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Spatial configuration and climatic drivers of post-infestation resilience in Honduran pine forests.

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Abstract

Pine forests in Honduras are increasingly affected by extreme weather events, land use change, and bark beetle outbreaks, primarily caused by *Dendroctonus frontalis*, posing significant challenges to ecosystem resilience. This study evaluates how spatial configuration and climatic conditions interact with forest structure, species composition, and regeneration dynamics to shape post-infestation recovery. We combined field-based forest inventories with satellite-derived vegetation indices (NDVI, GCI, ARVI) to assess recovery patterns across twenty-seven pine forest patches differing in size and shape. Environmental variables, including precipitation and elevation, were integrated to identify the main drivers of post-disturbance resilience.

Our results indicate that precipitation and elevation are the strongest climatic drivers of vegetation recovery, while patch shape plays a central role in determining structural and compositional trajectories. Elongated patches, despite experiencing higher initial mortality, exhibited greater regeneration potential of *Pinus* species, likely due to increased light availability and reduced competition. In contrast, compact patches retained higher basal area, greater canopy continuity, and a higher relative abundance of broadleaf associates such as *Quercus* and *Liquidambar*. Species diversity was consistently higher in control plots, highlighting the contribution of non-pine species to long-term structural stability.

By integrating spectral, structural, and compositional indicators, this study demonstrates that spatial configuration is a key determinant of forest resilience following bark beetle infestation in Central America. These findings underscore the importance of adaptive management strategies that consider patch geometry, climatic variability, and multispecies regeneration to enhance the resilience of pine-dominated landscapes under increasing environmental change.

INTRODUCTION

Pine forests in Honduras are increasingly affected by extreme weather events, land-use change, and recurrent bark beetle outbreaks, primarily caused by *Dendroctonus frontalis*. The frequency and severity of these disturbances have intensified under changing climatic conditions, resulting in extensive tree mortality and substantial degradation of forest structure (Billings et al. 2004; Raffa et al. 2008; Gomez et al. 2020). The most recent large-scale outbreak, occurring between 2014 and 2016, affected more than 500,000 ha of pine forests, highlighting both the magnitude of the disturbance and the urgent need to understand the mechanisms that govern post-infestation recovery (ICF 2017; Carias et al. 2018). Historical records indicate that bark beetle infestations have recurred in Honduras since the early twentieth century, often associated with drought events and regional climatic oscillations (Rojas 2010; Darr 2019). These outbreaks rank among the most severe natural disturbances in Central American forest ecosystems and provide a critical context for examining forest resilience under increasing climatic stress.

Pine–oak forests extend from the southwestern United States to Nicaragua and represent one of the most widespread forest ecosystem types in Mesoamerica. In Honduras, coniferous and mixed forests

cover approximately 42% of the national forest area and supply essential ecosystem services, including water regulation, carbon storage, biodiversity conservation, and livelihood support for rural communities (Vasquez et al. 2020). These forests are dominated by *Pinus oocarpa* and *Pinus caribaea*, with *P. maximinoi* and *P. pseudostrobus* occurring mainly at higher elevations. Broadleaf associates such as *Quercus sapotifolia*, *Liquidambar styraciflua*, and *Alnus jorullensis* contribute to nutrient cycling, structural heterogeneity, and long-term ecosystem stability. The interaction between coniferous and broadleaf species plays a central role in determining regeneration pathways following large-scale mortality events, making it essential to understand how these functional groups reorganize after disturbance.

Forest resilience is commonly defined as the capacity of ecosystems to reorganize following disturbance while maintaining their structure, composition, and key ecological processes (Holling 1973; Folke 2006). In the context of bark beetle outbreaks, resilience is influenced by the interaction of climatic conditions, elevation, forest density, and the spatial configuration of forest patches (Seidl et al. 2017; Sommerfeld et al. 2023). Evidence from temperate and subtropical regions indicates that homogeneous pine stands are more vulnerable to infestations, whereas structurally diverse forests and well-connected landscapes tend to exhibit greater resistance and faster recovery (Anderegg et al. 2015; Dhar et al. 2016; Windmuller Campione et al. 2021). In Honduras, strong seasonal variability in infestation intensity has been documented (Vásquez et al. 2020), and more than one quarter of the country's pine forests were affected between 2019 and 2023 (Orellana et al. 2025). Management responses have focused primarily on sanitation logging and containment measures, including the establishment of biological corridors (Gomez et al. 2020; Carias et al. 2018). However, the factors that control the pace and trajectory of post-disturbance recovery remain insufficiently quantified.

