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# Functional Trait Adaptations Drive Enhanced Post-Hurricane Resilience on Serpentine Soils

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## ABSTRACT

**Questions:** Understanding how plant functional traits mediate ecosystem resilience to extreme events is central to predicting ecological responses under variable climates. We asked: does edaphic filtering in serpentine versus volcanic soils shape plant functional composition in ways that determine forest stability (resistance, resilience, temporal stability, and recovery) following a major hurricane (Hurricane Maria)? We hypothesized that stress-tolerant serpentine plant communities would be more resistant but recover less quickly from environmental disturbances, while volcanic plant communities would show the opposite pattern, less resistance but faster recovery.

**Location:** Puerto Rico.

**Methods:** We combined trait-based analyses with remote sensing and environmental data across forest plots spanning serpentine and volcanic soils. We calculated community-weighted means and functional diversity metrics and analyzed their relationships with soil properties, storm impact (cumulative rainfall and maximum wind), and NDVI-based forest stability indicators.

**Results:** Contrary to expectations, serpentine communities exhibited greater than expected resilience and recovery, whereas volcanic communities exhibited greater than expected resistance after accounting for storm impact. Foliar iron content, functional evenness, and functional dispersion emerged as key correlates of forest stability.

**Conclusions:** Our findings suggest that nutrient-poor serpentine soils select for stress-tolerant traits that confer greater ecological resilience compared to forests on more fertile volcanic soils, challenging assumptions of serpentine vulnerability and highlighting the role of soil properties and traits in mediating ecosystem responses to extreme climatic events.

## 1 | Introduction

Ecological stability, a long-standing framework for assessing the persistence of populations, communities, and ecosystems (Pimm 1991), fundamentally involves recovery from disturbance. As extreme climatic events (like hurricanes) reshape forests worldwide, predicting responses to disturbance is both a pressing ecological and socio-economic challenge. This is especially true for tropical forests, where the potential for ecological tipping points may accelerate fundamental changes in ecosystem stability (Wunderling et al. 2024), threatening ecosystem services like carbon storage and thermal regulation in regions that sustain dense human populations. Yet, predicting responses to disturbance is challenging due to the inherent complexity of forests, which vary in structure and diversity, and occur across climatic and edaphic gradients, all of which influence forest stability and disturbance responses (Toledo-Aceves et al. 2011; Estrada-Villegas et al. 2020; Chytrý et al. 2022). Quantitative metrics further complicate our understanding. The variety of metrics used to measure forest stability (e.g., Pirrone et al. 2005; Hillebrand et al. 2018; Graham et al. 2021; Buma 2021) is as varied as the types and intensities of disturbances and ecosystem types, and one-dimensional approaches are unable to capture the many aspects of stability, making the search for generalities across ecosystems difficult.

The multidimensional stability framework (Hillebrand et al. 2018) is a promising solution. This framework describes four distinct dimensions of stability: resistance, resilience, recovery, and temporal stability. Resistance is the ability to withstand an immediate disturbance. Resilience and recovery describe the rate and the degree of return to a pre-disturbance baseline, respectively. Finally, temporal stability is the variation around the resilience slope. These metrics are calculated from log response ratios, which ensures that differences between pre- and post-disturbance values are normalized (Hedges et al. 1999), thereby facilitating comparisons across ecosystems and disturbance types (Harrison 1979; Donohue et al. 2016; Kéfi et al. 2019). As a result, the multidimensional stability framework has become a widespread tool for assessing population and community level responses to disturbances (Hillebrand and Kunze 2020) and is increasingly used to assess ecosystem level responses too (Mathes et al. 2021). Despite its popularity and broad adoption, the application of the multidimensional stability framework in tropical forests is limited (Hillebrand and Kunze 2020; Patrick et al. 2022). Understanding whether or why some forests are more stable than others requires identifying the ecological and functional attributes that mediate forest stability.

For this reason, coupling the multidimensional stability framework with a trait-based approach offers a mechanistic lens for identifying the ecological and functional underpinnings of stability across environmental gradients (de Bello et al. 2021). When functional traits are linked to stability outcomes, it is possible to identify the proximate drivers of forest responses to disturbance. In particular, soil properties exert a strong influence on plant functional composition (Vitousek et al. 1995; ter Steege et al. 2006; Jager et al. 2015) and can act as powerful filters shaping species traits, abundances, and ultimately, community resilience (Suding et al. 2008; Wonkka et al. 2016). Contrasting edaphic conditions, like those found on serpentine versus volcanic substrates, offer a natural experiment to test how plant traits mediate forest stability following major disturbances like hurricanes.

Here, we apply the multidimensional stability framework to disentangle how tropical forests on contrasting soil types respond to an acute and extreme climatic disturbance: Hurricane Maria. While functional traits have been linked to plant survival and recovery following storms (Ibanez et al. 2024), the specific pathways through which traits mediate forest stability are not well understood, particularly in tropical systems. Studies linking functional traits to forest stability have mostly focused on wood density, which appears to play a prominent role in resistance to hurricanes (Zimmerman et al. 1994; Curran et al. 2008; Webb et al. 2014; Uriarte et al. 2019). Changes in functional traits after disturbances also appear to shift from resource acquisition toward conservative strategies (Dent et al. 2013; Peñuelas et al. 2013; Monoy et al. 2016; Bauters et al. 2019; Ibanez et al. 2024; Keppel et al. 2024). However, most studies come from lowland tropical rainforests with limited heterogeneity in rainfall or soil substrates. We know, for example, that functional trait changes after tropical dry forest disturbance exhibit the opposing pattern from conservative to acquisitive strategies (Lohbeck et al. 2013; Buzzard et al. 2016). We also know that while tropical rainforests regenerate post-hurricane primarily through recruitment in newly created light gaps (Alonso-Rodríguez et al. 2022; Smith-Martin et al. 2022), tropical dry forests recover through resprouting (Van Bloem et al. 2007; Curran et al. 2008). Together, this evidence underscores the need to study the contribution of environmental properties and community-level functional traits in determining stability. In Puerto Rico, nutrient-poor serpentine soils select for conservative, stress-tolerant plant strategies (Ewel and Whitmore 1973), whereas the more fertile volcanic soils support acquisitive, fast-growing species (Ping et al. 2013). It has been proposed that the traits associated with edaphic stress tolerance may enhance resistance to disturbance (Damschen et al. 2011), though this has not been well studied. These sharply contrasting edaphic environments thus create a natural experiment for testing how trait-based ecological strategies and soil properties jointly influence ecosystem stability.

