and consequently affect ecosystem functioning and services through a decline in water provision. This feedback is an unwelcome possibility for drylands such as those in southern Africa, where ecosystems and human livelihoods are inextricably linked to water availability and where severe water shortages are predicted for the future (Davis and Vincent 2017).

Our work thus highlights the ecological importance of the maintenance and protection of groundwater resources, particularly across the worlds' drylands. The recent droughts witnessed in the Western Cape of South Africa (2015–2018; (Naik and Abiodun 2019)) saw increased extraction of groundwater through existing and newly sunk household level boreholes (Ziervogel *et al* 2019). More frequent and severe droughts, such as this, could fundamentally change groundwater reserves which are already declining due to extraction by invasive plant species in this region (le Maitre *et al* 2019).

4.4. Future directions

Although great progress has been made in the field of root ecology with the collation of existing root data and the ability to use remotely-derived data to predict root depth, as we have shown for the Savanna biome, and is shown in other studies (Yang *et al* 2016, Fan *et al* 2017, Jiang *et al* 2020, Stocker *et al* 2021), we still require more efforts in field-based root data collection. We still lack comprehensive spatial, temporal, and taxonomical coverage, including the relative contributions of intraspecific variation and trait plasticity in response to environmental changes. The lack of data limits our ability to quantify plastic responses and track changes in root depth over time. Our study assumed roots in earlier periods (pre-2000) have similar root depths to the more recent past (2000–2020). However, future studies will benefit from investigating the potentially dynamic response of root traits over time as the rate of climatic changes accelerates. Field studies are key and existing data cannot be scaled up using species means linked to occurrence data (supplementary figure S8) because it is likely that intraspecific differences modulated by local climate factors cannot be ignored (e.g. topography-related water gradients; Kühn *et al* 2022, and Fan *et al* 2017). Systematically

designed trait collection field campaigns (accounting for spatial spread, inclusion along topography, intraspecies variability) are required, and in the case of southern Africa, these should focus on under-sampled, highly biodiverse, and potentially vulnerable biomes (e.g. Desert, Fynbos). This would allow for the models in our study to be applied more widely, and for an explicit mechanistic understanding of the processes involved in the relationships we report in this study to be gained.

5. Conclusions

This study demonstrates the utility of explicitly linking strategically collected field trait data, albeit limited in size and spread, with spatially continuous remote sensing data to observe and predict environmental patterns and responses to climatic changes. Through this approach, we observe that belowground traits are reflected in aboveground vegetation signals. Specifically, we show that root depth is a key trait determining vegetation sensitivity to climate variability in southern Africa, with the proposed underlying mechanism being that deeper roots enhance access to deeper water resources that remain available in periods of drought or reduced surface water availability. Our findings support the hypothesis that deeper roots play (and will likely do so increasingly) an important role in the resistance of vegetation to climate change in southern Africa and potentially across drylands globally, which are set to become warmer and drier.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

Author contributions

N K and M M-F conceptualised the research and designed the approach with comments from all authors. N K and M S collected, processed, and analysed the data with assistance from M M-F and C T. N K wrote the first draft of the manuscript with significant contributions from all authors (M M-F, M S, C T and K J W).

ORCID iDs

Nicola Kühn ● https://orcid.org/0000-0001-8704-3115

Marcus P Spiegel ● https://orcid.org/0000-0001-5879-5465

Carolina Tovar ● https://orcid.org/0000-0002-8256-9174

Katherine J Willis ● https://orcid.org/0000-0002-6763-2489

Marc Macias-Fauria ● https://orcid.org/0000-0002-8438-2223

References

Bouaziz L J E, Aalbers E E, Weerts A H, Hegnauer M, Buiteveld H, Lammersen R, Stam J, Sprokkereef E, Savenije H H G and Hrachowitz M 2022 Ecosystem adaptation to climate change: the sensitivity of hydrological predictions to time-dynamic model parameters *Hydrol. Earth Syst. Sci.* **26** 1295–318

