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Large-statured vegetation with conservative strategies exhibits greater resilience in global terrestrial ecosystems

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Research Article

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Abstract

The resilience of vegetation, defined as its capacity to withstand and recover from perturbations, is fundamental to maintaining the global carbon cycle and biodiversity. However, the roles of functional traits and their trade-offs in governing resilience at a global scale remain elusive. Combining complementary Normalized Difference Vegetation Index (NDVI) and Vegetation Optical Depth (VOD) data, we quantified global vegetation resilience via variance- (λ_{Var}) and lag-one autocorrelation- (λ_{AC1}) based recovery rates, linking these metrics to both individual traits and their trade-offs. Results reveal canopy height as the predominant driver of global vegetation resilience across both NDVI and VOD metrics (λ_{Var} and λ_{AC1}). While NDVI-based resilience is governed by leaf economic traits (leaf nitrogen content (LNC), leaf dry matter content (LDMC), and specific leaf area), VOD-based resilience is dominated by the LDMC, leaf N:P ratio (LNPR) and hydraulic conductivity. Spatially, stronger resilience is consistently coupled with greater height and conservative traits (lower LNC or LNPR) across nearly all land-cover types, confirming that a combination of large physical stature and conservative resource-use strategies maximizes ecosystem resilience. These findings underscore the significant role of functional traits in regulating ecosystem resilience, offering a trait-based framework to predict vegetation responses to global environmental changes.

Introduction

Global terrestrial ecosystems have experienced more frequent and severe disturbances due to ongoing climate change and intensifying human activities [1–4]. The capacity of ecosystems to withstand and recover from external disturbances, referred as resilience, plays a critical role in determining their responses and feedbacks under global change [5–7]. According to the critical slowing down (CSD) theory, declining resilience has been widely recognized as an early warning signal of abrupt ecosystem transitions [8,9], which can lead to profound transformation in ecosystem functions and structure [1,10,11]. For example, abrupt transitions from rainforest state to alternative savannah state in tropical regions can substantially alter the carbon sequestration capacity of ecosystems [12]. Therefore, clarifying the key drivers of ecosystem resilience is essential to accurately projecting future dynamics of terrestrial ecosystems.

Functional traits, which represent plant adaptations to their living environments and govern responses to environmental changes [13–15], have been widely utilized to explain vegetation resilience to disturbances in recent years [16–18]. Morphological traits, such as leaf dry matter content (LDMC), are critical for maintaining resilience. For instance, species with higher LDMC often exhibit greater temporal population stability [18,19]. Beyond morphology, resilience to disturbances such as drought is linked to chemical traits like leaf nitrogen content (LNC), where higher LNC is typically associated with increased sensitivity to precipitation fluctuations [20]. Furthermore, hydraulic traits regulate growth responses to climate change, with drought-resistant species often possessing lower hydraulic conductivity and higher hydraulic safety [21,22]. However, most existing findings are derived from plot-based studies limited to specific ecosystems,

such as grasslands or forests, thereby neglecting global-scale trait effects. To overcome this limitation, satellite observations offer an opportunity to evaluate the links between functional traits and the resilience of diverse vegetation types globally.

Crucially, these individual traits do not operate in isolation, rather, trade-offs among functional traits are widely recognized as prevalent across diverse taxa and ecosystems [23–26].A prominent example is the Leaf Economics Spectrum (LES), which defines a continuum of plant strategies, ranging from resource acquisitive (fast-growing) to conservative (slow-growing) [26]. Generally, resource-conservative plants prioritize energy allocation toward structural investment, resource storage, and defense, which bolsters their stress tolerance and results in enhanced functional constancy [27,28]. However, recent evidence from semi-arid grasslands suggests that acquisitive strategies can dampen fluctuations in ecosystem productivity through drought escape and avoidance mechanisms, characterized by rapid growth and reproduction prior to drought onset, as well as more sensitive stomatal regulation to mitigate biomass loss during dry periods [29,30]. Additionally, large-scale studies across the Tibetan and Inner Mongolian Plateaus demonstrate that grassland communities dominated by fast-growing species exhibit lower productivity variability at the local scale [31]. Conversely, experimental evidence from North American and European grasslands suggests that the community-weighted means of 'fast–slow' functional traits have no consistent effect on aboveground biomass fluctuations [32]. These divergent findings across spatial scales and habitats highlight a knowledge gap regarding whether a universal trade-off between acquisitive and conservative strategies governs vegetation resilience at a global scale. Considering the variability in disturbance regimes and regional heterogeneity, how trait trade-offs govern vegetation resilience on a global scale requires further, more systematic investigation.

This study aims to elucidate how Community Weighted Mean (CWM) functional traits govern global-scale vegetation resilience to external disturbances across diverse ecosystem types. Utilizing a suite of remote sensing observations, we quantify vegetation resilience through two recovery rate metrics derived from variance (λ_{Var}) and lag-one autocorrelation (λ_{AC1}), which have been widely adopted as robust early-warning indicators for forthcoming critical transitions [33,34]. By dividing the globe according to the International Geosphere-Biosphere Programme (IGBP) land cover classification, we analyzed the impacts of economic, morphological, and hydraulic traits - as well as their combinations - on resilience. Specifically, this analysis aims to: (1) determine whether a global-scale trade-off between acquisitive and conservative strategies serves as a universal driver of vegetation resilience; (2) disentangle the relative contributions of multidimensional functional traits to resilience at a global scale; and (3) examine the robustness of these trait-resilience relationships across different land cover types.

Results

1 Global pattern of vegetation resilience

Over the past decades, both variance- and AC1-based vegetation resilience maps estimated from NDVI and VOD have generally shown similar spatial patterns (Fig. 1), although a large portion of resilience metrics derived from NDVI were excluded due to lower reliability (mainly in dense forests, Fig. 1a, b). Overall, a consistent latitudinal pattern was observed, in which vegetation resilience decreased from the equator toward higher latitudes, with regions near15°N, 50°N and 30°S demonstrating low resilience levels (Fig. 1c, f). Significant regional differences were observed: the Amazon, tropical African, and Southeast Asia exhibited the highest resilience, while vegetation in Central Aisa, Australia, and the southwestern region of North America typically had low resilience. Regarding different landcover types, forests showed higher resilience than savannas and grasslands based on recovery rate derived from both NDVI and VOD data (Fig. 2). Specifically, Evergreen Broadleaves Forests (EBF) had the highest resilience, whereas Closed Shrublands (CSHB), Open Shrublands (OSHB), and Grasslands (GRA) exhibited the lower resilience. Among forests, broadleaf forests generally had higher resilience than needleleaf forests.

