

Title page: Spatial patterns govern vegetation shifts

Land-cover-specific network reconfiguration and spatial trajectories govern abrupt vegetation regime shifts across global drylands

Yuning Chen, Yu Peng*

College of Life and Environmental Sciences, Minzu University of China, Beijing 100081, China

*Corresponding author: yuupeng@163.com

Abstract

Aim: In drylands, abrupt vegetation changes may signal declining resilience and regime shifts, yet global assessments have largely focused on greenness trends while overlooking the role of spatial organization.

Location: Global.

Time period: 2000 – 2020.

Major taxa studied: Terrestrial vegetations.

Method: Here we analyzed 15,898 1-km² landscape units across global drylands (aridity index < 0.65) using 30-m land cover and NDVI time series. We quantified multidimensional spatial structure via landscape metrics, patch co-occurrence networks, semivariogram-based indicators, and texture features, then examined associations with abrupt NDVI step shifts using PCA, XGBoost, and correlation networks.

Results: Spatial structure consistently resolved into two orthogonal axes: fragmentation–connectivity and configurational complexity/interspersion. Associations were strongly state-dependent: increasing fragmentation and complexity were more consistently linked to negative steps (abrupt browning) than to positive steps (abrupt greening). Positive steps were explained by fewer predictors, dominated by stable contiguity, whereas negative steps involved broader predictors including area proportion and fragmentation trajectories. Regime-dependent rewiring of correlation networks further indicated coordinated spatial breakdown under browning versus constrained reorganization under greening.

Main conclusions: We conclude that dynamic, land-cover-specific spatial structure provides mechanistic and predictive information on abrupt vegetation change beyond static fragmentation or mean greenness. Browning and greening represent distinct modes of spatial reorganization, supporting a shift from static assessments toward trajectory- and network-informed monitoring of dryland vulnerability and resilience.

Keywords: drylands; regime shifts; landscape structure; texture; self-organization; patch networks; spatial trajectories; land-cover types

1. INTRODUCTION

39

40 Abrupt and potentially irreversible ecosystem changes, often described as regime shifts, pose
41 major risks to Earth-system functioning and human well-being (Lenton et al., 2008; Scheffer et al.,
42 2009; Rocha et al., 2018). Such shifts can emerge when gradual external forcing is amplified by
43 nonlinear feedbacks, pushing ecosystems across critical thresholds into alternative states
44 (Armstrong McKay et al., 2022). Explaining the mechanisms that govern ecosystem stability,
45 vulnerability and tipping behaviour has therefore become a central challenge in global-change
46 ecology.

47 Drylands cover more than 40% of the terrestrial surface and are among the biomes most
48 vulnerable to abrupt ecological change because vegetation dynamics are tightly constrained by
49 climate variability, water limitation and land-use pressure (Reynolds et al., 2007; Zhu et al., 2016).
50 Widespread dryland greening and browning have been documented from regional to global scales,
51 but most broad-scale assessments have focused on temporal forcing and mean trends in vegetation
52 indices (Pettorelli et al., 2005; Zhu et al., 2016; Verbesselt et al., 2010). By contrast, the spatial
53 processes that determine whether vegetation change unfolds gradually or shifts abruptly remain
54 much less well understood. This gap limits both mechanistic inference and practical monitoring,
55 because resilience loss may be expressed not only as declining mean vegetation activity, but also
56 as the reorganization of spatial structure within landscapes.

57 A large body of work in landscape ecology has shown that spatial pattern regulates ecological
58 processes, persistence and resilience (With et al., 1997; Fahrig, 2003; Zhou et al., 2017; Wiegand
59 et al., 2021). In drylands, spatial self-organization, patch connectivity and heterogeneity influence
60 runoff redistribution, resource concentration and vegetation – soil feedbacks, thereby stabilizing
61 vegetation cover or, once critical spatial structure is lost, accelerating degradation (D’Odorico et
62 al., 2006; Kéfi et al., 2007; Rietkerk et al., 2004; Berdugo et al., 2017). Spatial vegetation patterns
63 have therefore been proposed as indicators of alternative stable states and incipient desertification
64 (Kéfi et al., 2007; Berdugo et al., 2017). Yet many global analyses still rely on coarse summaries,
65 such as mean NDVI trends or generic fragmentation indices, that can obscure land-cover-specific
66 dynamics and the temporal character of spatial reconfiguration (Li & Wu, 2004; Fischer &
67 Lindenmayer, 2006; Riitters et al., 2000). This limitation is increasingly consequential in light of
68 mounting evidence for abrupt vegetation shifts across drylands and for biome-dependent
69 relationships between fragmentation and resilience (Berdugo et al., 2022; Su et al., 2025).

70 Two conceptual gaps motivate this study. First, spatial structure is inherently multidimensional,
71 encompassing configuration and connectivity, heterogeneity, texture and network topology
72 (Forman & Godron, 1986; Turner, 1989, 2010; Haralick, 1979). These dimensions are often
73 quantified separately and interpreted in isolation, even though they are likely to interact in shaping
74 ecohydrological feedbacks, disturbance propagation and the emergence of thresholds. Texture
75 metrics derived from remote sensing can capture structural heterogeneity not evident from mean
76 greenness alone (Wood et al., 2012; Farwell et al., 2021), whereas network approaches represent
77 patch mosaics as graphs whose topology can encode connectivity, robustness and resilience-

relevant organization (Barberón et al., 2012; Delmas et al., 2018; Guimarães Jr, 2020; Rayfield et al., 2010; Marini et al., 2019; Shackelford et al., 2018). However, these perspectives have rarely been integrated within a common analytical framework for studying regime shifts in drylands.

Second, spatial structure is dynamic. Temporal trajectories of spatial metrics may contain more information about ecosystem stability than static snapshots, especially near critical thresholds, where early warning signals can be weak, transient or obscured by noise (Bestelmeyer et al., 2011; Dakos et al., 2012, 2015, 2019). Both theory and empirical evidence indicate that indicators such as critical slowing down and increasing correlation can reveal declining resilience in temporal and spatial data (Dakos et al., 2011; Kéfi et al., 2024), and practical frameworks for spatial early warning are now beginning to emerge (Nijp et al., 2019; Bashirzadeh et al., 2022). Yet global analyses have only started to test whether directional changes in spatial organization can systematically distinguish abrupt vegetation loss from abrupt vegetation gain.

A further expectation is that degradation and recovery should be asymmetric. Resilience theory predicts hysteresis and state dependence, such that degradation may spread rapidly through reinforcing feedbacks, whereas recovery may proceed more slowly and depend on legacy spatial organization and disturbance history (Holling, 1973; Gunderson, 2000; Folke et al., 2004; Haddad et al., 2015). Empirical studies likewise suggest that regime shifts involve coupled changes in ecosystem structure and function rather than simply large-magnitude changes in state variables (Bestelmeyer et al., 2011; Dakos et al., 2019). Determining whether browning and greening are associated with distinct forms of spatial-network reconfiguration is therefore important both for mechanistic understanding and for the design of monitoring strategies.