We hypothesized that serpentine plant communities would exhibit high resistance but slow recovery (lower resilience) following disturbance, due to stress-tolerant functional traits that enhance survival but limit rapid regrowth. In contrast, we anticipated that volcanic plant communities, influenced by more fertile soils, would exhibit lower resistance but faster recovery (greater resilience) due to resource-acquisitive strategies. We expected these patterns to persist after accounting for differences in storm impact. To assess this, we combined trait-based analyses with remote sensing and environmental data across soil types in Puerto Rico. Our method allowed us to quantify and compare the multidimensional stability responses (resistance, resilience, recovery, and temporal stability) of serpentine and volcanic communities and to identify the traits and environmental filters that most strongly predict these outcomes. Fundamentally, we ask whether soil properties and plant traits can serve as predictive indicators of ecosystem stability in edaphically heterogeneous tropical forests.

## 2 | Methods

### 2.1 | Study Area

Puerto Rico, part of the Caribbean Biodiversity Hotspot, supports diverse ecosystems shaped by climatic and edaphic gradients linked to its topography and geology (Gómez-Gómez et al. 2014). We selected existing forest inventory plots on serpentine soils in Susúa and Maricao State Forests and on volcanic soils in the Luquillo Experimental Forest, also known as El Yunque National Forest (Figure 1). We selected four volcanic plots representing the major forest types on volcanic substrates and six serpentine plots to capture a comparable elevational range and environmental heterogeneity across systems. For the six serpentine plots, we obtained species abundance data

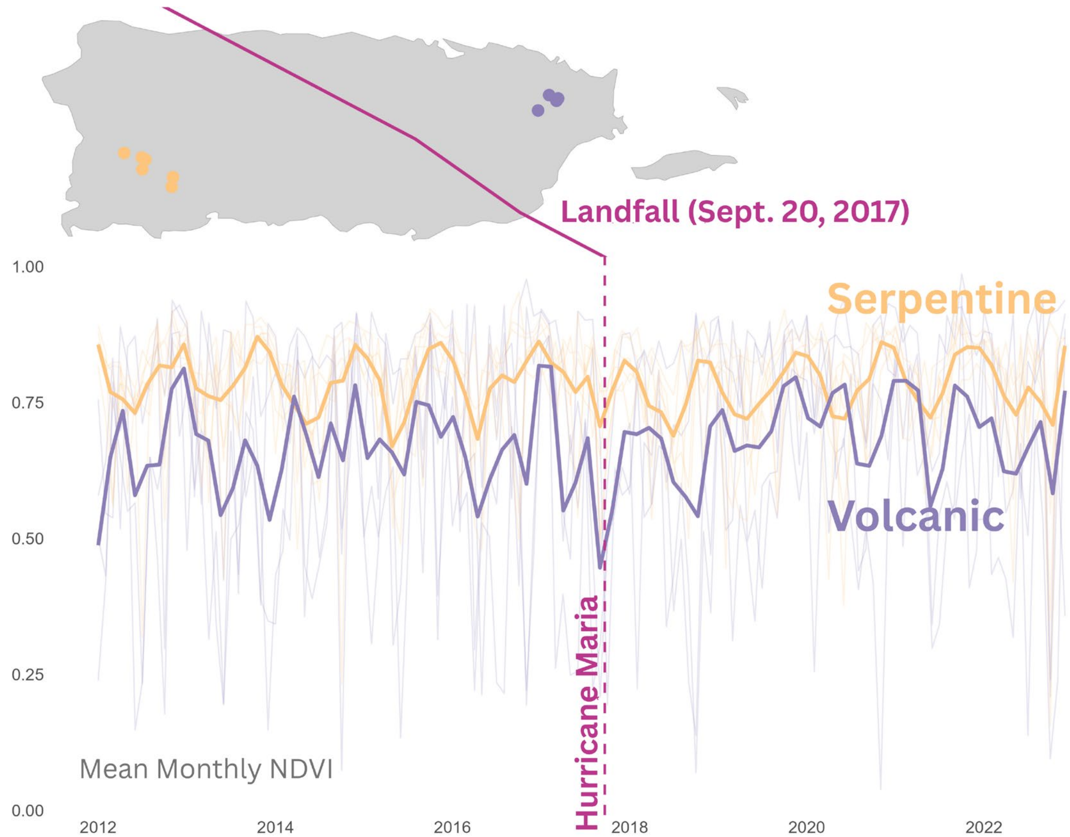


**FIGURE 1** | Sampling sites and vegetation dynamics following Hurricane Maria. Time series of mean monthly NDVI (2012–2022) for each site (grayed out), smoothed with loess curves by soil type. The vertical dashed line indicates the landfall of Hurricane Maria on September 20, 2017, illustrating the impact on vegetation and subsequent recovery. The map inset shows sampling sites grouped by soil type: Serpentine (yellow) and volcanic (purple), and the hurricane trajectory (solid line).