2 Vegetation resilience variations along PC axes of traits

The first two principal components (PC1 and PC2) captured approximately 62% of the variation in the original functional traits (Fig. 3). PC1 accounted for 44% of the total variation and was defined by leaf economics traits (including LDMC, SLA and LNC) and canopy height. This axis captures a spectrum of plant growth strategies, ranging from fast-growing, resource-acquisitive strategies to slow-growing, resource-conservative ones. PC2 accounted for approximately 18% of the variation and was mainly determined by LNPR, LPC, and canopy height. According to Figure S1, the forests landcover types were distributed in the left part of the PCs plane, whereas shrublands and grasslands mainly located on the right. Along the PC2 axis, shrublands and savannas, including OSHB, Woody Savannas (WSAV) and Savannas (SAV), tended to locate on the negative part, while most forest types did not exhibit clear patterns. Global vegetation resilience was generally low in the upper right part of the PCs planes across different metrics and vegetation indices (Fig. 3). Whereas high resilience was primarily observed in the left part, particularly in the bottom left regions. This indicated that the PC1 of traits play a more important role in determining vegetation resilience than PC2. Vegetation resilience was increased as PC1 decreased, suggesting that vegetation with traits associated with the conservative resources strategies and high canopy height tended to have higher resilience. PC2 has a strong influence on vegetation resilience in the regions where PC1 > 0, where resilience generally increased as PC2 decreased. Thus, vegetation with higher LPC and canopy height, as well as lower LNPR tended to exhibit stronger resilience.

For each landcover type, the proportion of variance explained by each principal component and the loadings of individual traits exhibited differences, although the leaf economics spectrum (LES) was generally observed (Fig. S2-5). Consequently, resilience patterns on the PCs planes also varied across different landcover types. Significant patterns were identified in some landcover types, such as DBF (Deciduous Broadleaf Forests), OSHB, WASV, and GRA, across metrics and vegetation indices. For example, in GRA, resilience was higher in the right part of the PC1 plane, where the traits were

associated with the conservative resource strategies and greater height. However, resilience patterns differed significantly between NDVI- and VOD-based metrics for certain landcover types. While no notable patterns were found in EBF and MF for NDVI-based resilience, the VOD-based resilience metrics were generally lower in regions with higher SLA and LNC, but stronger with greater canopy height and LPC. For ENF (Evergreen Needleleaf Forests) and SAV, although certain distribution patterns were observed for VOD-based resilience on the PCs planes, the relationships between resilience and traits remained relative weak.

3 Influences of traits on vegetation resilience

Machine learning models based solely on vegetation traits explained 64–78% of the spatial variance in resilience, which was comparable to the variance explained by climatic factors alone (67–75%). When integrating both trait and climatic predictors, our models demonstrated that the plant functional trade-off (PC1) is a critical driver of global vegetation resilience (Fig. S6). Specifically, vegetation characterized by conservative strategies (lower PC1) is consistently associated with higher resilience, a robust pattern observed across all resilience metrics and vegetation indices. Among individual traits, canopy height was the dominant predictor of vegetation resilience, although the relative importance of other traits varied between NDVI- and VOD-based metrics (Fig. 4). For NDVI-based resilience, leaf economic traits, such as LNC, LDMC, and SLA, ranked higher in importance. While LDMC maintained high importance for VOD-based resilience, the influence of LNPR and HC increased. This hierarchy was largely consistent across specific landcover types, where canopy height remained the primary driver, and the top three influential traits were consistent with those identified in the aggregate model (Fig. S7-10).

Canopy height and LNC consistently exerted significant influences on NDVI-based vegetation resilience, both globally and across various landcover types (Fig. 5). Specifically, height exhibited a pervasive positive relationship with resilience, whereas higher LNC generally contributed to reduced resilience (i.e., increasing SHAP values) across the majority of analyzed landcover types. For VOD-based resilience, vegetation with greater height and lower LNPR generally exhibited stronger resilience (indicated by lower SHAP values). In contrast, the influence of LDMC was less consistent and highly variable across different indicators. For instance, despite its high importance rank in all models, LDMC displayed divergent effects on resilience between NDVI- and VOD-based metrics. Specifically, for VOD-based resilience, higher LDMC was generally associated with higher resilience at the aggregate level, yet marked discrepancies in the direction of this influence were observed across different landcover types.

Discussion

In this study, our findings demonstrate that vegetation characterized by taller canopy height and conservative resource strategies exhibits higher resilience, a phenomenon that is consistently observed across long-term NDVI and VOD datasets. This relationship remains robust notwithstanding the inherent heterogeneity observed among land-cover types and resilience metrics.

Canopy height was found to play a critical role in determining vegetation resilience, with great height enhancing resilience. Numerous studies have demonstrated that canopy height regulate a series ecological process including productivity, drought response, across different scales from individual plants to ecosystems [35–38]. Taller forests generally have deeper root systems [39,40], their photosynthesis was found less sensitive to variations in precipitation [41], which enhance their resistance to drought. In this study, a strong relationship was also found between canopy height and root depth (Fig. 3). Therefore, more extensive and deeper root system that could access deeper water may be one of the primary reasons for the greater resistance of taller vegetation, since Smith and Boers [42] found that global vegetation resilience was associated with water availability and variability. On the other hand, a taller canopy tends to possess greater species richness and structural complexity [43–45], both of which enhance ecosystem resistance and recovery in response to disturbances [46,47]. Notably, while most above-mentioned studies focused on forest ecosystems, our study demonstrates that canopy height remains a pivotal determinant of resilience across diverse biomes (Fig. S7-10), suggesting a dominant role of canopy height in governing vegetation resilience. These global scale findings are consistent with localized field observations across different ecosystems. A transect study spanning over 2,000 km in grassland ecosystems of northern China reveals a significant positive correlation between height and resilience under moderate human activity intensity [45]. Similarly, in U.S. wetlands, community-level plant size exhibited the strongest positive association with the temporal stability of productivity, a trend which remained consistent across various wetland types and levels of human disturbance [48].