Recent advances in forest ecology and entomology have expanded understanding of beetle–forest interactions beyond immediate tree mortality. Studies have shown that bark beetle outbreaks influence decomposition rates, nutrient cycling, soil respiration, and longer-term regeneration processes (Clay et al. 2024; Siegert et al. 2024). Regional analyses have identified strong climatic and elevational gradients associated with the distribution and activity of *Dendroctonus* species (Saenz Romero et al. 2023), while experimental and observational studies demonstrate that drought and heat stress increase host vulnerability to infestation (Bernal et al. 2023). Together, these findings underscore the need for integrative analyses that combine climatic variability, forest structure, species composition, and spatial configuration to explain heterogeneous recovery patterns across landscapes.

In this study, forest resilience is interpreted as the capacity of individual forest patches to regain pre-disturbance canopy attributes, species composition, and functional diversity over time (DeRose and Long 2014; Xu et al. 2016). Recovery is expected to vary with precipitation, elevation, and spatial configuration, which jointly influence exposure to edge effects, microclimatic stress, and resource availability (Laurance et al. 2018). Elongated or fragmented patches may experience higher initial mortality but can create favorable conditions for regeneration through increased light availability and reduced competition, particularly for pioneer species such as *Pinus oocarpa*. In contrast, compact

patches may retain higher basal area and preserve broadleaf associates that contribute to long-term structural stability.

The objective of this study is to evaluate the recovery capacity of pine forest patches in Honduras following bark beetle infestation and to identify the main climatic and spatial drivers of post-disturbance resilience. Structural attributes, including tree density, basal area, regeneration ratios, and species diversity, were analyzed alongside vegetation indices and biophysical variables to assess recovery across patches differing in size, shape, precipitation, and elevation. Two hypotheses were tested: (1) compact and less fragmented patches maintain greater canopy continuity and higher species diversity, whereas elongated patches, despite higher initial mortality, exhibit stronger regeneration due to increased light availability and reduced competition; and (2) climatic variables, particularly precipitation and elevation, are positively associated with vegetation recovery following disturbance. By integrating structural, compositional, and spectral indicators, this study provides new insights into the mechanisms shaping forest resilience in Central America and offers a scientific basis for adaptive forest management under increasing environmental variability.

METHODOLOGY

Study area and environmental conditions

Sampling plots were established across a broad range of climatic, topographic, and landscape conditions in Honduras, spanning elevations from 500 to 2,000 m a.s.l. This gradient encompasses substantial variation in temperature, precipitation, soil properties, and forest structure. Mean annual temperatures range from 18 to 26°C in lowland areas and can decrease to approximately 10°C at higher elevations during cooler months. Annual precipitation varies between 1,200 and 2,500 mm, with higher rainfall occurring in upper montane zones. Climatic data were obtained from the TerraClimate dataset (Abatzoglou et al. 2018) and complemented with records from the National Meteorological Service and the Permanent Commission of Contingencies.

Soil characteristics also vary along the altitudinal gradient. Lowland areas are dominated by volcanic soils with high water retention capacity, whereas mountain soils are generally shallow and rocky, leading to seasonal water stress. These edaphic differences influence regeneration potential and forest recovery processes (Turner et al. 2015). Soil information was derived from the National Territorial Information System. Slopes range from gentle to steep, exceeding 60% in some mountainous locations, and strongly affect water retention, microclimatic conditions, and post-disturbance recovery (Wang et al. 2020). Figure 1 shows the spatial distribution of sampling plots and their location within areas affected by the 2014–2016 bark beetle outbreak.

Sampling design and data collection

An exploratory and correlational study design was applied to integrate landscape, bioclimatic, topographic, and socioeconomic variables. Sampling sites were selected from pine forest patches affected by *Dendroctonus* spp., ensuring representation across a range of patch sizes, shapes, and disturbance intensities. To ensure field accessibility, only patches located within 1,000 m of roads were considered. From a total of 11,840 eligible patches, 27 were randomly selected using a stratified approach to ensure balanced representation of patch categories.