Here, we link land-cover-specific spatial structure and its temporal trajectories to abrupt vegetation step shifts across global drylands. We integrate dryland land-use/land-cover products (2000 – 2020) with satellite-derived vegetation time series and a broad suite of spatial descriptors, including landscape pattern metrics, texture and self-organization indicators, and patch-network topology measures (Figure 1). Specifically, we test three hypotheses. First, dryland spatial structure should resolve into a small number of dominant axes reflecting fragmentation – connectivity and configuration complexity. Second, abrupt browning should be associated with synchronized degradation of spatial structure across multiple land-cover types, whereas abrupt greening should reflect more selective and land-cover-specific reorganization. Third, trajectories of land-cover-specific spatial metrics should explain vegetation step shifts better than static fragmentation measures or mean greenness trends alone. By moving beyond static fragmentation towards a trajectory- and network-informed framework, we aim to identify the spatial mechanisms underpinning dryland stability and abrupt change, and to provide spatially explicit leverage points for resilience-based monitoring and management under intensifying aridity and land-use pressure.

2. MATERIALS AND METHODS

2.1 Study area and data

Global drylands were defined as regions with an aridity index (annual precipitation divided by potential evapotranspiration) < 0.65 (Zhu et al., 2016). Vegetation regime-shift information was obtained from a published global dataset that classified $\sim 1\text{-km}^2$ spatial units according to NDVI trajectory type during 2000–2020, including linear, curvilinear and step changes for both positive and negative trends (Berdugo et al., 2022). In the source dataset, 24,555 vegetation state-change units were screened from 41,830 sampling points distributed across global drylands, with an approximate spacing of 1 km between points (Berdugo et al., 2022). Following this framework, we excluded units with neutral vegetation trends and those lacking complete annual land-use/land-cover data, yielding 15,898 spatial units for analysis (Fig. 1).

Based on the overall NDVI trajectory for each spatial unit, vegetation dynamics were classified into eight categories: two neutral trajectories (linear and curvilinear), three positive trajectories (linear, curvilinear and step) and three negative trajectories (linear, curvilinear and step) (Berdugo et al., 2022). Linear trajectories represent monotonic change or no trend, curvilinear trajectories represent nonlinear changes with acceleration or deceleration, and step trajectories represent abrupt changes in which NDVI remains relatively stable until a specific year, shifts rapidly, and then stabilizes again.

To characterize temporal dynamics in spatial structure while remaining aligned with the mid-period occurrence of many vegetation step shifts, spatial metrics were calculated at 5-year intervals (2000, 2005, 2010, 2015 and 2020) (Li & Wu 2004; McGarigal et al., 2012). This interval is widely used in landscape-pattern change analysis because land use/cover typically changes more slowly than short-term vegetation activity (Wu et al., 2002; Li and Wu, 2004). Moreover, because many regime-shift points, especially step shifts, occurred during the middle of the 2000–2020 period in the original dataset, spatial metrics from the earlier years (2000, 2005 and 2010) may be more informative as potential early warning signals (Scheffer et al., 2009; Dakos et al., 2012). Detecting spatial early warning signals requires that the monitoring resolution match, or exceed, the scale at which amplifying feedbacks are spatially expressed (Nijp et al., 2019). The 30-m spatial resolution used here meets that requirement for the $\sim 1\text{-km}^2$ landscape units analysed (Berdugo et al., 2022).

2.2 Quantification of multidimensional spatial structure

We characterized spatial structure using four complementary sets of metrics derived from 30-m land-cover data (GLC_FCS30/GLC30) (Zhang et al., 2021): landscape pattern metrics, patch co-occurrence network parameters, spatial self-organization indicators and land-cover texture metrics. Together, these metrics were intended to capture fragmentation, connectivity, configurational complexity, spatial autocorrelation and local heterogeneity.

2.3 Patch-, class- and landscape-scale metrics

Patch-, class- and landscape-scale metrics were calculated within a 500-m buffer around the centre of each sample point using the Global Land Cover Maps (1985–2020) dataset (GLC30; Zhang et

al., 2021). This dataset was developed on the Google Earth Engine platform by combining Landsat time-series imagery, training data from the Global Spatial Temporal Spectral Library (GSPECLib), and locally adaptive random forest models to map the spatial distribution of land-use/land-cover types globally. It adopts the Climate Change Initiative Land Cover (CCI_LC) classification system and includes 16 first-level land-cover classes (Supplementary Material 2, Table S1). Validation based on 44,043 global reference samples reported an overall accuracy of 82.5% and a Kappa coefficient of 0.784 (Liu et al., 2021). The dataset has also been applied in studies of seasonal wildfire and leaf chlorophyll retrieval across land-use/cover types (Tang et al., 2022; Zhang et al., 2022).

To characterize landscape fragmentation, heterogeneity and complexity, we calculated a broad set of established landscape metrics (McGarigal et al., 2012; Forman & Godron 1986). Fragmentation-related metrics included number of patches (NumL), total edge length (TE, m), edge density (ED), mean nearest-neighbour distance (MNN, m), and mean proximity index (MPI), which together describe patchiness, connectivity and edge effects (Ma et al., 2023; Su et al., 2025; Zhou et al., 2025). Heterogeneity metrics included patch richness (PR), Shannon–Wiener index (SDI) and Simpson index (SEI). Complexity metrics included patch-size coefficient of variation (PSCoV), mean shape index (MSI), area-weighted mean shape index (AWMSI), mean patch fractal dimension (MPFD), area-weighted mean patch fractal dimension (AWMPFD), landscape shape index (LSI), largest patch index (LPI) and interspersed and juxtaposition index (IJI). At the patch scale, we additionally quantified patch area (m²), the percentage of a given land-use type within the landscape (ClassP, %), perimeter–area ratio (pShp), double-log fractal dimension (DLFD), number of patches (NumP), mean patch shape index (pMSI) and total edge length (pTE, m). These metrics were selected to capture multiple dimensions of landscape structure based on established landscape-ecology theory, edge-effect studies and our previous work (Cao et al., 2024; Fan et al., 2017; Peng et al., 2016; Peng et al., 2019; Jin et al., 2024; Xu et al., 2025). In total, 1,936 patch-, class- and landscape-scale metrics were calculated using the landscapemetrics package in R (Hesselbarth et al., 2019) (Supplementary Material Table S1).

2.4 Land-use co-occurrence network parameters

To represent landscape mosaics as spatial association networks, patches within each landscape unit were treated as nodes in a co-occurrence network. Network structure was intended to reflect ecosystem functional complexity and the organization of interactions among patch types (Messier et al., 2019; Craven et al., 2016; Marini et al., 2019). Metrics commonly used in ecological network analysis, including connectivity, modularity, nestedness and robustness, can quantify both the spatial relationships among patches and the emergent properties of the landscape as a whole, thereby providing information relevant to ecosystem function and resilience (Guimarães Jr., 2020; Rayfield et al., 2010).

Landscapes with high effective connectivity and centrality may facilitate more rapid and efficient reorganization following disturbance, thereby enhancing landscape resilience (Delmas et

al., 2018). Ordered structures composed of multiple core patches may also promote the propagation of ecological flows across the landscape, increasing functional diversity and redundancy (Delmas et al., 2018). By contrast, high modularity indicates weak connections among patch groups, or strong within-group links coupled with pronounced discontinuities in function and structure. Such modularity may limit the spread of disturbances such as fire, windthrow and pest outbreaks, thereby increasing landscape-level resilience (Aquilué et al., 2018). Network robustness reflects the stability of the overall network following random patch loss, with higher robustness implying a lower probability of vegetation regime shifts.

Patch co-occurrence networks were constructed from patch association indices following Barberán et al. (2012). We calculated 10 network parameters: number of nodes, number of edges, mean degree (meanedge), network diameter, network density, modularity, mean betweenness centrality, proportion of positive associations (positive prop), proportion of negative associations (negative prop), and network robustness. These metrics were used to characterize both landscape context and potential interactions among patches, thereby capturing resilience-related properties of regional ecosystem structure (Evans et al., 2016).