Resilience was found to be higher in vegetation with leaf traits representing conservative resources strategies, which in accordance with the widely believed view that conservative growth strategies of plants are crucial for sustaining ecosystem stability [27]. Previous studies found that more conservative species, such as that characterized by higher leaf dry matter content (LDMC) and lower relative growth rates, tended to have more stable populations [18,19,49], and the communities that dominated by plant species with slow leaf functional traits (greater LDMC, lower SLA, and lower LNC) were more stable [32,50]. Leaf traits represent the resource investment strategy that adapted to resource availability in living environment. Plants with conservative strategies (slow return on nutrients investments) tend to have lower relative growth rate and longer leaf lifespan [26], leading to higher potential of buffered growth. They could endure the unfavorable years through utilizing the resources stored from previous favorable year, consequently enhance the stability of population growth [18,25].

Although the multi-trait trade-offs, like economics spectrum, are essential to recognize the major axis of differentiation among plants, previous studies suggested that individual traits may predict growth stability more effective due to their more relevant ecological functions [19,51]. LDMC was generally found to have more consistent and stronger effects on the temporal variability of plant growth than other leaf traits such as SLA and LNC. Which could probably be explained by its tight linkage with growth rate, more reliable measurement, stronger reflection of the growth-defense trade-off, and better representation of the response to water stress [19]. However, in this study, we found LNC was the most

important leaf trait for the resilience metrics estimated from NDVI, which also showed more consistent effects across landcover types. Compared to LDMC, LNC (related to the chlorophyll and enzymes in leaf) is more tightly linked to plant photosynthetic strategy [52–54]. At the same time, NDVI, calculated based on the difference between near-infrared (which vegetation strongly reflects) and red light (which vegetation absorbs), primarily reflect more information related to leaf chlorophyll concentration and photosynthetic activity [55]. This may be the main reason of the observed relationship between LNC and NDVI-based resilience metrics. For VOD based metrics, LDMC is the most important leaf trait influencing vegetation resilience. Since VOD is sensitive to the water content and biomass of plant [56], above-mentioned strong connection of LDMC with plants response to water stress could potentially be the main underlying reason.

We also found LNPR and hydraulic conductance play important roles in determining the VOD-based resilience. Specifically, a higher LNPR was associated with reduced resilience, a relationship likely driven by several pathways. Regarding intrinsic plant physiology, community-level leaf N:P serve as a frequent indicator of nutrient limitation, where an elevated LNPR typically signifies P-limitation [57,58]. Given that phosphorus is a fundamental building block for the synthesis of nucleic acids and proteins [59,60], P-deficiency can constrain vegetation photosynthesis, thereby diminishing vegetation resilience [61,62]. Crucially, this vulnerability is amplified by extrinsic environmental stressors, such as drought and atmospheric nitrogen deposition. By impeding P-diffusion and root uptake, drought aggravates existing P-limitations [63], thereby heightening the sensitivity to water stress in vegetation with higher LNPR [64,65]. Similarly, intensifying nitrogen deposition can also elevate LNPR, which has frequently been found to reduce community temporal stability [66–68]. Hydraulic conductivity represents the trade-off in plants to balance water transport efficiency and safety [69–71]. Although higher hydraulic conductance could enhance the water transportation that support photosynthesis and growth under favorable conditions, it often comes at the cost of increased vulnerability to xylem cavitation, particular under drought. A tree-ring analysis study by Duan et al. [21] on seven pine species in semi-arid environments demonstrated that species with higher hydraulic conductivity and photosynthetic capacity were more sensitive to drought stress, exhibiting greater growth fluctuation to extreme drought events. Conversely, plants with lower hydraulic conductance tend to be more resistant to hydraulic failure, thus showed higher stability. An analysis of 100 global observation sites indicates that forests dominated by species with high hydraulic safety exhibit greater resistance to drought [22]. Overall, the relative importance of individual traits in predicting vegetation resilience is governed by the eco-physiological alignment between the traits themselves and the specific indices employed to derive stability metrics. While leaf-level economic traits (LNC, LDMC, SLA) couple more effectively with the photosynthetic signals inherent in NDVI, structural and hydraulic traits (LDMC, LNPR, HC) exhibit superior explanatory power for the water-sensitive and biomass-related signals characteristic of VOD.

Although the optical vegetation indices like NDVI were widely used in previous related studies, their reliability to estimate vegetation resilience were questionable, particular in ecosystems with dense

structure, such as tropical and boreal forests [33]. Following previous study [34], we assessed the reliability of resilience estimation by the consistence of AC1 and VAR based metrics, and excluded the pixels with $\lambda_{Var}/\lambda_{AC1}$ less than 0.5 or greater than 2. In addition, we also calculated the same metrics using VOD to improve the reliability of resilience estimation. Another major source of uncertainty comes from the trait datasets. The CWM traits used in this research were derived using machine learning techniques based on optical remote sensing data, climate data, and in-situ measured traits [72], thus may not represent the actual trait values. Furthermore, the plant functional traits were highly time-varying under climate change, disturbances, and human activities [73,74], which could also compromise the reliability of the relationship between vegetation resilience and traits. Future work should integrate the spaceborne and near-surface remote sensing, big data processing, machine learning techniques, and field observation to enhance the accuracy and resolution of multifaceted vegetation monitoring, and refine our understanding of the plant functional traits and their influences on ecosystem functions in a changing earth.

Conclusion

Our results identify canopy height as a predominant driver of vegetation resilience at the global scale across multiple indices, implying the fundamental importance of plant stature in buffering ecosystems against external perturbations. This suggests that taller, more structurally complex forests may possess an inherent stability that shorter-stature vegetation may lack. Furthermore, we found that vegetation adopting conservative strategies characterized by slow leaf turnover demonstrates higher resilience compared to acquisitive counterparts. Regarding trait-resilience relationships, taller canopy height is associated with greater resilience, whereas LNC and LNPR exhibit the opposite trend. In contrast, LDMC does not display a clear or consistent pattern globally. Notably, these sensitivities exhibit significant cross-biome heterogeneity. By integrating multidimensional remote sensing metrics with community-weighted mean traits, our trait-based framework offers a mechanistic pathway to predict terrestrial ecosystem responses to intensifying environmental stressors and inform the strategic management of global carbon sinks.