At each site, nested circular plots were established following a randomized spatial arrangement to minimize selection bias. Each patch contained three nested plots: 1,000 m² for adult trees, 100 m² for saplings, and 5 m² for seedlings. All trees were identified to species level and measured for diameter at breast height (DBH) and total height. Cut stumps were recorded to quantify human intervention related to pest control activities. This design enabled the assessment of regeneration by size class and differentiation between *Pinus* and non-*Pinus* species.

To control background environmental variability, each affected patch was paired with a nearby unaffected stand with similar site conditions. This paired-site design allows direct comparison of affected and control plots and is commonly used in studies of post-disturbance forest dynamics (DeRose and Long 2014). In total, 54 nested plots were sampled, comprising 27 affected and 27 control sites.

Spatial data on precipitation, elevation, and bark beetle-affected areas were obtained from the National Institute of Forest Conservation and Development and integrated into a GIS database as shapefiles. Additional socioeconomic and bioclimatic indicators for 2014, 2017, and 2019 were obtained from the Inter-American Development Bank to characterize land-use context and accessibility.

Forest patch classification

Forest patches were classified based on two spatial attributes: size and shape. Patch size was categorized as small (< 0.1 ha), medium (0.1–1 ha), or large (> 1 ha). Patch shape was classified as moderately circular, elongated, or very elongated using the compactness index described by Cañibano and Gandini (2018). The combination of size and shape resulted in nine distinct patch types. Patch geometry was quantified using GIS tools and metrics derived from FRAGSTATS 4.2 (McGarigal et al. 2012).

To further characterize spatial heterogeneity, a K-means clustering algorithm (Jain 2010) was applied to group patches according to shared physical and bioclimatic attributes. Variables included patch size and shape, slope, distance to rivers and populated areas, and climatic variables (precipitation and temperature) derived from TerraClimate. This classification provided a spatial framework for comparing forest structure, regeneration, and species composition among patch types.

Remote sensing data and vegetation indices

Vegetation recovery was assessed using Landsat 7 ETM + imagery for 2012–2013 and Landsat 8 OLI imagery for 2014–2023, all with a spatial resolution of 30 m. Images were corrected for atmospheric and radiometric effects using the LEDAPS algorithm. Three vegetation indices were calculated:

- Normalized Difference Vegetation Index (NDVI)
- Green Chlorophyll Index (GCI)
- Atmospherically Resistant Vegetation Index (ARVI)

These indices were used as proxies for canopy greenness and photosynthetic activity and enabled temporal assessment of vegetation recovery (Kennard 2002; Dupuy et al. 2011; Guerra Martínez et al. 2020). Annual composite images were generated for the 2012–2023 period, and vegetation indices were averaged at the patch level to match the spatial scale of field measurements.

Statistical and analytical procedures

Data analysis followed a multistep approach integrating field-based and remote sensing indicators of resilience. Structural variables (basal area, tree density, and species richness) were compared between affected and control plots using one-way ANOVA and Games–Howell post hoc tests with a significance level of 0.05 (Fettig and McKelvey 2014; Turner et al. 2019).

Regeneration ratios were calculated as the combined number of seedlings and saplings divided by the number of adult trees for both *Pinus* and non-*Pinus* species. Shannon and Simpson diversity indices were computed to assess compositional resilience and compared between affected and control plots. Species-level structural importance was quantified using the Importance Value Index (Curtis and McIntosh 1951).

Spearman correlation analyses were conducted to evaluate relationships between vegetation indices and environmental variables, including precipitation, temperature, slope, elevation, distance to rivers, and patch geometry. Generalized Linear Models (GLMs) with a Gamma distribution and log link function were used to quantify the influence of patch shape, size, elevation, slope, and distance to rivers on regeneration ratios and basal area recovery.

Principal Component Analysis (PCA) was applied to summarize relationships among structural, compositional, and environmental variables, followed by cluster analysis to identify groups of patches with similar resilience characteristics.

All statistical analyses were performed in R version 4.3.2 using the packages *stats*, *lme4*, and *vegan* (Bates et al. 2015). Spatial analyses and map production were conducted using ArcGIS Pro version 3.2.