All data processing and analyses were conducted in R version 4.4.3. Before network construction, extremely rare patch types were removed to reduce spurious associations driven by low-abundance patches. Spearman correlation coefficients among patches were calculated using the spaa package to quantify association strength (Zhang et al., 2023b). The variance ratio (VR) method and W statistic were then used to test the significance of patch co-occurrence patterns. Raw data were preprocessed using the psych and reshape2 packages. Following Barberán et al. (2012), valid associations were retained using thresholds of $|r| \geq 0.6$ and $p \leq 0.01$. Final network parameters were calculated using the igraph package in R.

2.5 Spatial self-organization indicators

Because dryland resilience is often associated with the emergence, maintenance or breakdown of spatial self-organization, we quantified self-organization using semivariogram-based parameters. Previous studies have shown that variation in distances among patches can indicate impending shift types (Bastiaansen et al., 2020), and that spatial autocorrelation among vegetation patches can provide early signals of degradation (Blaschke et al., 2024). We therefore used semivariogram analysis to characterize the degree of spatial self-organization within each landscape unit (Wiegand et al., 2021). Using a lag distance of 100 m, we estimated four spatial autocorrelation parameters: nugget, sill, range and spatial variability.

The nugget effect (c_0) is the semivariance at zero distance and reflects random variation unrelated to spatial self-organization, including measurement error and microscale heterogeneity. Lower nugget values indicate weaker random influence and stronger regularity of self-organized structure, whereas higher nugget values suggest greater stochasticity and weaker self-organized pattern formation. The sill ($c_0 + c$) is the asymptotic semivariance reached when the semivariogram stabilizes and represents total spatial heterogeneity. Higher sill values indicate

stronger overall heterogeneity. When the partial sill accounts for a larger share of total variance, this implies that organized processes such as biological aggregation and resource differentiation contribute more strongly to the observed pattern. The range was defined as the distance at which the semivariogram reached 95% of the sill; beyond this distance, spatial units were considered effectively uncorrelated. It therefore represents the effective spatial scale over which self-organization operates. Spatial variability was expressed as the partial sill ($c = \text{sill} - \text{nugget}$) and used as a reference index of spatial autocorrelation and structural organization (Sun et al., 2025). All self-organization metrics were calculated using the gstat package in R (Pebesma, 2004).

2.6 Land-use/cover texture metrics

To capture local heterogeneity and granularity not fully represented by categorical patch metrics, we calculated a set of Gray-Level Co-occurrence Matrix (GLCM) texture features from the GLC30 land-cover data (Haralick, 1979). Texture analysis has been widely used in dryland image analysis, often as a complementary source of structural information for machine-learning applications (Pain et al., 2019). Here, we used symmetric GLCMs to derive texture metrics describing the spatial distribution of land-cover intensities within each landscape unit, including mean, variance, contrast, correlation, energy, dissimilarity, entropy, second moment and homogeneity (Haralick, 1979). These metrics are commonly used to summarize different aspects of local spatial heterogeneity and organization (Wood et al., 2012; Farwell et al., 2021). Texture was calculated over neighbourhoods of 9, 21 and 33 pixels, corresponding to 270, 630 and 990 m, respectively. These window sizes were selected because texture metrics derived at multiple extents within a ~1-km landscape unit are often strongly correlated, yet still provide a useful multiscale representation of vegetation structural patterns (Farwell et al., 2021; Wood et al., 2012). The study landscapes were intentionally located in areas with heterogeneous land-cover mosaics, such as mixtures of forest, shrubland and grassland, making them suitable for classified land-cover texture analysis.

The GLCM quantifies the joint probability distribution of pairwise comparisons between a focal pixel and neighbouring pixels at fixed geometric offsets (Haralick, 1979). In a completely homogeneous image, values are concentrated on the GLCM diagonal; noise causes values to spread around the diagonal, whereas increasing texture produces more on- and off-diagonal elements (Pain et al., 2019). The resulting texture features summarize different aspects of this distribution. Although such features do not, on their own, identify the ecological mechanisms generating vegetation shifts, they provide comparable descriptors of spatial organization among shift states and can help identify candidate structural features associated with vegetation change. Contrast measures local variance and gives greater weight to pixel pairs with large intensity differences. Correlation measures linear dependence between intensities, ranging from -1 to 1. Energy (angular second moment) summarizes spatial uniformity, ranging from 0 to 1. Homogeneity measures the closeness of the distribution to the diagonal, also ranging from 0 to 1. Texture metrics were calculated using the glcm and exactextractr packages in R, yielding 24

multiscale texture variables (8 metrics at 3 scales in the implemented workflow).

2.7 Spatial trajectories, dimensionality reduction and prediction of step shifts

2.7.1 Quantifying the magnitude and rate of spatial change

To summarize temporal variation in spatial structure over 2000–2020, we quantified change for 1,936 landscape pattern variables, 10 co-occurrence network variables, 4 self-organization variables and 24 texture variables. Overall temporal variability was measured using the coefficient of variation (CV), calculated as the variance of each variable across the study period divided by its mean. To assess when changes occurred and whether different time windows were differentially informative for vegetation regime shifts, we also calculated percentage change rates for 5-year, 10-year, 15-year and 20-year intervals. Change rate was defined as:

$$\text{Change rate} = \frac{\text{Value}_{\text{end}} - \text{Value}_{\text{start}}}{\text{Value}_{\text{start}}} \times 100\%$$

Across all combinations of start and end years, this procedure generated 10 temporal intervals per variable, yielding 19,740 change-rate variables for subsequent analysis.

2.7.2 Characterizing spatial trajectory shape

We further assumed that spatial variables whose temporal trajectories resemble vegetation trajectories may be particularly informative predictors of vegetation step shifts. To classify the trajectory shape of each of the 1,974 base spatial variables, we fitted alternative statistical models relating each variable to year for each spatial unit. Following Berdugo et al. (2022), trajectories were classified into six categories: increasing linear, decreasing linear, increasing curvilinear, decreasing curvilinear, increasing step and decreasing step.

Three model types were used to represent these alternative temporal behaviours: linear models for linear trajectories, quadratic models for curvilinear trajectories, and threshold regression models for step trajectories. Linear and quadratic models were fitted using the generic `lm` function in R, whereas step models were fitted using the `chngpt` package (Fong et al., 2017). This procedure provided a standardized classification of spatial trajectory shape that could then be compared with NDVI trajectory type.

2.7.3 Variable selection and dimensionality reduction

The full predictor set included annual spatial variables (1,974 variables $\times$ 5 years = 9,870), interval-based change variables (1,974 $\times$ 10 intervals = 19,740), coefficients of variation for all spatial variables (1,974 variables), and trajectory-shape descriptors (1,974 variables), yielding a total of 33,558 variables. To reduce redundancy and mitigate multicollinearity, we applied a correlation-based screening procedure before further analysis.

First, pairwise Spearman correlation coefficients were calculated among all spatial variables. Second, Spearman correlations were calculated between each spatial variable and NDVI-based vegetation regime-shift type. When the absolute correlation coefficient between two spatial

variables was ≥ 0.9 , only the variable with the stronger correlation with vegetation regime-shift type was retained, following Bashirzadeh et al. (2022). This filtering procedure was repeated iteratively until no highly correlated pairs remained. The final reduced predictor set contained 1,986 variables.