Methods

Vegetation index

The AVHRR GIMMS-3g+ NDVI (0.083°, bi-weekly 1982–2022, [75]) and VOD (0.25°, Ku-Band, daily 1987–2017, [56]) were used to examine global vegetation dynamics over the past decades. Only the NDVI data pixels flagged as ‘high quality’ were used in our analysis. The VOD data was resampled using bi-weekly medians to align with the sampling time of NDVI data. MODIS landcover data (MCD12C1, 0.05°, 2001–2022) was used to mask out non-vegetated areas and classify pixels into different International Geosphere-Biosphere Programme (IGBP) landcover types. We further excluded pixels with any landcover change from 2001 to 2022 to minimize the influences of ecosystem transitions or anthropogenic

influence on our results. The landcover data was adjusted to 0.083° and 0.25° using nearest-neighbor resampling to match the resolutions of the NDVI and VOD data. Finally, we applied a rolling-mean detrender to remove the long-term trend and a harmonic fit deseasoner to remove the seasonal patterns in both vegetation time series on each pixel [34]. While NDVI primarily reflects photosynthetic activity and leaf greenness, VOD captures the dynamics of whole-canopy water content and structural biomass. Therefore, integrating both metrics allows for a comprehensive assessment of ecosystem resilience, capturing both the physiological recovery of the leaf canopy and the structural persistence of the whole-plant hydraulic system.

Estimating vegetation resilience

We estimated vegetation resilience using two recovery rate indices based on the variance (λ_{Var}) and the lag-one autocorrelation (λ_{AC1}). Compared to the empirical resilience that is calculated from the local vegetation time series which have actually experienced abrupt perturbations, the variance- and AC1-based metrics can yield spatially homogeneous resilience metrics, even in locations where no significant disturbance occurred. Both variance and AC1 have been widely adopted in previous studies to quantify the resilience of vegetation ecosystems and serve as early-warning indicators for forthcoming critical transitions [76–80]. This can theoretically be explained through the linearization of the stochastic dynamics at a particular equilibrium point [33,34,42]. The vegetation recovery rate from perturbations can be shown as the recovery rate λ of a linearized version of the dynamics around a given equilibrium, which could be described by an Ornstein-Uhlenbeck process:

$$dX_t = \lambda X_t dt + \sigma dW$$

for deviations X_t from the equilibrium, where $\lambda < 0$ for stable dynamics, and increasing (decreasing) recovery rate λ indicates a loss (gain) of resilience. The above Ornstein-Uhlenbeck process could be discretized into equal time steps of size Δt. Consequently, the variance and AC1 of the resulting order-one autoregressive process are then related to the restoring rate λ via:

$$Var[X] = -\frac{\sigma^2}{2\lambda} = \frac{\tilde{\sigma}^2}{1 - e^{2\lambda \Delta t}}$$

For the variance, and

$$a = e^{\lambda \Delta t}$$

For the AC1 (a). The variance and AC1 are larger when λ is close to zero, indicating lower vegetation resilience. Finally, we estimated the resilience based on variance and AC1 by the following equations, respectively:

$$\lambda_{Var} = \frac{1}{2\Delta t}\log(1 - \frac{\tilde{\sigma}^2}{Var[X]})$$

$$\lambda_{AC1} = \frac{1}{\Delta t}\log(a)$$

Because of the logarithm in both equations, the recovery rate λ cannot be calculated for pixels where either a<0 or $\frac{\tilde{\sigma}^2}{Var[X]}$ > 1.

Previous studies have suggested that the vegetation resilience estimated from optical remote sensing data may be problematic in regions with high biomass density, such as tropical and boreal forests [33]. To enhance the reliability of vegetation resilience estimates, we excluded pixel where $\lambda_{Var}/\lambda_{AC1}$ less than 0.5 or greater than 2.

Vegetation traits

Plant functional traits influence the strategies and capacities of plants to respond to various kinds of disturbances. We extracted five community mean leaf traits, including specific leaf area (SLA, mm^2 mg^{-1}), leaf dry matter content (LDMC, g g^{-1}), leaf nitrogen content (LNC, mg g^{-1}), leaf phosphorus content (LPC, mg g^{-1}), and leaf nitrogen/phosphorus ratio (LNPR g g^{-1}) from the global leaf trait maps provided by Moreno-Martínez et al. [72]. These maps were derived using machine learning techniques based on optical remote sensing data, climate data, and in-situ measured leaf traits. Canopy height (HEI, m) was obtained from the global canopy height model published by Lang et al. [81], which was produced by a deep learning model that fused sparse height data from the Global Ecosystem Dynamics Investigation (GEDI) space-borne LiDAR mission with dense optical satellite images from Sentinel-2. The effective rooting depth (RD, m) and hydraulic conductance (HC, mm day^{-1}) of global vegetation were estimated from daily microwave vegetation optical depth (VOD) by Liu et al. [82]. All trait maps were resampled to match the resolutions of the two kinds of vegetation data.

Climate data

The 2-m air temperature and total precipitation data were obtained from the monthly ERA5-Land dataset (0.1°), which is the fifth-generation atmospheric reanalysis produced by the European Centre for Medium-Range Weather Forecasts [83]. Based on this dataset, we calculated the mean annual temperature and total precipitation, as well as normalized inter-annual precipitation variability for the period 1982–2022. The aridity index was derived from the Global Aridity Index and Potential Evapotranspiration Database, version 3 (30') [84]. This index was defined as the ratio of mean annual precipitation to mean annual reference evapotranspiration, which was calculated using the FAO-56

Penman-Monteith equation. This database was computed using the WorldClim dataset version 2.1, which describes long-term surface water conditions for the period 1970–2000.

Principal components analysis (PCA)

We performed PCAs on global plant functional traits and separately for each landcover type to examine how different traits combinations relate to vegetation resilience. Specifically, we investigated the variations in vegetation resilience along the leading PCA axes. Since the functional traits were measured on different scales, all trait variables were log-transformed and standardized using z-transformation (by subtracting its mean value and then dividing by its standard deviation) before PCA. The proportion of variance explained by each principal component and the loadings of individual traits were used to interpret the dominant functional gradients.