Integration of field and spectral indicators

Vegetation indices capture temporal patterns of canopy greenness and structural recovery but do not directly measure forest health. To obtain a comprehensive assessment of resilience, spectral indicators were integrated with field-based metrics of structure and composition, including basal area, regeneration ratios, species diversity, and Importance Value Index values. This integrated framework enabled identification of both structural recovery and compositional shifts, providing a multidimensional perspective on post-disturbance resilience in pine-dominated ecosystems. The combined use of field and remote sensing indicators enhances early detection of recovery signals and supports long-term monitoring of Honduran pine forests under increasing climatic stress.

RESULTS

General patterns of recovery

The twenty-seven sampled sites were classified into nine patch types based on patch size and shape, providing a spatial framework for evaluating structural and spectral recovery across the landscape. This classification captured substantial variability in regeneration conditions associated with differences in topography, microclimate, and disturbance intensity among sites.

Relationship between vegetation indices and precipitation

Vegetation recovery showed a significant positive correlation with precipitation (Spearman's $\rho = 0.193$, $p < 0.05$). Sites receiving higher annual rainfall exhibited greater increases in vegetation indices, indicating enhanced canopy greenness and photosynthetic activity following infestation. Correlation coefficients between vegetation indices (NDVI, ARVI, GCI) and environmental variables are presented in Table 1.

Table 1
Correlation coefficients between vegetation indices (NDVI, ARVI, GCI) and environmental variables (2012–2023).

Evaluated Variables	Shapiro-Wilk normality test	p-value	Rho Coefficient
Fires	2.20E-16	0.79	0.01
Precipitation	1.43E-08	0.00**	0.19
Maximum Temperature	1.57E-14	0.67	0.02
Minimum Temperature	1.76E-10	0.59	-0.03
Distance to Populated Areas	6.28E-09	0.16	0.08
Distance to Rivers	2.20E-16	0.88	-0.01
Slope	6.67E-10	0.46	0.04
Elevation	4.37E-15	0.50	-0.04
Shape and Size	Categorical Variable	0.52	NA
Notes. *p < 0.05 indicates statistical significance. NA = Not applicable (categorical variable).*			

Vegetation indices captured broad patterns of canopy recovery but showed complementary information when combined with field-based indicators such as basal area, regeneration ratios, and species diversity.

Table 1. Correlation coefficients between vegetation indices (NDVI, ARVI, GCI) and environmental variables (2012–2023).

Temporal and spatial trends in vegetation recovery

Analysis of NDVI, ARVI, and GCI time series from 2012 to 2023 revealed three distinct phases. The years 2012–2013 represented pre-disturbance baseline conditions, whereas the period from 2014 to 2019 showed a pronounced decline in vegetation indices corresponding to the bark beetle outbreak. From 2019 onward, all indices exhibited a consistent increasing trend, indicating widespread canopy recovery across affected areas (Fig. 2).

By 2023, vegetation indices in several patches reached or exceeded pre-disturbance values, although recovery trajectories varied among patch types.

Figure 2. Mean vegetation indices for sampled plots before, during, and after bark beetle infestation (2012–2023).

Influence of patch characteristics on recovery

Recovery patterns differed markedly among the nine patch types. Relative increases in vegetation indices ranged from approximately 150% in small, moderately circular patches to more than 550% in

large, very elongated patches (Table 2). These results indicate that spatial configuration strongly influenced regeneration dynamics.

Table 2
Mean recovery (%) of vegetation indices (NDVI, ARVI, GCI) in 2023 relative to 2012 baseline, by patch type

Patch type	Shape category	Size class	N plots	Mean recovery (%)	Standard deviation	Dominant structural pattern
1	Moderately circular	Small	3	145	35	Stable canopy, low regeneration
2	Moderately circular	Medium	3	178	42	Balanced structure
3	Moderately circular	Large	3	210	57	High basal area retention
4	Elongated	Small	3	295	64	Moderate regeneration
5	Elongated	Medium	3	340	71	Active canopy renewal
6	Elongated	Large	3	365	83	High pine recruitment
7	Very elongated	Small	3	415	90	Strong regeneration pulse
8	Very elongated	Medium	3	498	106	Rapid canopy recovery
9	Very elongated	Large	3	552	118	Highest regeneration potential

Notes. Values represent the mean percentage change in vegetation indices (NDVI, ARVI, GCI) between 2012 and 2023 for each patch type. Classification follows the combined typology of shape (moderately circular, elongated, very elongated) and size (small < 0.1 ha; medium 0.1–1 ha; large > 1 ha). Higher values indicate greater vegetation recovery and structural regeneration. Standard deviations estimated from within-group variability.