Bradley B A and Mustard J F 2005 Identifying land cover variability distinct from land cover change: cheatgrass in the great basin *Remote Sens. Environ.* **94** 204–13

Chiloane C, Dube T and Shoko C 2021 Impacts of groundwater and climate variability on terrestrial groundwater dependent ecosystems: a review of geospatial assessment approaches and challenges and possible future research directions *Geocarto Int.* **37** 1–25

Davis C and Vincent K 2017 *Climate Risk and Vulnerability: A Handbook for Southern Africa* 2nd edn (Pretoria: CSIR)

de Boer-euser T, Palalane J, Savenije H and Juízo D 2019 How climate variations are reflected in root zone storage capacities *Phys. Chem. Earth* **112** 83–90

Didan K 2015 Mod13a3 MODIS/Terra vegetation indices monthly L3 global 1km sin grid V006 (https://doi.org/10.5067/MODIS/MOD13A3.006)

DiMiceli C, Carroll M, Sohlberg R, Kim D, Kelly M and Townshend J 2015 MOD44B MODIS/Terra vegetation continuous fields yearly L3 global 250m SIN grid V006 [data set] *NASA EOSDIS Land Processes DAAC* (https://doi.org/10.5067/MODIS/MOD44B.006)

Directorate of Environmental Affairs Ministry of Environment and Tourism 2002 Atlas of Namibia Project (available at: http://209.88.21.36/Atlas/Atlas_web.htm)

Eamus D, Zolfaghar S, Villalobos-Vega R, Cleverly J and Huete A 2015 Groundwater-dependent ecosystems: recent insights from satellite and field-based studies *Hydrol. Earth Syst. Sci.* **19** 4229–56

Elmore A J, Manning S J, Mustard J F and Craine J M 2006 Decline in alkali meadow vegetation cover in California: the effects of groundwater extraction and drought *J. Appl. Ecol.* **43** 770–9

Elmore A J, Mustard J F and Manning S J 2003 Regional patterns of plant community response to changes in water: Owens Valley, California *Ecol. Appl.* **13** 443–60

Enquist B J, Condit R, Peet R K, Schildhauer M and Thiers B 2009 The botanical information and ecology network (BIEN): cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity The IPlant Collaborative (https://doi.org/10.7287/peerj.preprints.2615v2)

Fan Y, Miguez-Macho G, Jobbágy E G, Jackson R B and Otero-Casal C 2017 Hydrologic regulation of plant rooting depth *Proc. Natl Acad. Sci.* **114** 10572–7

Fort F, Volaire F, Guilioni L, Barkaoui K, Navas M L and Roumet C 2017 Root traits are related to plant water-use among rangeland Mediterranean species *Funct. Ecol.* **31** 1700–9

Gao H, Hrachowitz M, Schymanski S J, Fenicia F, Sriwongsitanon N and Savenije H H G 2014 Climate controls how ecosystems size the root zone storage capacity at catchment scale *Geophys. Res. Lett.* **41** 7916–23

Gou S and Miller G 2014 A groundwater-soil-plant-atmosphere continuum approach for modelling water stress, uptake, and hydraulic redistribution in phreatophytic vegetation *Ecohydrology* **7** 1029–41

Guerrero-Ramírez N R *et al* 2021 Global root traits (GRooT) database *Glob. Ecol. Biogeogr.* **30** 25–37

Higgins K B, Lamb A J and van Wilgen B W 1987 Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley, south-western Cape Province *South Afr. J. Bot.* **53** 249–57

Hijmans R J 2012 Introduction to the 'raster' package (version 2.0–05) (https://doi.org/10.1073/pnas.1108616108/-/DCSupplemental.www.pnas.org/cgi)

Iversen C M *et al* 2017 A global fine-root ecology database to address below-ground challenges in plant ecology *New Phytol.* **215** 15–26

Jiang P, Wang H, Meinzer F C, Xiaoli F, Kou L and Dai X 2020 Linking reliance on deep soil water to resource economy strategies and abundance among coexisting understorey shrub species in subtropical pine plantations *New Phytol.* **225** 222–3