2.7.4 Principal component analysis of spatial variation

To further summarize dominant patterns of spatial variation while retaining as much information as possible, we performed principal component analysis (PCA) on the reduced variable set. PCA transforms correlated variables into a smaller number of orthogonal principal components representing independent gradients of spatial variation. Components with eigenvalues > 1 and explaining a high cumulative proportion of variance were retained for subsequent interpretation and contribution analyses. These components were used to examine the relative contributions of different dimensions of land-use/cover spatial structure, including landscape configuration, patch co-occurrence network structure, spatial self-organization and texture, to vegetation regime shifts.

In addition, PCA was performed on annual spatial variables to examine how the principal dimensions of spatial organization changed through time from 2000 to 2020. This helped distinguish temporally stable versus shifting dimensions of spatial structure and improved interpretation of long-term spatial trajectories.

2.7.5 Predicting vegetation step shifts with XGBoost

To evaluate the explanatory and predictive power of spatial trajectories for vegetation regime shifts, we fitted separate binary classification models for Positive Step and Negative Step occurrence using eXtreme Gradient Boosting (XGBoost) (Chen et al., 2021). In each analysis, step occurrence was treated as the binary response variable within a given trend direction, with linear and curvilinear trajectories combined as the non-step reference category. Thus, one model predicted “stepness” within positive NDVI trajectories and the other predicted “stepness” within negative NDVI trajectories.

All analyses were conducted in R using the xgboost implementation. For each model, 70% of the data were used for training and the remaining 30% for validation. The gbtrees booster was used, and because the response variable was binary, the objective function was specified as binary logistic regression. Model performance was evaluated using classification error. Hyperparameters tuned during model fitting included learning rate (eta), maximum tree depth (max_depth), regularization parameter (gamma), minimum child weight (min_child_weight), subsample ratio (subsample), number of folds for cross-validation (nfold), feature subsampling ratio (colsample_bytree) and number of boosting rounds (nrounds) (Supplementary Material Table S2). These parameters were optimized using Bayesian optimization implemented in the parBayesianOpt package. During optimization, the xgb.cv function was used with 10-fold cross-validation to minimize overfitting, and model performance was evaluated using test-set error rather than training error, following Berdugo et al. (2022).

To interpret fitted models, we quantified predictor contributions using SHAP (SHapley Additive exPlanations) values, which provide feature-level explanations for individual predictions from tree-based models (Berdugo et al., 2022). SHAP values can be interpreted as the contribution of each predictor to the predicted response for a given sample, analogous to additive terms in a multivariate model. By relating predictor values to their SHAP values, we derived response curves describing the marginal effects of predictors on step occurrence. SHAP values were extracted using the fastshap package in combination with functions implemented in xgboost, following Berdugo et al. (2022). We additionally used XGBoost “gain” as a complementary importance measure, representing the improvement in the objective function attributable to splits on a given feature. The spatial units used in this study were previously shown to be sufficiently independent that random-forest-type model results were not substantially affected by spatial autocorrelation (Berdugo et al., 2022).

3. RESULTS

3.1 Multidimensional structure and temporal stability of dryland spatial patterns

Principal component analysis (PCA) revealed stable and interpretable dimensions of spatial structure across dryland vegetation types and benchmark years from 2000 to 2020 (Fig. 2; Supplementary Material 2). The PCA integrated nine fragmentation metrics and three composite indices describing structural, connectivity and aggregation fragmentation. Across vegetation types and years, the first two principal components (PCs) consistently explained most of the variance and resolved dryland spatial structure into two largely orthogonal axes.

PC1 represented a fragmentation–connectivity axis. Metrics describing patch subdivision and topology, including number of patches (np%), node-related descriptors and mean radius of gyration (gyrate_mn%), loaded strongly and positively on PC1 across years (loadings > 0.7; for example, np% = 0.92–0.97 and gyrate_mn% = 0.85–0.91), whereas cohesion and metrics describing patch spatial extent loaded negatively (for example, cohesion% = –0.68 to –0.75). Higher PC1 scores therefore corresponded to landscapes with greater patch subdivision, altered connectivity structure, lower cohesion and reduced spatial influence of patches.

PC2 captured a largely independent axis of configuration complexity and spatial arrangement heterogeneity (PC1–PC2 correlation < 0.1). This axis was dominated by metrics describing patch shape and interspersions/juxtaposition for specific land-cover classes, particularly deciduous broadleaf forest (LC_61/62) and sparse vegetation classes (LC_150/152/153). Landscape shape index (lsi%) and interspersions and juxtaposition index (iji%) showed strong positive loadings (lsi% ≈ 0.82–0.88), whereas within-class shape regularity metrics for LC_61/62 (shape_mn%, para_mn%) loaded negatively (shape_mn% ≈ –0.71). Thus, landscape mixing and boundary complexity could vary substantially without corresponding shifts in fragmentation intensity.

Cross-temporal PCA further showed that these two spatial axes were structurally stable through time: the same variables repeatedly contributed most strongly and with consistent loading signs.

However, the rate of change along these axes differed among vegetation types. Deserts (LC_200) showed comparatively rapid changes, in some cases exceeding 3% yr⁻¹, particularly in subdivision-related metrics involving woody components such as LC_61/62. By contrast, forest systems showed smaller but persistent shifts that were more consistent with gradual erosion of connectivity than with abrupt reorganization.

3.2 State-dependent correlations between spatial change and step-shift regimes

We next quantified associations between changes in spatial pattern variables across four subperiods (2000–2005, 2005–2010, 2010–2015 and 2015–2020) and two step-shift trajectory types, Positive Step (abrupt greening) and Negative Step (abrupt browning), using Spearman correlations (Fig. 3; Supplementary Material 2). The analysis included more than 150 variables spanning global indices and land-cover-specific metrics for 21 land-cover classes (LC codes 10–220).

At the global scale (VegType = Overall), increasing fragmentation and configuration complexity were more consistently associated with Negative Step than with Positive Step across periods. For example, during 2000–2005, patch density (pd%) was positively correlated with Negative Step ($\rho = 0.00166$, $p < 0.001$) and more weakly correlated with Positive Step ($\rho = 0.00107$, $p < 0.001$). Landscape shape index (lsi%) showed the same directional pattern during the same interval. Although effect sizes were small at this highly aggregated global level, the consistency of sign and relative magnitude across periods pointed to regime-dependent coupling between spatial deterioration and abrupt vegetation change.

These associations were strongly land-cover dependent and temporally heterogeneous. Several metrics associated with deciduous broadleaf forest (LC_62) and deciduous shrubland (LC_122) showed their strongest correlations, especially for Positive Step trajectories, during 2000–2010, with weaker but still significant associations during 2010–2020. Thus, the spatial correlates of step shifts varied not only by shift direction but also by land-cover type and time window, indicating that abrupt vegetation change is linked to temporally specific forms of spatial reorganization rather than to a single universal fragmentation response.

3.3 Asymmetric spatial predictors of greening and browning steps

XGBoost attribution analysis showed pronounced asymmetry in the spatial predictors of abrupt greening (Positive Step) versus abrupt browning (Negative Step) (Fig. 4; Supplementary Material 3). Classification models fitted separately for the two shift directions indicated that Positive Steps were explained by a relatively small set of high-impact predictors, whereas Negative Steps were associated with a broader and more evenly distributed pool of predictors.