Table 2. Mean recovery of vegetation indices (NDVI, ARVI, GCI) in 2023 relative to the 2012 baseline by patch type.

Compact patches retained higher basal area and canopy continuity, whereas elongated patches exhibited stronger regeneration signals. Changes in vegetation indices across patch types are shown in Fig. 3.

Figure 3. Changes in mean vegetation indices (NDVI, ARVI, GCI) in affected areas between 2012 and 2023.

Patch shape emerged as a stronger determinant of recovery patterns than patch size. Moderately circular, elongated, and very elongated patches followed distinct post-disturbance trajectories associated with differences in canopy openness and structural continuity.

Structural recovery, regeneration, and species composition

Significant differences were observed between affected and control plots for vegetation indices ($F = 5.536$, $p = 0.0225$; Table 3). Affected plots exhibited lower canopy greenness and density during the post-outbreak period, whereas control plots maintained higher values. These contrasts are illustrated in Fig. 4.

Table 3
ANOVA results comparing affected and control plots (NDVI, ARVI, GCI, basal area, tree density).

Variable	F-value	df	p-value	Significance
NDVI	5.536	1, 52	0.0225	*
ARVI	4.982	1, 52	0.0290	*
GCI	5.210	1, 52	0.0251	*
Basal area	6.415	1, 52	0.0143	*
Tree density	3.972	1, 52	0.0486	*
Notes. * indicates statistical significance at α = 0.05. df = degrees of freedom.				

Table 3. ANOVA results comparing affected and control plots (NDVI, ARVI, GCI, basal area, tree density).

Figure 4. Mean vegetation indices in affected (A) and unaffected (T) plots.

Basal area differed among patch types. Moderately circular patches contained larger trees and higher basal area, whereas very elongated patches had higher numbers of individuals due to abundant saplings and seedlings (Table 4).

Table 4
Differences in average basal area and number of trees between patch types.

Patch Shape	Total Basal Area ($m^2\ ha^{-1}$)	Pine Basal Area ($m^2\ ha^{-1}$)	Total Number of Pine Trees (ind. ha^{-1})	Average Pine Diameter (cm)
Moderately Circular	31.5a	28.2a	145.6ab	15.42a
Elongated	22.4b	20.1b	112.2b	9.84b
Very Elongated	18.9b	17.6b	250a	8.07b

Notes. Different letters (a, b, ab) indicate statistically significant differences between patch shapes according to post-hoc tests ($p < 0.05$). Values in bold represent the highest in each category. Moderately circular patches exhibited higher basal area and larger average diameters, while very elongated patches showed higher regeneration (number of individuals).

Table 4. Differences in average basal area and number of individuals among patch types.

Patch size did not significantly affect adult tree or sapling recovery. In contrast, patch shape significantly influenced regeneration ratios. Generalized Linear Models indicated higher regeneration ratios in elongated patches and higher basal area retention in compact patches (Table 5).

Table 5
Results of generalized linear models (GLM) for regeneration ratio and basal area recovery.

Variable	Estimate (β)	Std. Error	z-value	p-value	Significance
Patch shape (elongated)	0.423	0.112	3.77	0.0002	***
Patch size	0.056	0.048	1.17	0.241	ns
Elevation	0.318	0.097	3.28	0.001	**
Slope	-0.147	0.065	-2.26	0.024	*
Distance to rivers	-0.089	0.054	-1.65	0.099	ns
Intercept	1.204	0.183	6.58	< 0.001	***

Notes. GLM models fitted using Gamma distribution with log link. Dependent variable = regeneration ratio; model includes elevation, slope, patch geometry, and proximity to rivers. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant

Table 5. Results of Generalized Linear Models for regeneration ratio and basal area recovery.

Multivariate patterns of recovery

Principal Component Analysis explained 68% of the total variance along the first two axes. Basal area, elevation, and patch compactness were associated with the first component, whereas regeneration ratios and species diversity loaded strongly on the second component. The PCA separated compact

patches, characterized by higher basal area and elevation, from elongated patches, characterized by higher regeneration and diversity (Fig. 5).

Figure 5. PCA biplot showing the distribution of patch types based on structural and compositional attributes.