from the USDA Forest Inventory and Analysis (FIA) database (O'Connell et al. 2014), which measures stems > 2.5 cm diameter at breast height in nested subplots totaling approximately 700 m$^2$. For the four volcanic plots, we obtained abundance data from Gould et al. (2006), which measured stems > 2 cm diameter at breast height in plots totaling 900 m$^2$. Although plot size and minimum stem diameter differed slightly between datasets, our use of community-weighted mean traits and functional diversity metrics minimizes sensitivity to these differences by emphasizing dominant species contributions. Serpentine plant communities in Susúa and Maricao occur in moist to wet life zones across 250–875 m in elevation and are characterized by sclerophyllous leaves indicative of phosphorus limitation (Medina et al. 1994). These forests support complex vegetation structures ranging from tall trees (~15 m) to dense shrub canopies and exhibit high species diversity and woody plant density (Lugo et al. 2019). Notably, species richness was higher on serpentine soils than on volcanic soils (Tschirley et al. 1970). Volcanic plant communities in El Yunque National Forest are among the most extensively studied tropical montane forests in the Caribbean (Quiñones et al. 2018). These forests span an elevation gradient from 380 to 1000 m and encompass various forest types, including tabonuco, palo colorado, sierra palm, and elfin woodland (Gould et al. 2006). The tabonuco forests at lower elevations are characterized by tall canopy trees such as *Dacryodes excelsa* and *Sloanea berteriana*, with emergent individuals exceeding 20 m in height. At mid-elevations, palo colorado forests feature dense canopies and a significant presence of *Cyrilla racemiflora*. At the highest elevations, sierra palm (*Prestoea acuminata*) and elfin woodlands emerge (Gould et al. 2006).

## 2.2 | Storm Disturbance

In September 2017, Puerto Rico experienced two major hurricanes in rapid succession. Hurricane Irma (September 6), a Category 5 hurricane with sustained winds reaching 298 km/h, passed approximately 100 km northeast of the island. Two weeks later (September 20), Maria, the most powerful storm since 1928, made direct landfall as a Category 4 hurricane (Figure 1) with sustained winds reaching 250 km/h (www.nhc.noaa.gov, accessed June 2025). Overall, the US Caribbean lost 31% of its initial greenness after Hurricane Maria (Van Beusekom et al. 2020).

## 2.3 | Functional Trait Data

Because the Forest Inventory and Analysis (FIA) program intentionally offsets plot locations to protect site confidentiality, for serpentine sites, we limited our trait and soil sampling to the same elevation provided by FIA. For each plot (six on serpentine, four on volcanic), three to five individuals of all species accounting for at least 80% of the total abundance (Lavorel et al. 2007) were included for trait collection.

A total of 308 individuals representing 69 species were sampled for plant traits following standardized protocols (Perez-Harguindeguy et al. 2016) and were averaged by species per plot. The traits measured included specific leaf area (SLA; $cm^2 g^{-1}$), representative of the leaf economics spectrum (Wright et al. 2005); wood density (Bwd; $g\,cm^{-3}$), reflecting structural support and drought tolerance (Chave et al. 2009); xylem density (PoreDens; number pores $mm^{-2}$) and diameter (PoreDiam; mm), reflecting hydraulic strategies; and foliar nutrient concentrations (Ca, Fe, K, Mg, Mn) which were measured by ICP emission spectrometry at the International Institute of Tropical Forestry Chemical Laboratory (Río Piedras, Puerto Rico), following wet digestion protocols (Huang and Schulte 1985).

### 2.4 | Functional Composition and Diversity

Community abundance-weighted means (CWMs) were calculated to characterize dominant functional strategies. Functional diversity metrics, including functional richness (FRic), functional dispersion (FDis), and functional evenness (FEve), were calculated using the *dbFD* function from the *FD* package (Laliberté et al. 2014). Gower distances between species were calculated from scaled trait data, and a 'lingoes' correction was applied to address non-Euclidean distances.

### 2.5 | Abiotic Variables and Hurricane Impact

Site-level environmental data included elevation, soil carbon and nitrogen, soil pH, soil bulk density, and storm impact. For volcanic sites, soil data were obtained from Ping et al. (2013). For serpentine sites, soil samples were collected in triplicate per plot, composited, dried, and analyzed at the International Institute of Tropical Forestry for elemental content and physical properties following the same methodology as Ping et al. (2013). Total carbon was measured as $CO_2$ by an infrared detector, total nitrogen was determined as $N_2$ by a thermal conductivity cell, and both were reported as percentages. We used two key measures of hurricane impact: total cumulative rainfall and maximum wind speed (Pokhrel et al. 2021; https://www.eric21.org/environment).

### 2.6 | Remote Sensing and Multidimensional Stability Metrics

NDVI (Normalized Difference Vegetation Index) data, a proxy for canopy greenness and photosynthetic activity, were sourced from the MODIS (Moderate Resolution Imaging Spectroradiometer) Terra/Aqua satellite (MOD13Q1) at a 16-day temporal and 250-m spatial resolution for 5 years before and 5 years after Hurricane Maria (2012–2022). We processed the data using standard MODIS quality assurance flags to remove clouds and other atmospheric artifacts and then aggregated the NDVI data to monthly means for each sampling site to reduce high-frequency noise. For FIA plots on serpentine soils, we overlaid the plot coordinates on Google Earth imagery to confirm forest cover and placement within state forest boundaries rather than in urban or non-vegetated land cover. To quantify post-hurricane forest stability, we adopted the multidimensional stability framework proposed by Mathes et al. (2021) and Hillebrand et al. (2018), separating the response into four key metrics: the degree of initial change (resistance), the rate (resilience) and variability (temporal stability) of return to pre-disturbance levels, and the extent of return to pre-disturbance levels (recovery), all derived from temporal variation in NDVI and interpreted comparatively across soil types rather than as absolute measures. Following the methodology of Mathes et al. (2021), we used log response ratios to normalize our data and provide uniform contrasts between forests and between pre- and post-disturbance periods. The log response ratio (LRR) for a given NDVI value ($X_t$) at time $t$ relative to the pre-hurricane baseline ($X_{baseline}$) was calculated as:

$$\mathrm{LRR_t} = \ln\left(\frac{X_t}{X_{baseline}}\right)$$

The pre-hurricane baseline was defined as the mean monthly NDVI for the period from January 2012 up to August 2017, before Hurricane Maria's landfall in September 2017. We then calculated our stability metrics from these log response ratios: Resistance captures the initial magnitude and direction of the disturbance response. We calculated resistance as the log response ratio of the lowest NDVI value recorded in October 2017 (the month immediately following the disturbance), relative to the pre-hurricane baseline. A less negative value indicates higher resistance. Resilience captures the rate of return to the pre-disturbance state. We calculated resilience as the slope of the linear regression of the post-hurricane NDVI log response ratios against time (from October 2017 to the end of the study period in December 2022). A slope closer to zero indicates a faster rate of recovery. Temporal stability, a dynamic variable, represents the inter-annual variability of NDVI during the recovery period. We calculated temporal stability following Mathes et al. (2021) and Hillebrand et al. (2018) as the inverse of the standard error of the residuals from the linear regression used to calculate resilience. This captures inter-annual variability in NDVI after accounting for underlying recovery trends. This approach reflects the consistency of post-disturbance ecosystem function through time. Importantly, it is well suited to comparing systems that differ in baseline productivity or recovery trajectories, ideal for serpentine and volcanic forests given differences in forest structure. A larger temporal stability value indicates more stable, less variable post-disturbance NDVI values. Recovery summarizes the degree to which NDVI returns to or exceeds pre-disturbance rates. We calculated recovery as the log response ratio of the mean NDVI during the final year of our study (2022) relative to the pre-hurricane baseline. A value closer to zero indicates a more complete recovery. This multidimensional approach also reveals potential trade-offs between stability components, such as the often-reported trade-off between resistance and resilience (Miller and Chesson 2009; Nimmo et al. 2015).

### 2.7 | Statistical Analyses

For initial insights into the relationships driving post-hurricane recovery, we used Spearman's rank correlation coefficients (rho), adjusted for multiple comparisons using the

Benjamini–Hochberg method (Benjamini and Hochberg 1995) for functional diversity metrics, community-weighted mean traits, abiotic variables, storm impact, and forest stability metrics. The Benjamini–Hochberg method avoids excessive Type II error, thus more likely retaining biologically meaningful patterns. Then, we removed the confounding effect of storm intensity using residual-based models to link stability metrics to specific functional and edaphic drivers. We first performed standardized major axis regressions (SMA) for each stability metric against two key measures of hurricane impact: total cumulative rainfall and maximum wind speed. We used standardized major axis (SMA) regression because both our stability metrics and storm-impact variables contained inherent measurement error and natural variability, and neither variable could be considered a strictly independent predictor. SMA estimates the slope of the major axis through the joint variance of *x*- and *y*-axes, making it more appropriate for assessing proportional relationships between two ecological variables (Warton et al. 2006). The residuals from these regressions (i.e., the difference between the observed stability value and the value predicted by the storm impact model) became our new dependent variables (Figure 2a). We then regressed the residuals against explanatory variables (functional diversity metrics, traits, and abiotic variables), again