For Positive Steps, the most influential predictors were dominated by contiguity-related trajectory states, especially persistent “no change” conditions (for example, `contig_mn_10_tr_no change`), together with land-cover-specific aggregation metrics such as `clumpy_91_tr_decrease`. In contrast, predictor importance for Negative Steps spanned area proportion, contiguity and

fragmentation-intensity metrics, including PLAND, CONTIG and SPLIT, across grassland, shrubland, sparse vegetation and bare-land classes. Browning steps therefore appeared to integrate changes across multiple land-cover components rather than being associated with a narrowly defined subset of structural conditions.

Consistent with these spatial results, SHAP analyses from a single random forest model (ranger; 500 trees; min.node.size = 10) showed that environmental controls on abrupt change probability were also directionally asymmetric across global drylands (Fig. 5A–E). Aridity exerted opposing effects on the two shift types: SHAP values for Negative samples remained positive across the full aridity gradient (approximately 0.01–0.03), whereas SHAP values for Positive samples were predominantly negative or close to zero (approximately –0.02 to 0), approaching zero only under very high aridity (>0.8). Elevation showed threshold-like behaviour, with Positive samples shifting from weakly positive to negative contributions at around 150 m (to approximately –0.02), whereas Negative samples retained weakly positive effects across the gradient. Human footprint showed the strongest divergence between shift directions: Positive samples declined sharply with increasing pressure (to approximately –0.05), whereas Negative samples remained strongly positive (approximately 0.03–0.06). NDVI contributed monotonically and positively to Negative samples but only weakly to Positive samples.

Taken together, these results indicate that abrupt greening and browning are not mirror-image processes. Instead, browning risk increased most clearly along a composite axis defined by greater aridity and stronger anthropogenic pressure, while greening was associated with a narrower and more conditional set of spatial predictors.

3.4 Vegetation-type dependence of step-shift predictors

Predictor importance also varied among major dryland vegetation types (Supplementary Material 3, Fig. S1). In grasslands, Positive Step transitions were most strongly associated with fine-scale texture and spatial autocorrelation metrics for grassland cover (LC 130), whereas Negative Step transitions were dominated by fragmentation and subdivision indicators together with declining contiguity trajectories. In shrublands, Positive Steps were primarily associated with stable or increasing aggregation and cohesion in shrub classes (LC 120–122), whereas Negative Steps were more closely linked to increasing fragmentation and temporal variability. In forests, Positive Step transitions were associated with stability in medium- to large-scale texture and cohesion, whereas Negative Steps were linked to fragmentation metrics spanning multiple forest classes. Savanna and tundra showed the same directional contrast: Positive Steps were associated with maintained connectivity, while Negative Steps reflected combined fragmentation and declining spatial coherence. Overall, these vegetation-type-specific models indicate that the predictors of abrupt greening tend to be more selective and structurally conserved, whereas abrupt browning draws on a broader suite of indicators of spatial breakdown across vegetation contexts.

3.5 Regime-dependent reorganization of correlation networks among spatial factors

Correlation networks among landscape-pattern metrics further revealed regime-dependent reorganization of spatial relationships (Supplementary Material 4, Fig. S1, S2). Under Positive Step regimes, coupling was strengthened among temporal or sampling descriptors, including DataPoints_1520, DataPoints_0520 and DataPoints_0010. Correlations were especially strong between DataPoints_0520 and DataPoints_1520 ($r = 0.997$) and between DataPoints_0520 and DataPoints_0010 ($r = 0.995$). Sill_0005 also increased markedly and showed moderate positive correlations with DataPoints variables ($r = 0.709-0.731$). Positive Step thresholds ranged from 2.000 to 5.000 (mean 3.805 ± 1.109 ; median 4.000). At threshold 5.000, the probability of positive mutation increased 3.2-fold when Sill_0005 exceeded 10963.631 and DataPoints exceeded 4.440. By contrast, Negative Step regimes showed tighter coupling among fragmentation, cohesion and shape descriptors. DataPoints increased while indices of structural complexity declined, including correlation_11x11_0005 and entropy_3x3_0020. Data density and texture entropy were strongly and negatively coupled, for example between DataPoints_0510 and entropy_3x3_0020 ($r = -0.905$) and between DataPoints_0015 and entropy_3x3_0020 ($r = -0.867$). A threshold inflection occurred near 4.000 when DataPoints_0510 exceeded 2.707 and entropy_3x3_0020 fell below 25.228. Despite this regime-specific rewiring, DataPoints variables remained strongly intercorrelated across both regimes, suggesting the existence of an invariant correlation backbone onto which regime-specific structural changes were superimposed. More broadly, these network results support the inference from the PCA and machine-learning analyses that abrupt browning is associated with coordinated spatial breakdown across multiple structural dimensions, whereas abrupt greening involves a more constrained and selective form of reorganization.

4. DISCUSSION

Across global drylands, our analyses show that abrupt NDVI step shifts are associated not only with land-cover-specific spatial organization, but also with the temporal trajectories of that organization. These findings extend previous global assessments of dryland regime shifts by showing that abrupt vegetation change is embedded in dynamic spatial reorganization rather than being fully captured by mean greenness trends or static fragmentation summaries alone. Three main conclusions emerge.

First, dryland spatial structure resolved into a stable, low-dimensional space in which fragmentation–connectivity erosion and configuration complexity were largely separable. The first axis captured variation in patch subdivision, cohesion and connectivity, whereas the second reflected changes in patch shape, interspersation and spatial mixing. This distinction is important because it suggests that landscapes can be extensively reorganized in terms of adjacency structure and boundary complexity without a proportional increase in overall fragmentation intensity, and conversely that connectivity can erode without major changes in configurational mixing. Because fragmentation and connectivity regulate dispersal, recolonization and the redistribution of resources across patch mosaics (With et al., 1997; Fahrig, 2003; Haddad et al., 2015), separating

these axes helps explain why dryland landscapes with comparable vegetation cover can differ markedly in stability and vulnerability to abrupt change (Berdugo et al., 2022; Su et al., 2025). More broadly, our results support the view that dryland resilience is governed not by habitat amount alone, but by the spatial arrangement through which ecohydrological feedbacks are maintained or disrupted (D’Odorico et al., 2006; Kéfi et al., 2007; Berdugo et al., 2017; Rietkerk et al., 2004; Berdugo et al., 2022).

Second, abrupt browning and greening exhibited clear directional asymmetry in their spatial signatures. Negative-step regimes were associated with predictors distributed across multiple land-cover components and with stronger coupling among fragmentation, cohesion and shape descriptors, consistent with coordinated breakdown of spatial coherence. By contrast, positive-step regimes were associated with a smaller set of high-impact predictors, often dominated by stable contiguity-related trajectories, and with stronger temporal or sampling coherence. This asymmetry is consistent with resilience theory, which predicts that collapse can propagate through multiple interacting pathways once reinforcing feedbacks weaken, whereas recovery is often slower, more state dependent and constrained by legacy structure and a narrower set of stabilizing conditions (Holling, 1973; Gunderson, 2000; Folke et al., 2004; Haddad et al., 2015). In this sense, abrupt browning appears to reflect distributed deterioration across dryland mosaics, whereas abrupt greening appears to require more selective and spatially coherent reorganization. These results are also consistent with broader evidence that degradation and recovery are not mirror-image processes and may occupy different regions of system state space (Bestelmeyer et al., 2011; Dakos et al., 2019; Holling, 1973; Gunderson, 2000; Folke et al., 2004).