Explainable machine learning

The XGBoost machine learning algorithm along with the SHAP (SHapley Additive exPlanations) method were applied to evaluate the impact and relative importance of both environmental factors and functional traits on vegetation resilience. XGBoost is a decision-tree-based algorithm that can effectively process large-scale datasets and handle complex nonlinear relationships among features. We constructed three types of models: (1) using only climate factors, including mean annual temperature, mean annual total precipitation, normalized inter-annual precipitation variability, and the aridity index; (2) using only functional traits; (3) using both climate background factors and functional traits. Prior to model training, all functional traits were log-transformed. Specifically, to avoid the effects of collinearity, only LNC and LNPR were retained from among leaf nutrient traits. The datasets were split into training and validation sets to prevent overfitting. The key hyper-parameters of XGBoost models, including n_estimators, learning_rate, max_depth, subsample, colsample_bytree, and reg_alpha, were determined by Bayesian optimization algorithm and cross-validation. We first compared the performances of models with different input factors to simulating the estimated vegetation resilience. The marginal contributions of each functional trait on vegetation resilience were extracted using SHAP from the fitted models [85]. SHAP is a game theoretic approach to explain the output of machine learning model. Its value is the effect of the predictor of interest in the model output for a given prediction. Higher absolute SHAP values indicate a greater contribution of traits in explaining vegetation resilience. Specifically, positive SHAP values correspond to lower resilience levels, whereas negative SHAP values mean higher vegetation resilience. We examined the importance of each trait by calculated the mean absolute SHAP values. To compare influence of traits across different landcover types, we fitted linear models between the SHAP values and the trait values for the leading three traits respectively in each landcover type. In addition, we fitted XGBoost models using functional traits for each landcover type and assessed the contributions of traits to resilience.

Declarations

Data availability

All datasets used in this study are publicly available. GIMMS NDVI is available from https://daac.ornl.gov/VEGETATION/guides/Global_Veg_Greenness_GIMMS_3G.html. Long-term VOD is available from https://doi.org/10.5281/zenodo.2575599. MODIS landcover maps (MCD12Q1) are available from https://lpdaac.usgs.gov/products/mcd12q1v061. Community weighted mean leaf traits are available from https://www.try-db.org/TryWeb/Data.php#59. ERA5-land 2m-air temperature and precipitation are available from https://cds.climate.copernicus.eu. Aridity index is available from https://doi.org/10.6084/m9.figshare.7504448.v5.

Code availability

All Python codes essential for this analysis are available via Github at https://github.com/chaichenhao-HPU/Vege-Resilience

Competing interests

The authors declare no competing interests.

Author contributions

H.H. and C.C. designed the research and performed the analysis. H.H. drafted the manuscript with intensive input from all co-authors. P.L., X.L., and J.Z. contributed ideas, interpreted the results and were involved in the editing and writing of the paper.

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Figures

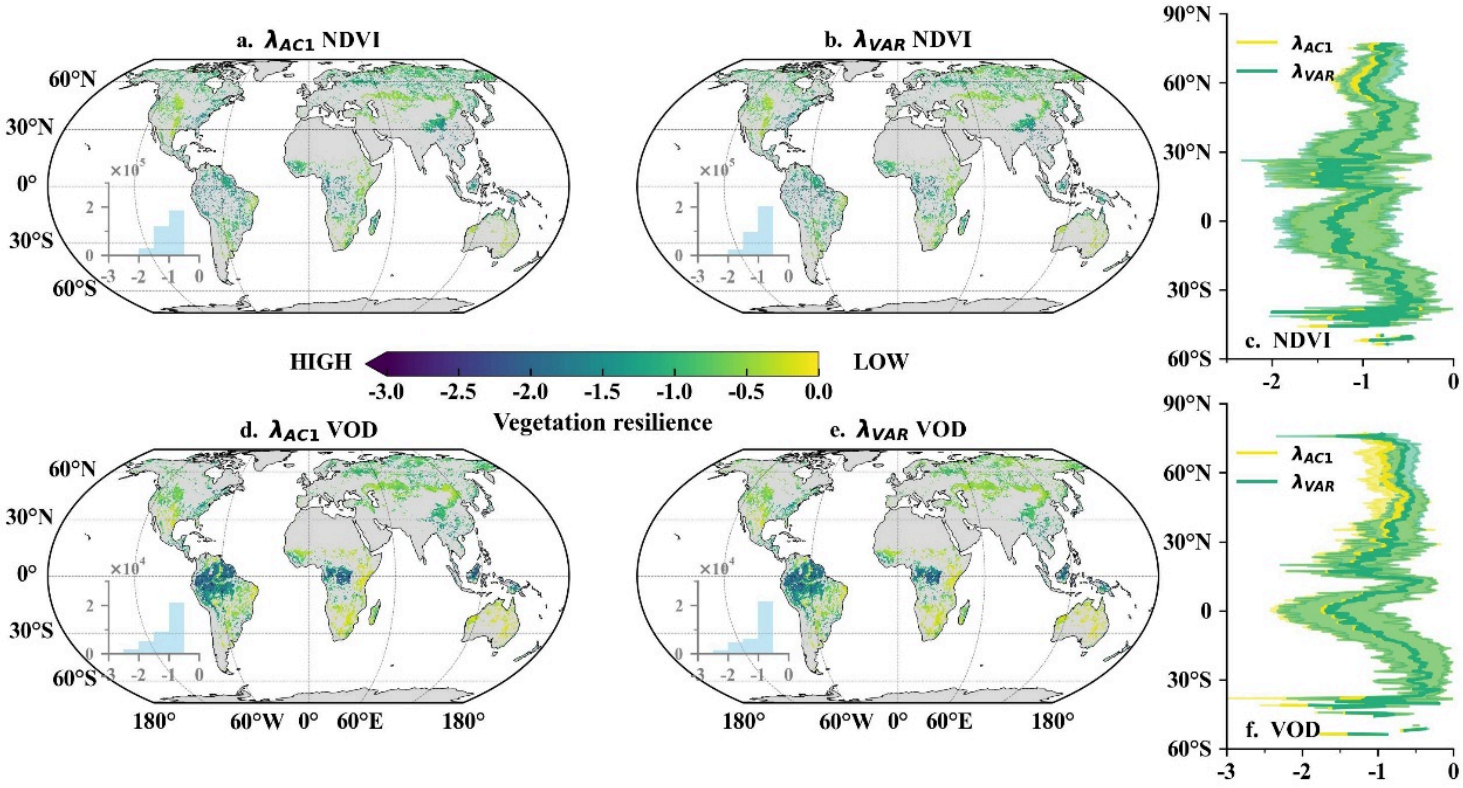


Figure 1

Spatial distributions and latitudinal variations of λ_{AC1} and λ_{Var} based vegetation resilience metrics derived from NDVI and VOD.