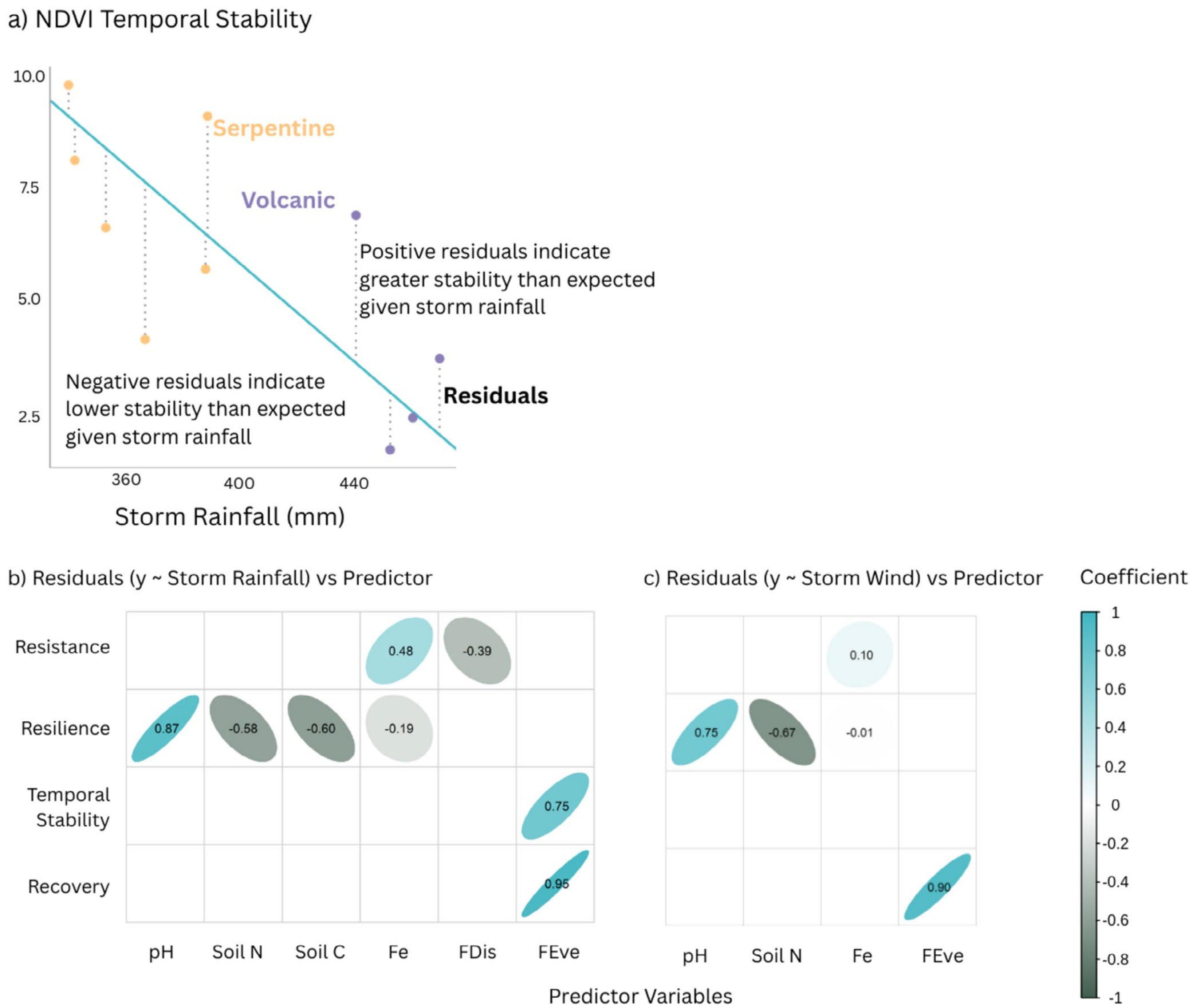


**FIGURE 2** | Disentangling the effects of storm impact from local environmental factors on forest stability metrics. (a) An example of how residuals were calculated to account for the confounding effect of storm impact. NDVI temporal stability (the dependent variable) is plotted against storm rainfall (a measure of storm impact). The solid blue line represents the standardized major axis regression. The residuals, or the distances between each data point and the regression line, represent the variation in forest stability independent of storm precipitation. We used these residuals for subsequent analyses. (b) A correlation matrix between the residuals of key forest stability metrics (resistance, resilience, and temporal stability) and storm rainfall (y ~ Storm Rainfall) and predictor variables: Soil pH, soil nitrogen (N), soil carbon (C), foliar iron content (Fe), and functional dispersion (FDis) and evenness (FEve). The shading and size of the ellipses correspond to the strength and direction of the correlation, with the coefficients shown within each ellipse. (c) A similar correlation matrix showing significant relationships between the residuals of forest stability metrics and storm peak wind speed and predictor variables. The results highlight the significant abiotic and functional correlates of resilience, after accounting for differences in storm impact.

using SMA regressions (and compared our results to those obtained from ordinary least squared regressions). This method allowed us to analyze the variation in forest stability that was not explained by the storm's intensity and answer the central question: in the context of increasing climate volatility, how do edaphic properties and functional traits determine patterns of forest resistance, resilience, temporal stability, and recovery from an extreme climatic event?

## 3 | Results

Our analysis revealed significant simple correlations among functional diversity metrics, traits, abiotic variables, and forest stability metrics (Figure 3, Table 1, Appendix S1). These correlations provide initial insights into the relationships driving post-hurricane stability. Given the limited number of plots per soil type, results are interpreted in terms of relative patterns. Resistance was positively correlated with wood (Spearman's rho $= 0.83$, $p = 0.0011$) and xylem density ($r = 0.64$, $p = 0.048$), and foliar Mg ($r = 0.64$, $p = 0.048$) and negatively correlated with cumulative storm rainfall ($r = -0.70$, $p = 0.034$), suggesting that sites with denser wood and plants with greater magnesium content were better at withstanding initial storm impacts, but that storm impact (specifically rainfall) reduced forest capacity for resistance. Resilience was positively correlated with functional evenness ($r = 0.73$, $p = 0.034$) and negatively correlated with foliar Mg ($r = -0.67$, $p = 0.042$), indicating a link between functional evenness and the rate of recovery, and was unaffected by either rainfall or wind speed (rain: $p = 0.054$; wind: $p = 0.89$). Temporal stability was positively correlated with functional richness ($r = 0.67$, $p = 0.048$) and xylem vessel density ($r = 0.87$, $p = 0.006$) and negatively correlated with foliar iron ($r = -0.81$, $p = 0.014$) and storm rainfall ($r = -0.76$, $p = 0.022$), suggesting that sites with a greater variety of functional traits and that experienced greater storm impact experienced less stable vegetation cover in the 5 years post-hurricane. Recovery was positively correlated with functional evenness ($r = 0.80$, $p = 0.021$) and unaffected by storm impact (rain: $p = 0.73$; wind: $p = 0.96$). Finally, resistance and resilience were negatively correlated ($r = -0.68$, $p = 0.038$), as expected. These simple correlations provide a preliminary understanding of the complex relationships at play and serve as a basis for the residual-based models in the next section.

Our residual-based models (Figure 2b,c, Table 1, Appendix S2), which accounted for the direct impact of the storm (cumulative rainfall and maximum wind speed), revealed key local drivers of forest stability. This approach allowed us to isolate the effects of edaphic properties and functional traits from the effects of storm impacts. In both the rain and wind models, foliar iron (Fe) was a significant positive predictor of resistance residuals (rain: adj $R^2 = 0.65$, $p = 0.0047$; wind: adj $R^2 = 0.46$, $p = 0.030$) and functional dispersion (FDis) was a negative predictor in the rain model (rain: adj $R^2 = 0.45$, $p = 0.033$), indicating that iron-deficient plants and a wider range of traits made communities less resistant than expected given storm impact. These trends remained unchanged when performing OLS regressions, which produced consistently lower slopes and lower $R^2$ values compared to SMA regressions (Appendix S2).