Third, trajectory-based spatial predictors were more informative than static snapshots for distinguishing step-shift regimes. The strong contribution of trajectory categories such as increase, decrease and no change in the XGBoost models indicates that abrupt vegetation shifts are better interpreted as outcomes of time-ordered spatial reconfiguration than as functions of instantaneous landscape structure. This result is conceptually consistent with early-warning theory, which emphasizes that dynamical signatures of resilience loss may emerge before clear state changes become visible and that spatial indicators can complement conventional time-series indicators (Scheffer et al., 2009; Dakos et al., 2012, 2015, 2011, 2019; Nijp et al., 2019; Bashirzadeh et al., 2022). Our findings therefore suggest that step shifts in drylands are preceded or accompanied by evolving structural changes across patch mosaics, and that these dynamics may provide mechanistic clues as to why some systems cross thresholds while others remain within the same basin of attraction.

The vegetation-type dependence of predictor importance further reinforces this interpretation. Across grasslands, shrublands, forests, savannas and tundra, positive-step transitions were typically associated with maintained connectivity, cohesion or stable texture, whereas negative-step transitions involved broader signals of fragmentation, subdivision and declining spatial coherence. This implies that the pathways to abrupt browning are not only broader than those to abrupt greening, but also more consistently shared across vegetation contexts. At the same time,

the land-cover specificity of many predictors indicates that dryland vulnerability cannot be understood solely through generic fragmentation indices. Instead, the same nominal landscape change may carry different ecological implications depending on whether it occurs in woody components, sparse-vegetation matrices or mixed shrub–grass mosaics. This helps reconcile why global drylands can exhibit common threshold behaviour while still expressing biome- and cover-specific manifestations of resilience loss (Berdugo et al., 2022; Su et al., 2025).

Our network analyses provide additional support for this interpretation by showing regime-dependent rewiring among spatial descriptors. Under browning, stronger coupling among fragmentation, texture and cohesion metrics suggests coordinated structural degradation across multiple dimensions of landscape organization. Under greening, by contrast, network changes were more constrained and centred more strongly on temporal or sampling coherence, consistent with selective reorganization rather than system-wide restructuring. Although some variables, particularly DataPoints descriptors, may partly reflect properties of temporal sampling or preprocessing, their stable correlation backbone across regimes suggests that they nonetheless capture meaningful structural regularities in how spatial information is organized through time. Together with the PCA and machine-learning analyses, these network results indicate that abrupt browning is associated with broad spatial breakdown, whereas abrupt greening is associated with more limited and conditional forms of reassembly.

These findings also have practical implications for dryland monitoring and management. For monitoring, regime-dependent rewiring among spatial indicators may provide operational signatures of emerging vulnerability. For example, tight negative coupling between DataPoints_0510 and entropy_3x3_0020 under browning suggests that declining structural complexity accompanied by increasing temporal concentration may signal incipient resilience loss before large changes in mean vegetation activity become apparent. More generally, the strong predictive contribution of land-cover-specific trajectories suggests that monitoring frameworks based on dynamic spatial indicators could improve early detection of vulnerable dryland landscapes beyond static fragmentation measures or mean NDVI trends alone (Pettorelli et al., 2005; Verbesselt et al., 2010; de Keersmaecker et al., 2015). For management, our results imply that reducing mosaic-wide fragmentation, maintaining contiguity in key matrix covers, and protecting woody or structurally stabilizing land-cover components that function as spatial anchors may help lower the likelihood of abrupt browning and enhance recovery potential (Rietkerk et al., 2004; Haddad et al., 2015; Newbold et al., 2015; Reynolds et al., 2007). Such actions are especially relevant in drylands, where local disruption of patch organization can rapidly alter runoff redistribution, resource concentration and vegetation–soil feedbacks (D’Odorico et al., 2006; Kéfi et al., 2007; Berdugo et al., 2017; Rietkerk et al., 2004; Reynolds et al., 2007).

Several limitations should be considered when interpreting these findings. First, land-cover classification uncertainty may propagate into some spatial metrics, particularly for classes with low areal extent or shifting boundaries. Second, percentage-change variables can be inflated where baseline values are very small, which may amplify apparent change in some rare metrics. Third,

although trajectory-based predictors improved discrimination of step-shift regimes, the analyses remain associational and cannot by themselves establish causal pathways from spatial reorganization to vegetation tipping. Finally, some temporal or sampling descriptors may partly encode data-structure constraints rather than purely ecological mechanisms. Even so, the consistency of the main patterns across PCA, correlation analyses, machine-learning attribution and correlation-network rewiring suggests that the core inference is robust: abrupt dryland vegetation shifts are closely linked to dynamic and land-cover-specific reorganization of spatial structure rather than to static structure alone (Li & Wu, 2004; McGarigal & Marks, 1995).

5. CONCLUSION

This study demonstrates that abrupt vegetation regime shifts across global drylands are governed not only by changes in vegetation state, but also by the dynamic reorganization of land-cover-specific spatial structure. Across 15,898 dryland landscape units, spatial variation consistently resolved into two dominant and stable axes: fragmentation–connectivity erosion and configuration complexity/interspersion. These dimensions were differentially associated with abrupt vegetation shifts, with negative-step events showing broader and more coordinated signatures of spatial breakdown than positive-step events.

By integrating landscape metrics, patch co-occurrence networks, semivariogram-based indicators of self-organization and multiscale texture features, we show that temporal trajectories of spatial organization contain mechanistic and predictive information beyond that provided by static fragmentation measures or mean greenness trends. Abrupt browning was associated with distributed deterioration across multiple land-cover components, whereas abrupt greening was associated with a narrower and more selective set of structural conditions, consistent with resilience theory and state-dependent recovery dynamics (Holling, 1973; Gunderson, 2000; Folke et al., 2004; Haddad et al., 2015).

Taken together, our findings support a shift from static fragmentation assessment towards trajectory- and network-informed monitoring of dryland vulnerability. Such an approach can improve the early detection of resilience loss and help identify spatial leverage points for management under intensifying aridity and land-use pressure. More broadly, the results highlight that spatial organization is not a secondary attribute of dryland ecosystems, but a central component of how resilience is maintained, lost and, in some cases, rebuilt.