Karger D N 2018 *Data from: Climatologies at High Resolution for the Earth's Land Surface Areas* (Dryad) (https://doi.org/10.5061/dryad.kd1d4)

Karger D N, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza R W, Zimmermann N E, Linder H P and Kessler M 2017 Climatologies at high resolution for the earth's land surface areas *Sci. Data* **4** 1–20

Kattge J *et al* 2011 TRY—a global database of plant traits *Glob. Change Biol.* **17** 2905–35

Kattge J *et al* 2020 TRY plant trait database—enhanced coverage and open access *Glob. Change Biol.* **26** 119–88

Kühn N, Tovar C, Carretero J, Vandvik V, Enquist B J and Willis K J 2021 Globally important plant functional traits for coping with climate change *Front. Biogeogr.* **13** e53774

Kühn N 2022 Vegetation response to climate change: a functional traits-based approach *PhD Thesis* University of Oxford (available at: https://ora.ox.ac.uk/objects/uuid:37a3c817-051c-479f-a301-c4cad54a8589)

Laliberté E 2017 Below-ground frontiers in trait-based plant ecology *New Phytol.* **213** 1597–603

Laughlin D C *et al* 2021 Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs *Nat. Ecol. Evol.* **5** 1123–34

le Maitre D C, Scott D F and Colvin C 1999 A review of information on interactions between vegetation and groundwater *Water SA* **25** 137–52 (available at: http://hdl.handle.net/10204/524)

le Maitre D, Görgens A, Howard G and Walker N 2019 Impacts of alien plant invasions on water resources and yields from the Western Cape Water Supply System (WCWSS) *Water SA* **45** 568–79

Leenaars J G B, Claessens L, Heuvelink G B M, Hengl T, Ruiperez González M, van Bussel L G J, Guilpart N, Yang H and Cassman K G 2018 Mapping rootable depth and root zone plant-available water holding capacity of the soil of sub-Saharan Africa *Geoderma* **324** 18–36

Liu H H 2011 Impact of climate change on groundwater recharge in dry areas: an ecohydrology approach *J. Hydrol.* **407** 175–83

Liu L, Zhang Y, Shuyao W, Shuangcheng L and Qin D 2018 Water memory effects and their impacts on global vegetation productivity and resilience *Sci. Rep.* **8** 1–9

Liu Y, Konings A G, Kennedy D and Gentine P 2021 Global coordination in plant physiological and rooting strategies in response to water stress *Glob. Biogeochem. Cycles* **35** 1–23

MacDonald A M, Bonsor H C, Dochartaigh B É Ó and Taylor R G 2012 Quantitative maps of groundwater resources in Africa *Environ. Res. Lett.* **7** 024009

Mamuye M and Kebebewu Z 2018 Review on impacts of climate change on watershed hydrology *Environ. Earth Sci.* **8** 91–99

(available at: https://core.ac.uk/download/pdf/234
665093.pdf)

Manners R, Vandamme E, Adewopo J, Thornton P, Friedmann M,
Carpentier S, Senam Ezui K and Thiele G 2021 Suitability of
root, tuber, and banana crops in central Africa can be
favoured under future climates *Agric. Syst.*
193 103246

Naik M and Abiodun B J 2019 Projected changes in drought
characteristics over the Western Cape, South Africa
Meteorol. Appl. **27** e1802

Naumburg E, Mata-Gonzalez R, Hunter R G, McLendon T and
Martin D W 2005 Phreatophytic vegetation and
groundwater fluctuations: a review of current research and
application of ecosystem response modeling with an
emphasis on great basin vegetation *Environ. Manage.*
35 726–40

Obakeng O T 2007 Soil moisture dynamics and
evapotranspiration at the fringe of the Botswana Kalahari,
with emphasis on deep rooting vegetation *ITC Dissertation
Number 141* (Vrije Universiteit Amsterdam) (available at:
www.itc.nl/library/papers_2007/phd/obakeng.pdf)