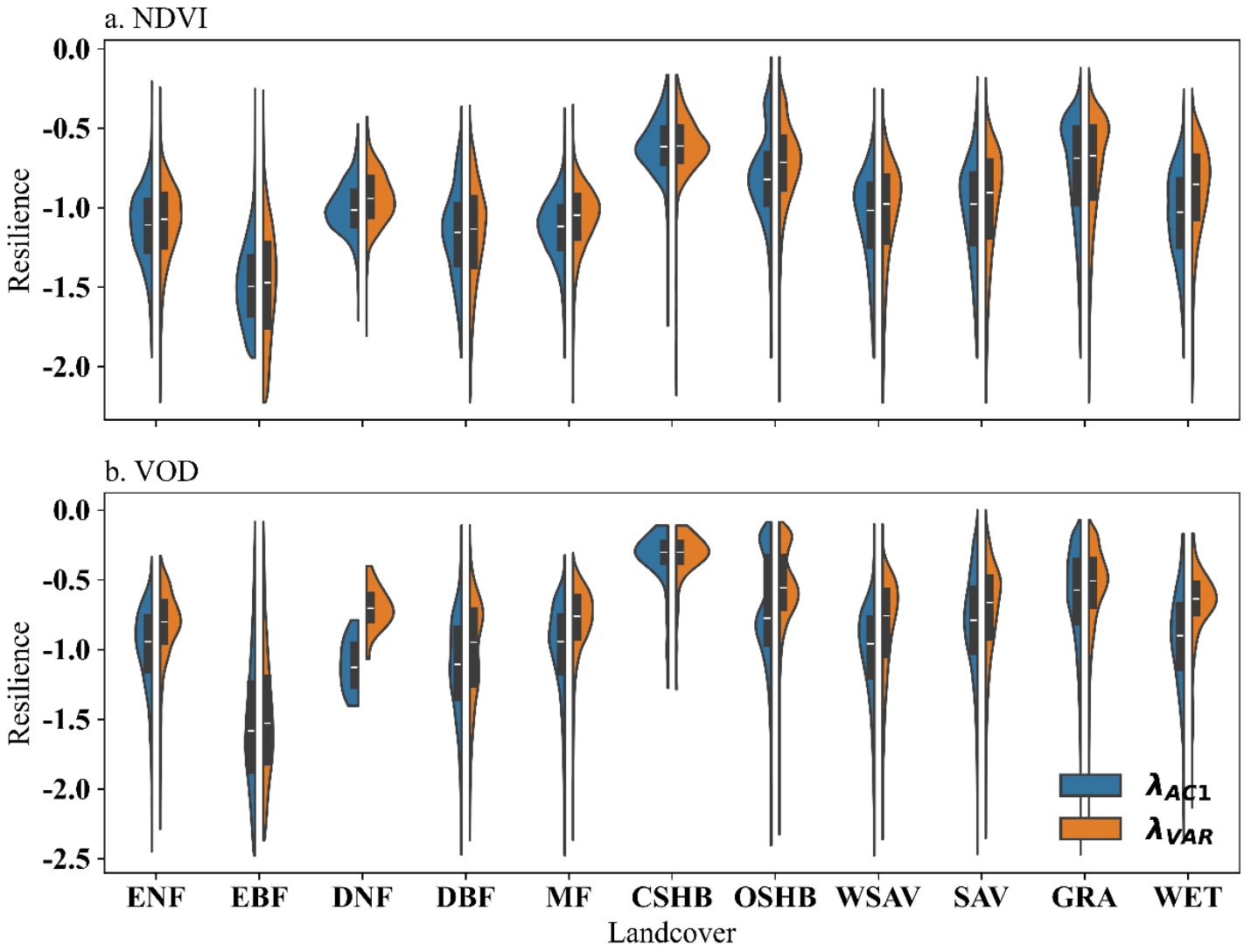


Figure 2

Vegetation resilience based on NDVI (a) and VOD (b) across IGBP land cover types. Resilience was quantified using two metrics: lag-one autocorrelation (λ_{AC1}, blue) and variance (λ_{Var}, orange). Violin plots depict the distribution of resilience values; white lines indicate medians, and black bars represent the interquartile range. ENF: Evergreen Needleleaf Forests, EBF: Evergreen Broadleaf Forests, DNF: Deciduous Needleleaf Forests, DBF: Deciduous Broadleaf Forests, MF: Mixed Forests, CSHB: Closed Shrublands, OSHB: Open Shrublands, WSAV: Woody Savannas, SAV: Savannas, GRA: Grasslands, WET: Permanent Wetlands.