Importance Value Index and functional composition

The Importance Value Index revealed clear dominance patterns. In affected plots, *Pinus oocarpa* accounted for 78% of basal area and 85% of individuals. Control plots showed a more balanced composition, with *Quercus*, *Liquidambar*, and *Alnus* contributing more substantially to basal area.

Regeneration of broadleaf species was more pronounced in elongated patches. Relative abundance, basal area, and Importance Value Index values for dominant species are summarized in Table 6.

Table 6
Relative abundance, basal area, and Importance Value Index (IVI) of dominant tree species in affected and control plots.

Species	Condition	Relative Density (%)	Relative Basal Area (%)	Relative Frequency (%)	Importance Value Index (IVI)
Pinus oocarpa	Affected	85.0	78.0	80.0	243.0
Pinus oocarpa	Control	60.0	52.0	55.0	167.0
Quercus sapotifolia	Affected	6.0	8.0	10.0	24.0
Quercus sapotifolia	Control	18.0	20.0	22.0	60.0
Liquidambar styraciflua	Affected	4.0	5.0	5.0	14.0
Liquidambar styraciflua	Control	12.0	10.0	10.0	32.0
Alnus jorullensis	Affected	3.0	4.0	3.0	10.0
Alnus jorullensis	Control	8.0	7.0	8.0	23.0
Other species	Affected	2.0	5.0	2.0	9.0
Other species	Control	2.0	11.0	5.0	18.0

Notes. Values in bold indicate the highest contribution per variable. The Importance Value Index (IVI) was calculated as the sum of relative density, relative basal area, and relative frequency (Curtis & McIntosh, 1951). Affected plots were dominated by Pinus oocarpa, while control plots exhibited greater balance among broadleaf species, reflecting higher compositional diversity.

Table 6. Relative abundance, basal area, and Importance Value Index of dominant species in affected and control plots.

DISCUSSION

Influence of patch shape on regeneration

Spatial configuration emerged as a central determinant of post-disturbance recovery in Honduran pine forests. Elongated patches consistently exhibited higher regeneration rates, suggesting that increased light availability and reduced competition created favorable microsite conditions for the establishment of *Pinus oocarpa* seedlings. These findings are consistent with studies showing that edge-associated microclimatic conditions can enhance regeneration when seed sources and soil conditions are adequate (Laurance et al. 2018). In contrast, compact patches retained greater canopy continuity and basal area but showed slower regeneration, indicating a trade-off between structural stability and recruitment opportunities following disturbance.

These results challenge the assumption that patch size alone is the primary predictor of forest resilience. Instead, spatial configuration and internal connectivity appear to exert a stronger influence by regulating light regimes, microsite heterogeneity, and the distribution of residual vegetation. The regeneration pulses observed in elongated patches are consistent with disturbance-mediated regeneration models described for pine-dominated systems (Millar et al. 2007; Turner et al. 2019). Although fire was absent from the study area, canopy openings created by bark beetle-induced mortality functioned similarly to moderate disturbances that facilitate pine recruitment. Comparable dynamics have been reported in Central American pine forests affected by bark beetle outbreaks (Billings et al. 2015), reinforcing the role of patch geometry as a key driver of regeneration trajectories.

Species composition, dominance, and diversity

Marked contrasts in species composition were observed between affected and control plots. Affected sites were strongly dominated by *Pinus oocarpa*, reflecting its rapid recruitment and central role in early structural recovery. In contrast, control plots exhibited higher compositional and structural diversity, with broadleaf species such as *Quercus sapotifolia*, *Liquidambar styraciflua*, and *Alnus jorullensis* contributing substantially to basal area. These patterns highlight complementary ecological roles between conifers and broadleaf associates during recovery processes.

Diversity indices indicated that bark beetle outbreaks reduce species evenness and structural heterogeneity in the short term. However, the presence of regenerating broadleaf individuals, particularly in elongated patches, suggests ongoing compositional renewal. This supports a dynamic view of resilience in which early recovery is driven primarily by pine recruitment, followed by the gradual reestablishment of broadleaf species that enhance long-term functional stability. Similar successional trajectories have been documented in pine–oak forests of Mexico and Central America (Saenz Romero

et al. 2023), indicating that structural recovery and compositional resilience operate on different temporal scales.