Soil pH, soil N, and foliar Fe were consistent predictors of resilience residuals in both storm impact models. Soil pH

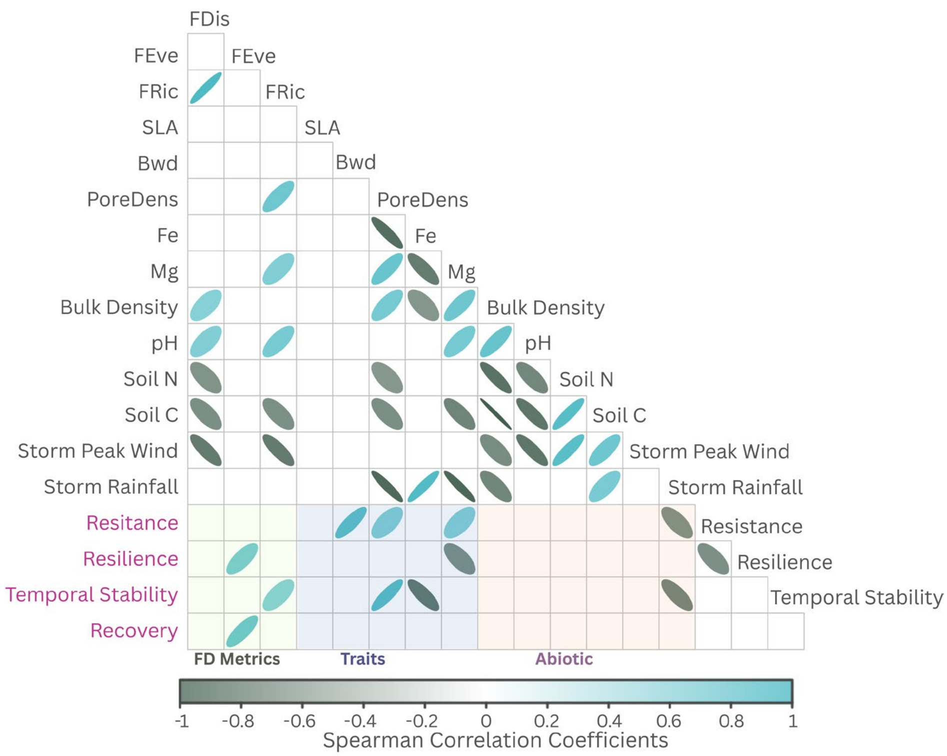


**FIGURE 3** | Functional and abiotic correlates of forest stability metrics. Colored ellipses illustrate the strength and direction of Spearman correlation coefficients; non-significant correlations are left blank. Notably, storm impact is not the sole driver of resistance and temporal stability, nor is it a significant driver of resilience or recovery. A trade-off between resistance and resilience is also evident.

was a positive predictor (rain: adj $R^2 = 0.53$, $p = 0.017$; wind: adj $R^2 = 0.45$, $p = 0.034$); thus, more acidic soils had a faster-than-expected recovery. Both soil N (rain: adj $R^2 = 0.44$, $p = 0.037$; wind: adj $R^2 = 0.42$, $p = 0.043$) and foliar Fe (rain: adj $R^2 = 0.46$, $p = 0.031$; wind: adj $R^2 = 0.41$, $p = 0.047$) were negative predictors.

Temporal stability residuals were positively predicted by FEve (adj $R^2 = 0.58$, $p = 0.017$) in the rain model only. In both the rain and wind models, functional evenness (FEve) was a significant positive predictor of recovery residuals (rain: adj $R^2 = 0.69$, $p = 0.0058$; wind: adj $R^2 = 0.64$, $p = 0.0092$), indicating that communities with a more even distribution of trait values exhibited a greater than expected recovery trajectory.

## 4 | Discussion

Our results revealed contrasting yet complementary patterns of forest stability across different soil types. Unexpectedly, serpentine plant communities, despite their nutrient-poor soils, showed greater than expected resilience, recovery, and temporal stability after Hurricane Maria, while volcanic plant communities demonstrated greater than expected resistance to initial damage, after accounting for storm impact. These differences stemmed from distinct functional and edaphic factors. High foliar iron and low functional dispersion were associated with greater resistance, emphasizing the role of dominant acquisitive species in mitigating storm impacts. Conversely, resilience correlated with soil pH, soil nutrients, and stress-tolerant traits typical of serpentine soils, indicating that pre-adaptation to chronic edaphic stress may enhance rapid recovery from acute disturbances. Recovery and temporal stability were most closely linked to functional evenness, highlighting the importance of balanced trait distributions for long-term stability. These findings illustrate a clear trade-off between resistance and resilience, influenced by soil properties and functional trait composition and support the notion that edaphic plant communities may be more resilient to disturbances.

### 4.1 | Resistance

The capacity of a forest to resist initial hurricane damage was primarily a function of plant functional traits. Our data consistently showed that communities with high foliar iron (Fe) were a strong positive indicator of greater than expected resistance in our residual-based models. Research in Puerto Rico has shown that leaf traits associated with efficient photosynthesis mediated faster tree growth after hurricanes (Umaña 2023), supporting the link between foliar iron (crucial for photosynthesis) and forest resistance found in our study. Because iron is essential to both photosystems, high foliar iron concentrations could theoretically support rapid repair of photosynthetic capacity following defoliation. Even though foliar iron is lost with complete canopy loss, it is quickly recycled via the pulse of post-hurricane litterfall (Lugo et al. 2011), enriching the soil and allowing for rapid reabsorption by regrowing foliage (Morrissey and Guerinot 2009), possibly buffering against the immediate shock of defoliation.