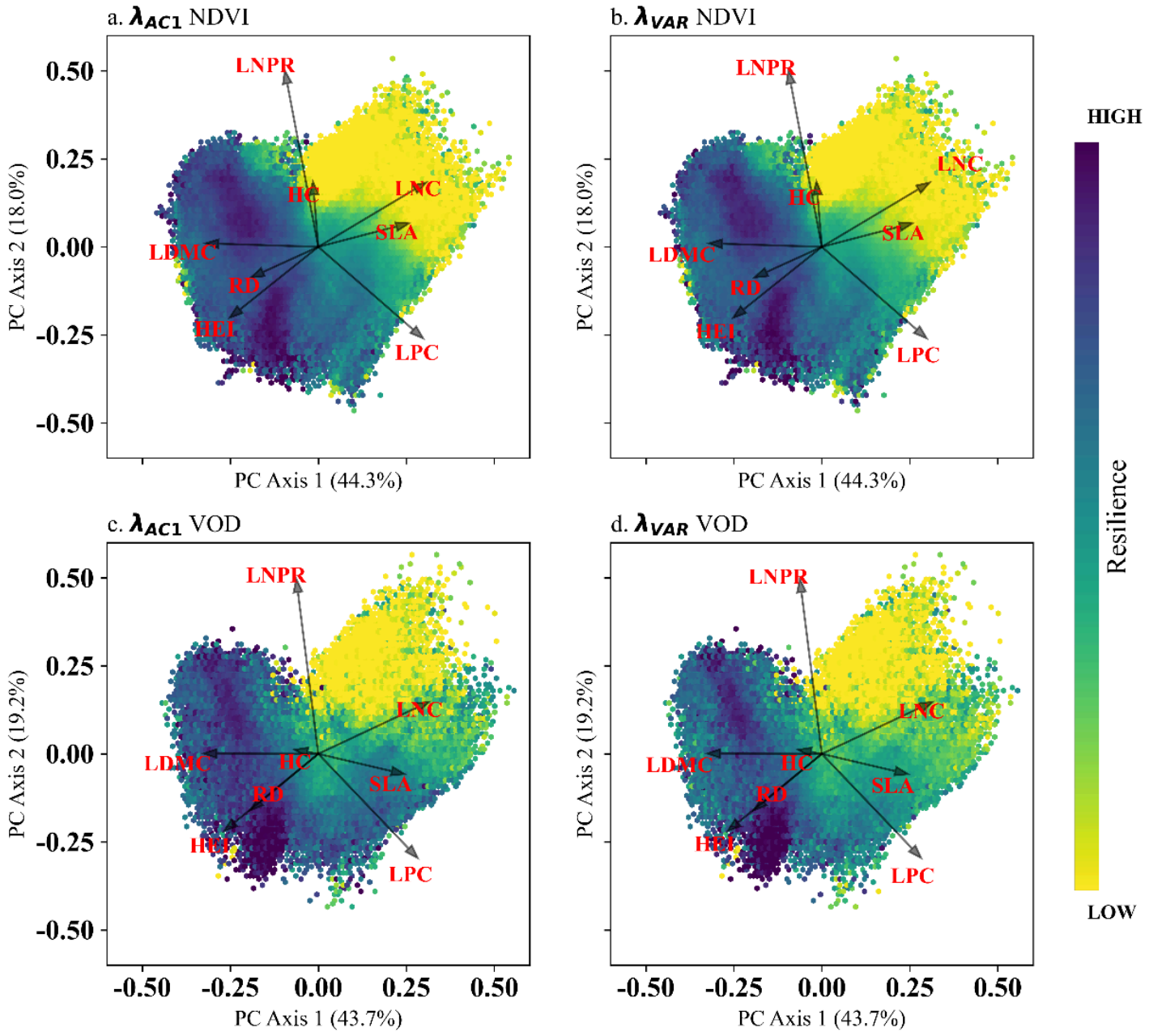


Figure 3

Distribution of vegetation resilience in principal component space of functional traits. Arrows indicate the loadings of plant traits in PCA space. The percentage on each axis indicates the proportion of total variance explained by the respective principal component. HEI: Canopy height, LNC: Leaf nitrogen content, LDMC: Leaf dry matter content, SLA: Specific leaf area, RD: Root depth, LPC: leaf phosphorus content, HC: Hydraulic conductivity, LNPR: Leaf N:P ratio. The color bar indicates a gradient of vegetation resilience, increasing from yellow (low) to purple (high).