Climatic drivers of recovery

Precipitation emerged as the most influential climatic driver of vegetation recovery. Its positive association with vegetation indices indicates that water availability regulates canopy greenness, seedling establishment, and the pace of post-disturbance recovery. Periods of increased precipitation coincided with accelerated recovery signals, highlighting the sensitivity of pine-dominated ecosystems to short-term hydroclimatic variability.

Although the temporal scope of this study does not allow attribution to long-term climate change, the results illustrate how interannual variability in precipitation influences regeneration success following disturbance. Regionally, bark beetle outbreaks are often associated with drought periods linked to El Niño events, which increase water stress and weaken host defenses (Gomez et al. 2020). The interaction between climatic variability and spatial configuration likely contributed to the heterogeneous recovery patterns observed across patches.

Regional implications and climate change context

Comparable patterns of bark beetle disturbance and recovery have been reported in pine–oak ecosystems of Mexico and the southwestern United States, where warming temperatures and prolonged droughts have intensified beetle activity (Anderegg et al. 2015). The present study demonstrates that spatial configuration, precipitation, and species composition jointly shape resilience in Honduran pine forests, and these mechanisms are likely applicable across Central America.

Beyond vegetation structure, bark beetle-induced mortality affects broader ecosystem processes, including nutrient cycling, soil respiration, and biogeochemical dynamics (Siegert et al. 2024). These processes may contribute to delayed or uneven regeneration in some patches and underscore the importance of considering multiple dimensions of recovery when assessing forest resilience.

Implications for adaptive forest management

The results indicate that bark beetle infestations, despite causing extensive mortality, can promote natural regeneration under favorable environmental conditions. The strong pine recruitment observed in affected areas is consistent with disturbance-mediated regeneration hypotheses (Raffa et al. 2008; Millar et al. 2007). Elongated patches functioned as regeneration hotspots due to increased canopy openness and favorable microclimates, whereas compact patches were characterized by greater structural stability.

From a management perspective, these findings suggest that adaptive strategies should account for spatial configuration and site-specific conditions. Practices such as selective thinning, assisted natural regeneration, and low-intensity prescribed burning may enhance regeneration, maintain structural heterogeneity, and reduce vulnerability to future disturbances. Incorporating patch geometry, topography,

and hydrological gradients into planning frameworks may improve restoration outcomes and long-term ecosystem stability.

Implications for forest health assessment

Integrating field-based and remote sensing indicators provided a robust framework for assessing post-disturbance recovery. Vegetation indices effectively captured temporal changes in canopy greenness but did not directly represent physiological condition or species composition. Combining spectral indicators with structural and compositional metrics, including basal area, regeneration ratios, diversity indices, and Importance Value Index values, enabled a more comprehensive assessment of resilience processes.

Future assessments would benefit from incorporating physiological indicators such as leaf water potential, mortality rates, and chlorophyll fluorescence to improve early detection of stress and enhance adaptive management decisions.

Limitations and future research

This study focused on short-term recovery patterns across twenty-seven sites, which limits broader generalization. Long-term monitoring is necessary to capture delayed responses, particularly among broadleaf species with slower regeneration dynamics. Future research should expand spatial coverage, integrate physiological and biogeochemical indicators, and incorporate climate projections to better understand resilience under compound stressors. Including landscape connectivity and hydrological modeling would further improve predictions of forest responses to repeated disturbance and increasing climatic variability.

CONCLUSIONS

This study shows that resilience in Honduran pine forests following bark beetle infestation is governed by the combined influence of spatial configuration, climatic variability, and species composition. By integrating structural, spectral, and compositional indicators, we found that precipitation and patch shape were the primary drivers of post-disturbance recovery. Compact patches tended to preserve canopy continuity and basal area, whereas elongated patches exhibited higher regeneration rates and greater species diversity, functioning as important regeneration nodes within the landscape. These results highlight spatial configuration as a critical determinant of post-disturbance recovery trajectories.

The dominance of *Pinus oocarpa* in affected sites confirms its role as a pioneer species that facilitates early structural recovery. In parallel, the presence and regeneration of broadleaf associates such as *Quercus sapotifolia*, *Liquidambar styraciflua*, and *Alnus jorullensis* underscore their importance for longer-term compositional stability. Together, these patterns indicate that structural recovery alone is insufficient to characterize resilience, which also depends on the reestablishment of species composition and functional diversity.