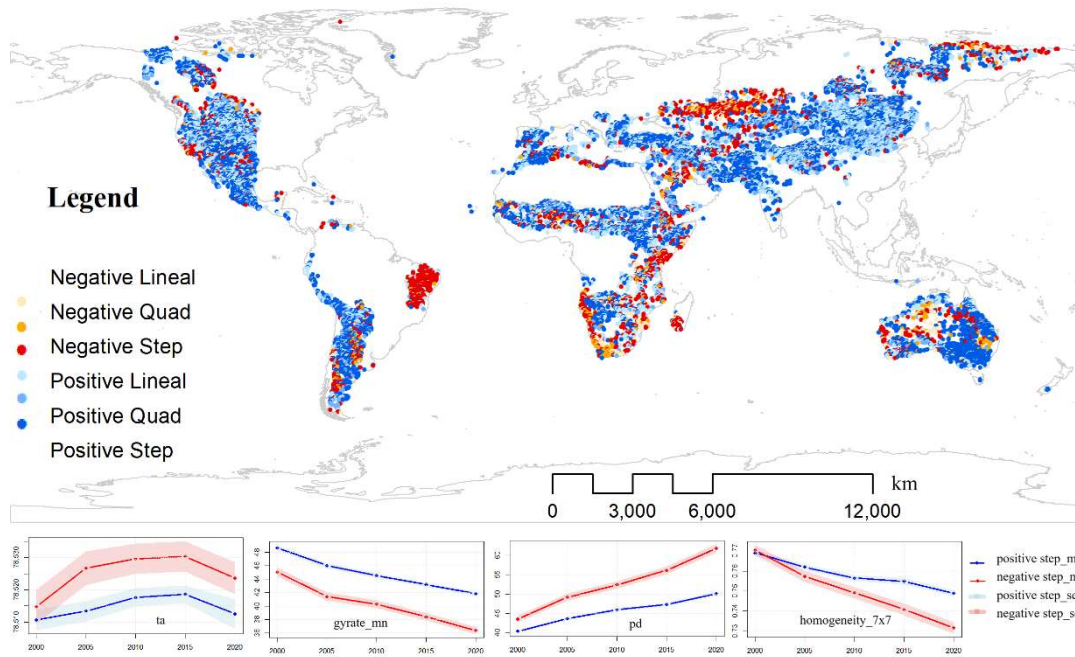


Fig. 1. Spatial distribution of global dryland vegetation step-shift quadrats and associated temporal dynamics of representative spatial metrics.

Map shows the locations of 1-km landscape units (quadrats) exhibiting NDVI-based Positive Step and Negative Step shifts across global drylands. Curves summarize changes (2000 – 2020) in selected landscape pattern metrics—total area (ta), mean radius of gyration (gyrate_mn), and patch density (pd)—and a texture metric (homogeneity_7x7) for Positive Step versus Negative Step shift regimes.

(Please see the clearer figures in the appendix)

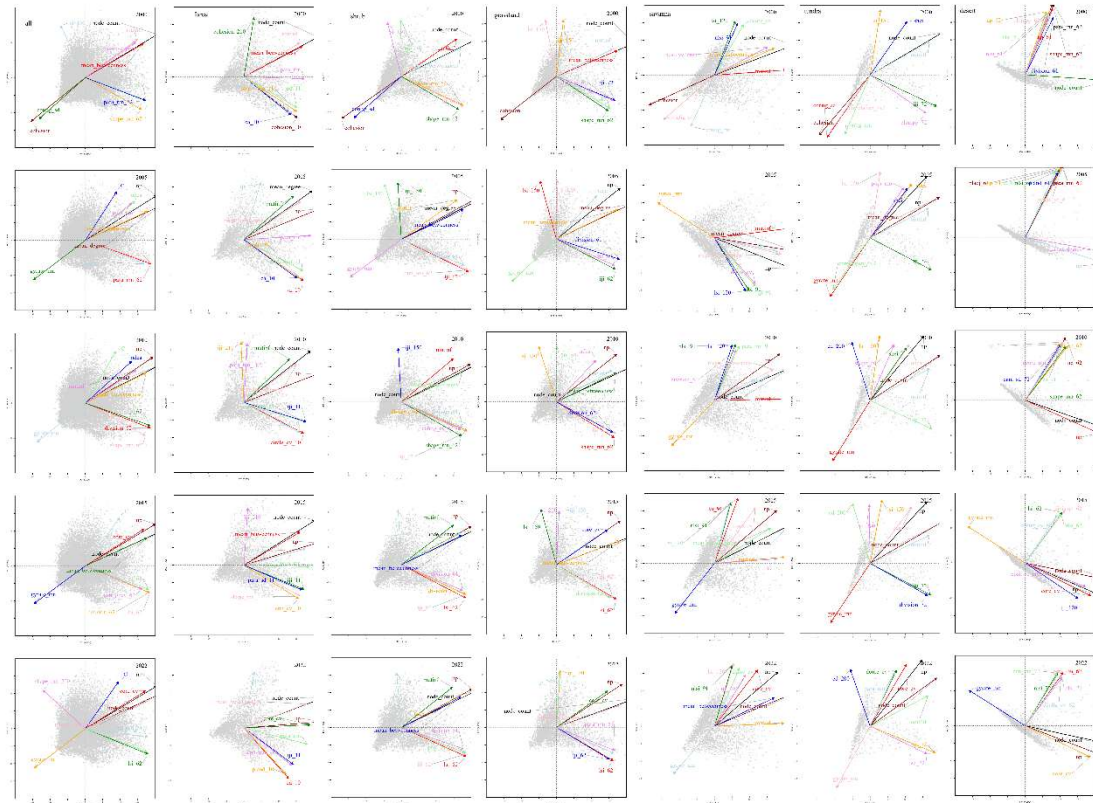


Fig. 2. Principal component analysis of spatial pattern metrics in global drylands (2000–2020). Principal component analysis (PCA) summarizing the dominant gradients of land use/cover spatial structure from 2000 to 2020. Panels show PCA scores for (A) all vegetation samples and for major vegetation types: forest, shrubland, grassland, savanna, tundra, and desert. For each sample unit, spatial metrics (landscape- and patch-level configuration/fragmentation indices, patch co-occurrence network parameters, self-organization metrics, and texture metrics) were computed at 5-y intervals (2000, 2005, 2010, 2015, 2020), and PCA was used to characterize temporal shifts in the principal component space. (Please see the clearer figures in the appendix)

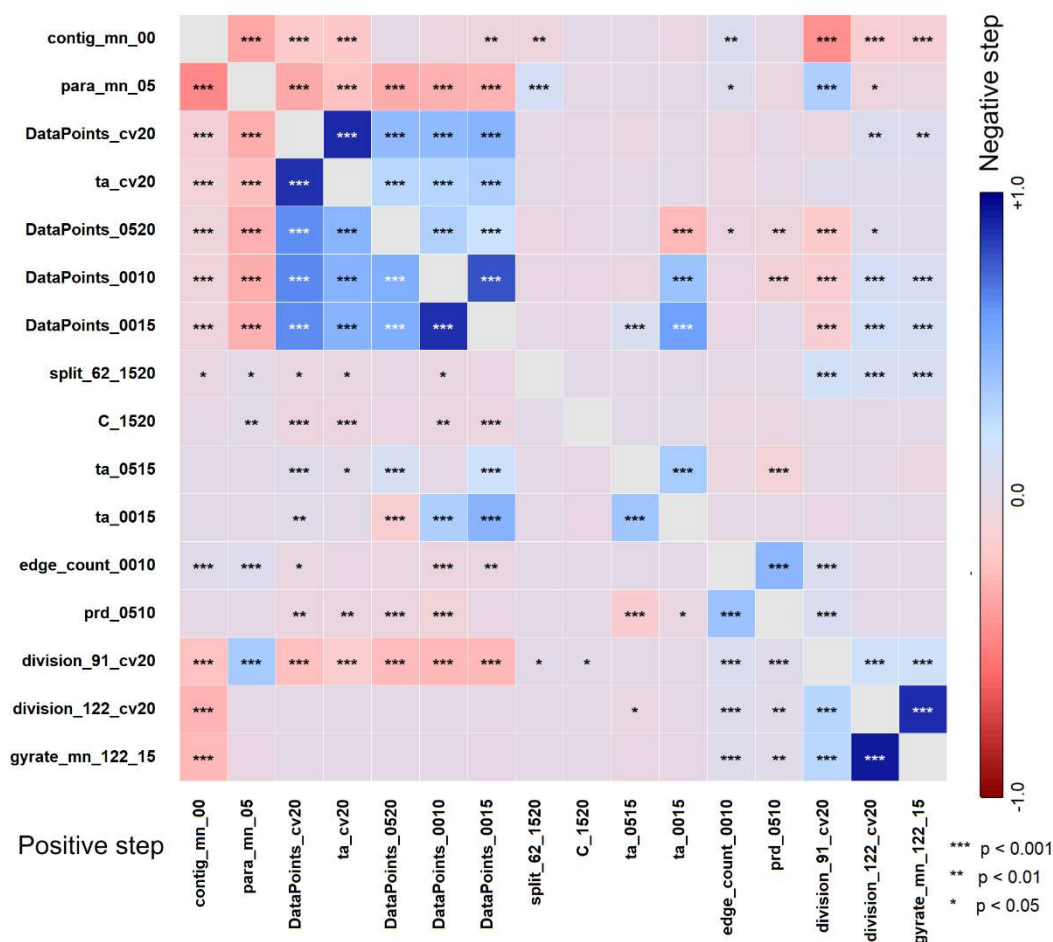


Fig. 3. State-dependent correlation structure of key spatial predictors under Positive and Negative Step shift regimes.