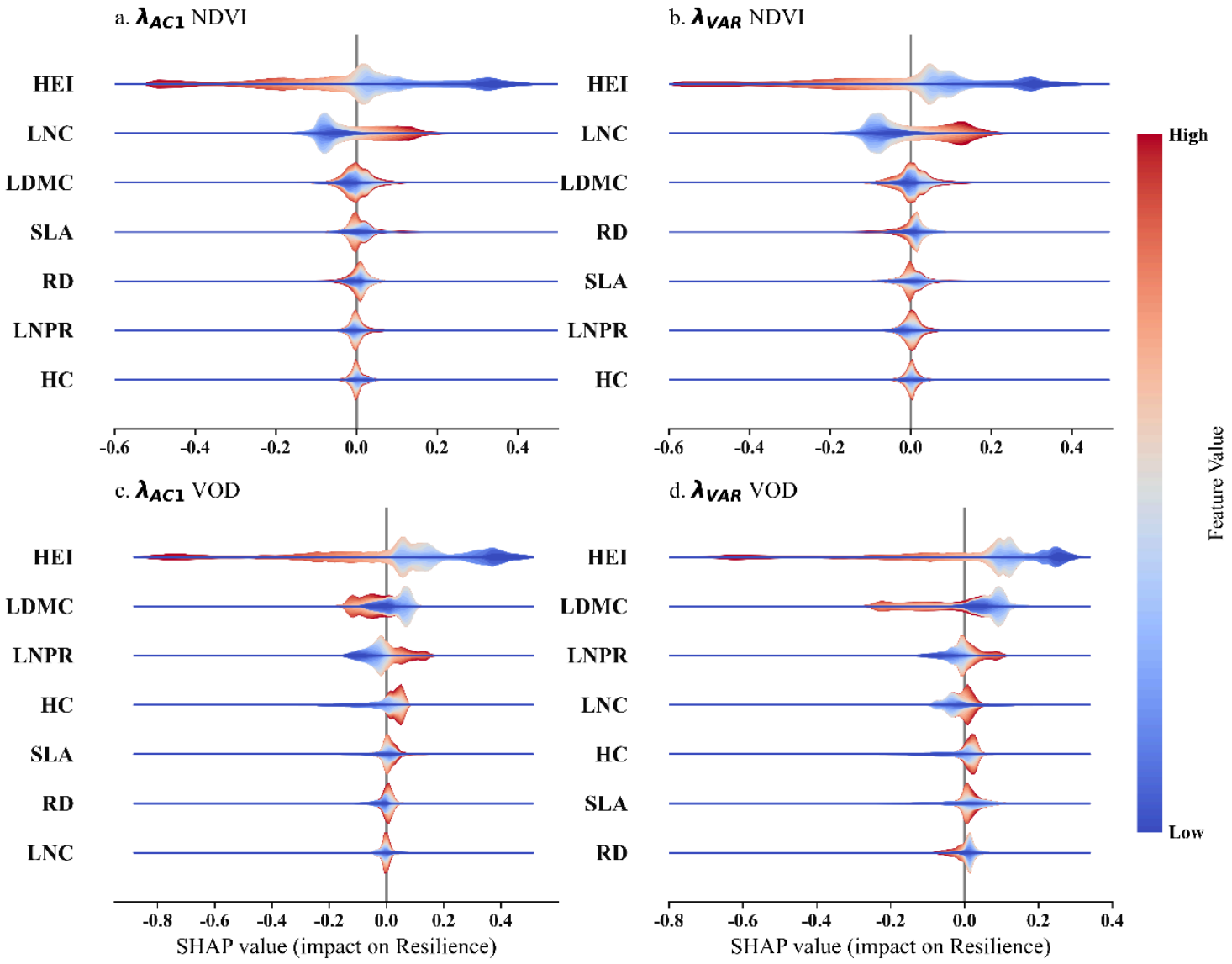


Figure 4

Relative importance and effects of plant functional traits on vegetation resilience. SHAP (SHapley Additive exPlanations) values showing the relative importance and directional influence of plant functional traits on vegetation resilience, as measured by four indicators: (a) λ_{AC1} NDVI, (b) λ_{Var} NDVI, (c) λ_{AC1} VOD, and (d) λ_{Var} VOD. Higher SHAP values indicate lower vegetation resilience. Each violin plot represents the distribution of SHAP values for a given trait, where color indicates the trait value (blue = low, red = high). Results are based on machine learning models trained to predict vegetation resilience from seven functional traits: HEI: Canopy height, LNC: Leaf nitrogen content, LDMC: Leaf dry matter content, SLA: Specific leaf area, RD: Root depth, HC: Hydraulic conductivity, LNPR: Leaf N:P ratio. Traits are ordered by their mean absolute SHAP values, reflecting their relative importance in the model.

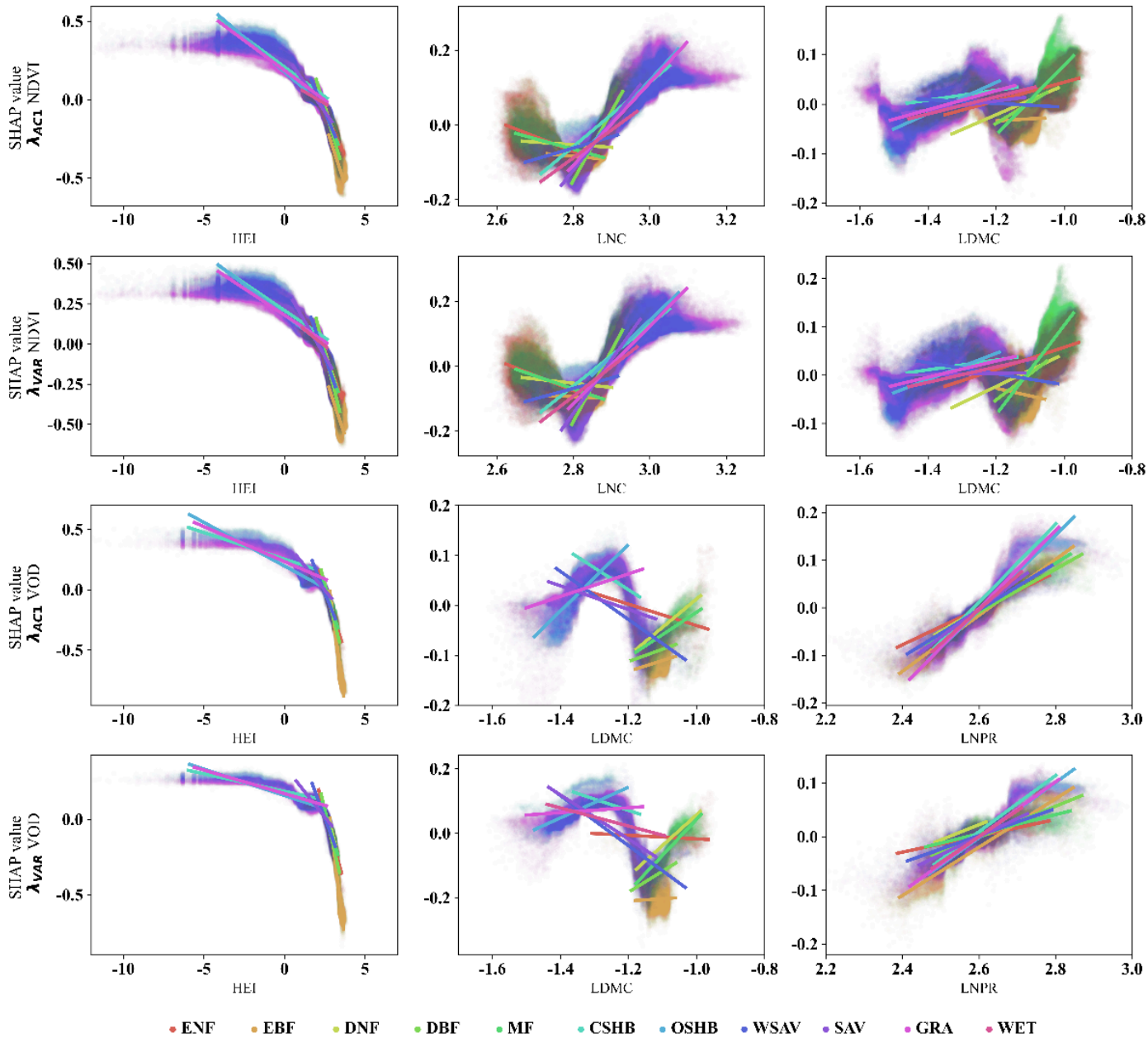


Figure 5

Influence of leading three functional traits on vegetation resilience across IGBP landcover types. ENF: Evergreen Needleleaf Forests, EBF: Evergreen Broadleaf Forests, DNF: Deciduous Needleleaf Forests, DBF: Deciduous Broadleaf Forests, MF: Mixed Forests, CSHB: Closed Shrublands, OSHB: Open Shrublands, WSAV: Woody Savannas, SAV: Savannas, GRA: Grasslands, WET: Permanent Wetlands.

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