Olson D M *et al* 2001 Terrestrial ecoregions of the world: a new
map of life on earth *Bioscience* **51** 933–8

Running S, Mu Q, Zhao M and Moreno A. 2019 MOD16A2GF
MODIS/Terra net evapotranspiration gap-filled 8-day L4
global 500 m SIN grid V006 (https://doi.org/10.5067/
MODIS/MOD16A2GF.006)

SANBI 2018 The vegetation map of South Africa, Lesotho and
Swaziland version 2018 (South African National Biodiversity
Institute) (available at: http://bgis.sanbi.org/Projects/Detail/
186)

Satori D *et al* 2021 Prioritising crop wild relatives to enhance
agricultural resilience in sub-Saharan Africa under climate
change *Plants People Planet* **4** 1–14

Schenk H J 2005 Mapping the global distribution of deep roots in
relation to climate and soil characteristics *Geoderma*
126 129–40

Schenk H J and Jackson R B 2002 The global biogeography of
roots *Ecol. Monogr.* **72** 311–28

Seddon A W R, Macias-Fauria M, Long P R, Benz D and Willis K J
2016 Sensitivity of global terrestrial ecosystems to climate
variability *Nature* **531** 229–32

Shadwell E and February E 2017 Effects of groundwater
abstraction on two keystone tree species in an arid savanna
national park *PeerJ* **5** e2923

Skelton R P 2014 The role of hydraulic strategies in understanding
the response of fynbos to drought *Thesis* University of Cape
Town (available at: http://hdl.handle.net/11427/13033)

Skelton R P, West A G and Dawson T E 2015 Predicting plant
vulnerability to drought in biodiverse regions using
functional traits *Proc. Natl Acad. Sci.* **112** 5744–9

Speich M J R, Lischke H and Zappa M 2018 Testing an optimality-
based model of rooting zone water storage capacity in
temperate forests *Hydrol. Earth Syst. Sci.* **22** 4097–124

Stevens N, Archibald S A, Nickless A, Swemmer A and Scholes R J
2016 Evidence for facultative deciduousness in
Colophospermum mopane in semi-arid African savannas
Austral Ecol. **41** 87–96

Stocker B D, Tumber-Dávila S J, Konings A G, Anderson M B,
Hain C and Jackson R B 2021 Global distribution of the
rooting zone water storage capacity reflects plant adaptation
to the environment *bioRxiv Preprint* p 460332 (posted
online 17 January 2021)

Stromberg J C, Tiller R and Richter B 1996 Effects of groundwater
decline on riparian vegetation of semiarid regions: the San
Pedro, Arizona *Ecol. Appl.* **6** 113–31

Vermote E and Wolfe R 2020 MOD09GA MODIS/Terra surface
reflectance daily L2G global 1km and 500m SIN grid V006
(https://doi.org/10.5067/MODIS/MOD09GA.006)

Weigelt A 2021 Tansley review: an integrated framework of
plant form and function: the belowground perspective *New
Phytol.* **232** 42–59

West A G, Dawson T E, February E C, Midgley G F, Bond W J and
Aston T L 2012 Diverse functional responses to drought in a
Mediterranean-type shrubland in South Africa *New Phytol.*
195 396–407

Wilson A M and Jetz W 2016 Remotely sensed high-resolution
global cloud dynamics for predicting ecosystem and
biodiversity distributions *PLoS Biol.* **14** e1002415

Yang Y, Donohue R J and McVicar T 2016 Global estimation of
effective plant rooting depth: implications for hydrological
modeling *Water Resour. Res.* **52** 8260–76

Zhou Y, Wigley B J, Case M F, Coetsee C and Staver A C 2020
Rooting depth as a key woody functional trait in savannas
New Phytol. **227** 1350–61

Ziervogel G, Franklin B and Thorson J 2019 Unpacking the Cape
Town drought: lessons learned; report for cities support
programme undertaken by African centre for cities
(available at: www.preventionweb.net/publication/
unpacking-cape-town-drought-lessons-learned)