Spearman rank correlations (ρ) among selected important spatial variables for global dryland vegetation step shifts. Correlations for the Positive Step regime are shown in the lower-left triangle and for the Negative Step regime in the upper-right triangle. Significance is indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

(Please see the clearer figures in the appendix)

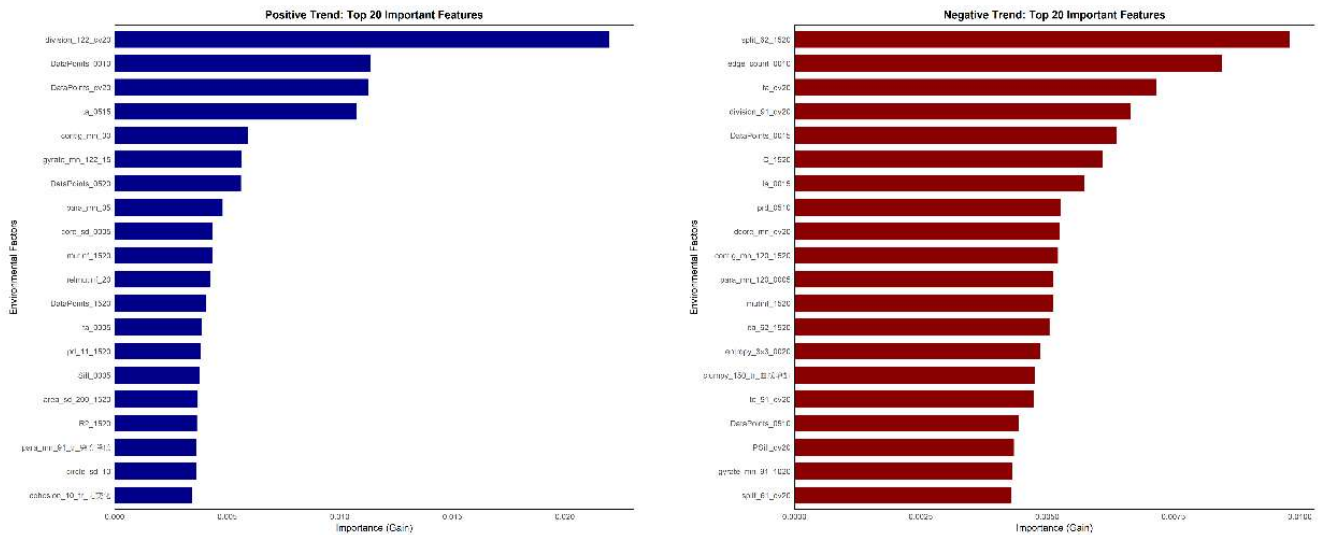


Fig. 4. Contrasting importance of spatial drivers of abrupt NDVI changes for greening versus browning trajectories. Ranked variable importance for predicting abruptness for (A) Positive Step (greening) and (B) Negative Step (browning) regimes. Importance is quantified as gain, defined as the improvement in model performance attributable to a predictor when used in tree splits. Models were fit using a random forest – type tree ensemble (XGBoost implementation) using 1,998 mutually uncorrelated predictors summarizing landscape- and patch-level metrics, patch co-occurrence network parameters, self-organization metrics, and land-cover texture metrics. (Please see the clearer figures in the appendix)

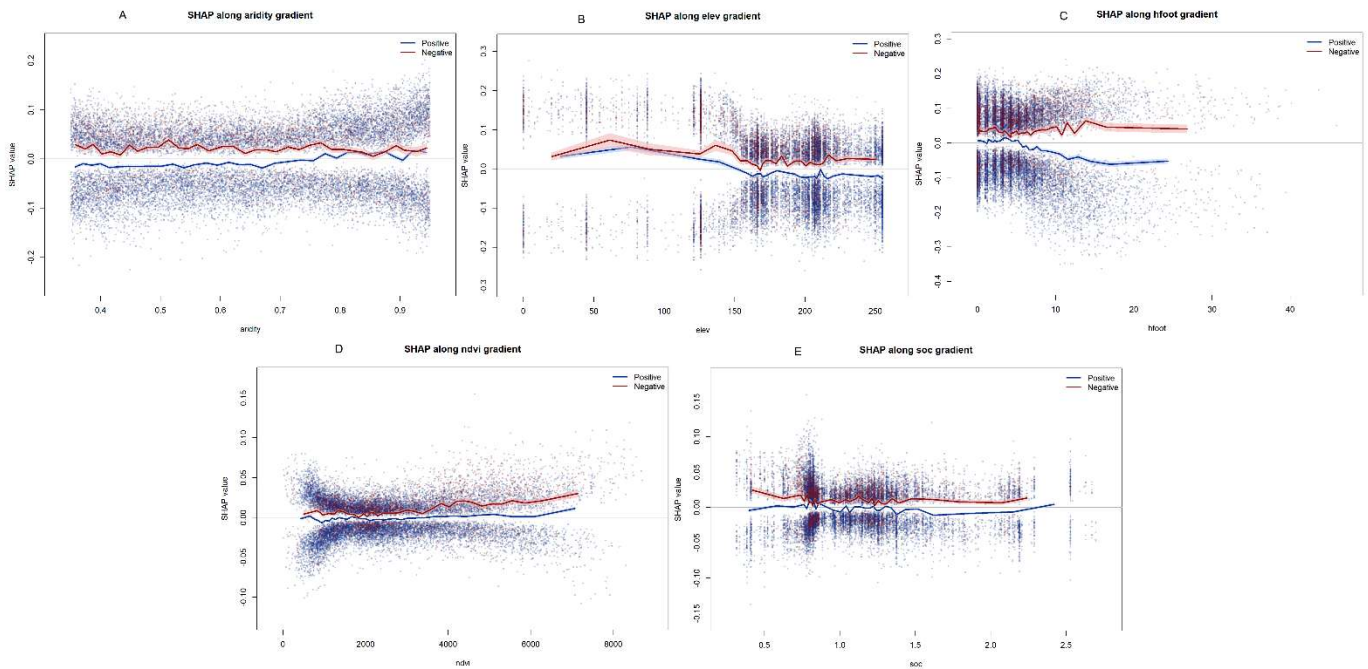


Fig. 5. Effects of environmental drivers of abrupt shifts depending on the NDVI trend analyzed. Effects of five factors (A-E: aridity, elevation, human footprint, NDVI and soil organic carbon) for negative (red) and positive (blue) abrupt changes. (Please see the clearer figures in the appendix)

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