**TABLE 1** | A synthesis of key results, ecological importance, and larger context.

| Finding | Biological significance | Supporting studies |
|---|---|---|
| Greater foliar Fe and lower FDis = greater resistance residuals | Photosynthetic rate may point to underlying mechanisms that buffer plant tissue from hurricane-induced canopy loss. Traits of dominant species predict resistance | Leaf traits associated with efficient photosynthesis mediated faster tree growth after hurricanes (Umaña 2023). Dominant trees were resistant to hurricanes (Bellingham et al. 1995) |
| Resilience increases with greater FEve (simple model) higher soil pH, lower soil N, soil C, foliar Fe (residual models) | Suggests functional diversity and soil mediate the rate of recovery to pre-disturbance levels. Evenly distributed strategies speed recovery via complementarity (i.e., resprouting) | Traits associated with stress tolerance may enhance forest resilience to hurricanes in tropical trees (Ibanez et al. 2024; Vargas et al. 2024). Functional diversity improved tropical forest resilience after a disturbance (Schmitt et al. 2020) |
| Temporal stability greater with greater FEve (residual model) | More balanced trait strategies result in less variability through buffering; one strategy may underperform, while other strategies maintain canopy greenness, reducing variation in NDVI | More balanced functional traits contribute to reduced variability in grassland ecosystem functioning during drought (van't Veen et al. 2020) |
| Recovery faster with greater FEve (simple and residual model) | Even trait distributions suggest complementary resource use and the portfolio effect | Complementarity enhances stability by reducing the abundance of risk-prone species (Wang et al. 2021) |

The negative relationship between resistance and functional dispersion (FDis) suggests that dominant species further shape forest resistance. Less functionally diverse communities, like the volcanic soils studied here, dominated by resource-acquisitive species (Ping et al. 2013), may be better equipped for resistance than is currently assumed. This finding contradicts the biodiversity-stability framework (Loreau and de Mazancourt 2013). Instead, it supports the mass ratio hypothesis, which argues that ecosystem function is primarily driven by the traits of the most abundant, or dominant, species (Grime 1998). This result underscores the necessity of distinguishing between different aspects of stability when analyzing ecosystem responses to extreme climatic events. Here, the functional uniformity of volcanic communities, dominated by resource-acquisitive species, acts as a form of resistance. The dominance of species on volcanic soils like the hurricane-resistant palm *Prestoea acuminata* (Hogan et al. 2018; Zhang et al. 2022) and *Dacryodes excelsa* means that their traits drive resistance. Indeed, *Dacryodes excelsa* forms complex root systems that can stabilize trees against extreme winds (Basnet et al. 1993) and stands dominated by *Prestoea* and *Dacryodes* experienced less damage after Hurricane Maria (Han et al. 2026). Thus, the dominance of fewer strategies (e.g., flexible petioles, stronger root anchorage) buffers forests from the initial impact, even if they are less functionally diverse. In montane forests of Jamaica, dominant trees were also resistant to hurricanes, with little long-term impact (Bellingham et al. 1995).

### 4.2 | Resilience

In contrast to resistance, the capacity for resilience appears to be governed by a different suite of factors related to soil nutrient availability. Although we expected the nutrient-rich volcanic soils to exhibit faster post-disturbance recovery, our findings reveal a more nuanced pattern. Resilience residuals were positively correlated with soil pH and negatively correlated with soil carbon, soil nitrogen, and foliar iron. In other words, nutrient-poor serpentine soils were more resilient than expected, after accounting for storm impact. In serpentine systems, strong edaphic filtering likely links soil properties and plant traits through both direct and indirect pathways, such that traits mediating forest stability reflect underlying soil constraints rather than independent effects. This supports the hypothesis that communities adapted to edaphic stress may also be inherently better adapted to disturbances (Damschen et al. 2012), a phenomenon we interpret as resilience through pre-adaptation (Rodgers and Gomez Isaza 2023). Traits common in serpentine floras (high root:shoot biomass ratio, high wood density, and leaf sclerophylly; Kruckeberg 1984) likely underlie this response by enabling survival and regrowth under conditions that constrain other species. This is consistent with studies showing serpentine resilience to other disturbance types, including invasion (Going et al. 2009), fire (Safford and Harrison 2004), and climate change (Harrison et al. 2015), though responses were weaker for mining (O'Dell and Claassen 2009), land use change (van der Ent et al. 2015), and drought (Coppi et al. 2022). We could not identify studies explicitly examining hurricane effects on serpentine communities; however, comparable patterns have been observed on other edaphically extreme substrates. Karst forests in Puerto Rico, which share similar stress-adapted traits like sclerophyllous leaves and shorter stature, exhibited minimal hurricane impacts due to high resprouting capacity (Van Bloem et al. 2006). Similar resilience has also been documented in karst dry forests of Jamaica (Wunderle Jr et al. 1992) and Mexico (Sánchez Sánchez and Islebe 1999; Whigham et al. 2024). Together, these findings suggest that traits associated with edaphic stress tolerance (especially resprouting) enhance forest resilience to hurricanes and possibly other disturbances. Under intensifying disturbance regimes, atypical soils may hold critical insight into trait-based resilience pathways (Hulshof et al. 2026). The greater species richness of serpentine forests in Puerto Rico (Tschirley et al. 1970) may reflect strong environmental heterogeneity and niche differentiation, which may enhance the diversity of responses to disturbance. Even though the relationship between species and functional diversity is known to be complex and context dependent, it is worth exploring further in these forests. Nevertheless, serpentine systems remain vulnerable to cascading risks. Their steep and rocky terrain makes them particularly susceptible to erosion and landslides (Brady et al. 2005), especially during intense rainfall events, which may offset the advantages of their trait adaptations. Understanding how serpentine and other atypical soils respond to compounding and extreme events like hurricanes remains a significant research gap, highlighting the need for targeted research to develop more generalizable models of ecological resilience.

### 4.3 | Recovery and Temporal Stability

Recovery and temporal stability were mediated by functional diversity. The strong positive correlation between recovery and temporal stability with functional evenness (FEve) supports the importance of complementarity and functional insurance for long-term stability. Communities with a balanced mix of functional strategies, where no single trait is overly dominant, demonstrated greater than expected recovery and temporal stability. In terms of recovery, functional evenness promotes niche complementarity post-disturbance; rapid resprouting restores leaf area while deep-rooted species stabilize soil and nutrient fluxes. In terms of temporal stability, a balanced set of strategies may buffer against year-to-year fluctuations post disturbance, minimizing the variance in ecosystem functioning. Indeed, ecosystem stability is known to increase with niche complementarity through portfolio or insurance effects (Isbell et al. 2011; Wang et al. 2021), with some species resistant and some resilient. We suspect that the higher functional richness on serpentine soils, and the lower species dominance relative to volcanic soils, promotes a diverse portfolio of coexisting ecological strategies, as shown in other serpentine ecosystems (Adamidis et al. 2014; Hidalgo-Triana et al. 2018, 2023), enhancing community-level insurance against disturbance (e.g., de Bello et al. 2021; Loreau et al. 2021), even though this translates to a trade-off with immediate resistance. The wide range of wood density across serpentine sites (Appendix S3) supports this idea. We also suspect that the greater xylem vessel density on serpentine soils and their wider range of values, indicating a greater variety of hydraulic strategies compared to volcanic soils, further contributes to reduced NDVI variance following disturbance.

### 4.4 | Trade-Offs and Storm Impact

Our results demonstrate a fundamental trade-off between resistance and resilience influenced by soil type and trait composition. Communities with acquisitive traits in volcanic soils exhibited greater than expected resistance to damage, whereas those characterized by stress-tolerant strategies in serpentine soils recovered more quickly than expected. Our analyses also showed that storm rainfall rather than wind speed was a more important driver of forest stability. This finding is critical because many hurricane studies emphasize wind as the dominant factor (Ibanez et al. 2024), highlighting a need to consider hydrological stress alongside mechanical disturbance (Hall et al. 2020). Crucially, rainfall, which constrained resistance and temporal stability, did not constrain resilience or recovery, which were dictated by the local edaphic and trait environment, confirming that different dimensions of stability are governed by fundamentally different processes.

### 4.5 | Limitations

Our study provides a framework for identifying the vulnerabilities of forest types to an extreme disturbance. However, we recognize that many uncertainties still exist regarding the influence of storm characteristics and storm frequency (Hogan et al. 2018), as well as interactions with other factors not considered here, like topography and microsite hydrology, or compounding disturbances like fire (Whigham et al. 2024) or drought (Smith-Martin et al. 2022; Matlaga et al. 2024). In addition, our temporal scale was limited to 5 years post-hurricane; some successional processes and full recovery trajectories may require longer timeframes than those observed here. Material legacies, resources that persist through disturbance and support ecosystem recovery (Johnstone et al. 2016), may further influence forest stability patterns as they may fundamentally differ between soil types (e.g., patterns of soil nutrient retention or reabsorption from a pulse of leaf litter). We also note that the number and placement of plots were constrained by the spatial distribution of edaphic systems, with volcanic plots representing major forest types and serpentine plots selected to span a comparable elevational range. While sample size necessarily constrains statistical power, the consistency of observed relationships across plots supports the use of these data for comparative inference between contrasting edaphic systems. Furthermore, recent work advocates for moving from pixel-based to crown-based remote sensing approaches to better capture forest responses to extreme storms (Han et al. 2026). Future comparative work across other atypical Caribbean soils, such as karst, or other serpentine outcrops, and across a range of spatial (e.g., Vargas et al. 2024) and temporal scales is thus needed to develop broader ecological generalizations. Finally, our models did not include several critical mechanistic traits. Future research should include hydraulic traits (e.g., resistance to embolism), physiological plasticity, and detailed root traits (e.g., rooting depth, root biomass ratio) to examine the structural and physiological mechanisms underlying the resistance–resilience trade-off. Serpentine outcrops are also vulnerable to erosion and landslides (Brady et al. 2005), which could impose a distinct, unmeasured constraint on the true stability of these ecosystems.

## 5 | Conclusions

Contrary to our expectations, serpentine forests demonstrated greater than expected resilience, highlighting that nutrient-poor systems can serve as models of ecological recovery under intensifying climate extremes. Our findings suggest that selection toward stress-tolerant traits across soil types enhances resilience to hurricanes and different aspects of functional diversity mediate different dimensions of forest stability. Low functional dispersion led to greater resistance, and high functional evenness led to greater temporal stability and recovery. Our results also reveal a resistance–resilience trade-off that is determined by soil–plant interactions, suggesting that nutrient-poor soils promote resilience at the expense of resistance, and the opposite is true for nutrient-rich soils. These findings suggest that conservation of functionally diverse forests may be key to maintaining ecosystem stability under intensifying climate extremes, particularly for atypical soils. Understanding the interacting effects of edaphic properties and functional traits remains crucial for forecasting forest responses to extreme events.

### Author Contributions

C.M.H. conceived the idea; C.G.D., G. González, R.A., G. Garay, M.M.R., and H.R. collected field data; C.G.D., G. González, and L.E.V.R. completed trait measurements and laboratory analyses; C.M.H. performed statistical analyses and data visualization with input from C.G.D.; C.M.H. wrote the original manuscript with input from C.G.D.; funding acquisition was led by C.M.H. and G. González; all authors reviewed and commented on the manuscript.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

All data are available from the Forest Service Research Data Archive (https://doi.org/10.2737/RDS-2026-0012).

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Correlation matrix of functional, edaphic, storm, and stability metrics. **Appendix S2:** OLS versus SMA stability residuals and drivers. **Appendix S3:** Comparison of functional diversity, CWM traits, and abiotic factors between soil types.