Vegetation indices provided valuable information on canopy dynamics over time, but their combination with field-based measurements of basal area, regeneration, diversity, and species importance offered a more comprehensive assessment of recovery processes. This integrated approach demonstrates how spectral indicators capture broad temporal trends, while field data reveal the structural and compositional mechanisms underlying forest reorganization.

Overall, this study provides new evidence on how spatial, climatic, and ecological factors interact to shape post-disturbance resilience in Central American pine forests. These findings contribute to a broader understanding of forest recovery dynamics following severe bark beetle outbreaks and provide a robust scientific basis for evaluating resilience under increasing climatic variability.

Declarations

ETHICS STATEMENT

This study did not involve human participants, personal data, or experiments with animals. All data were obtained through ecological field observations and analysis of satellite-derived imagery, in compliance with national forestry regulations. Therefore, ethical approval from an institutional review board was not required.

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Author Contribution

Juan Carlos Flores: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft.Julio C. Jut Solórzano: Methodology, Formal analysis, Data curation, Writing – review & editing.Bernardo Trejos: Investigation, Fieldwork coordination, Writing – review & editing.Marlon Granadino: Data analysis, Visualization, Writing – review & editing.All authors contributed to the final manuscript revision and approve its submission for publication.

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Figures

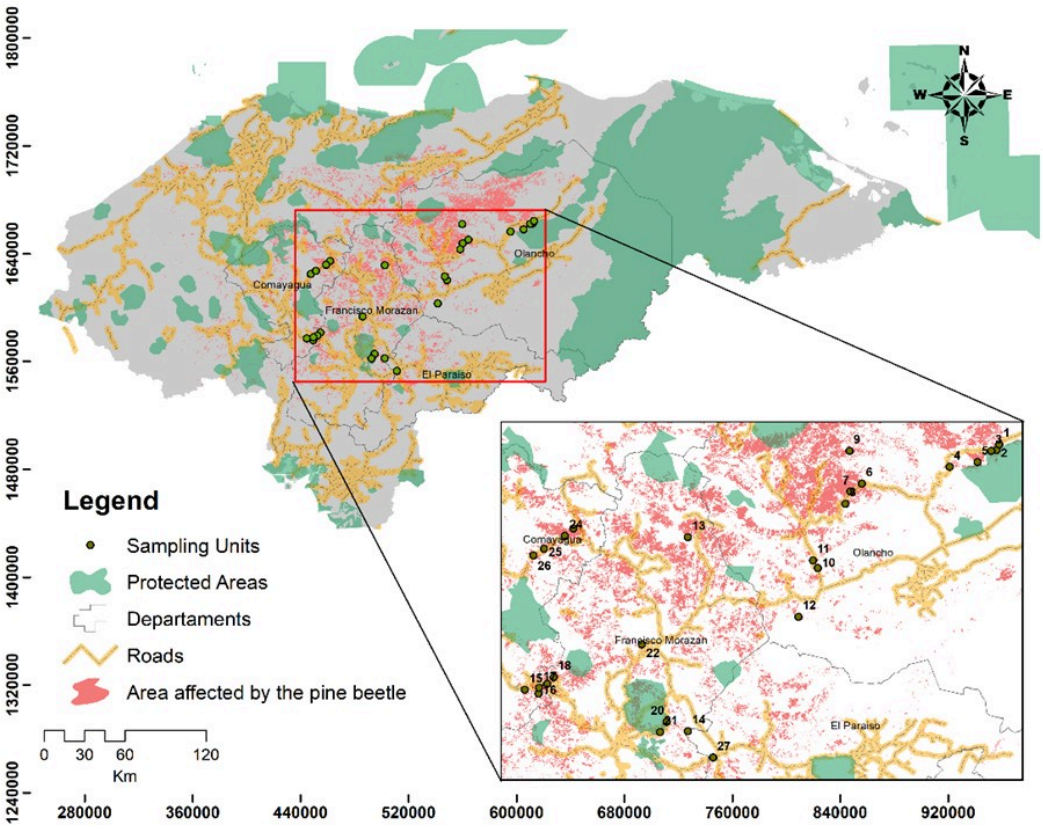


Figure 1

Location of the sampled points corresponding to areas affected by the bark beetle infestation.

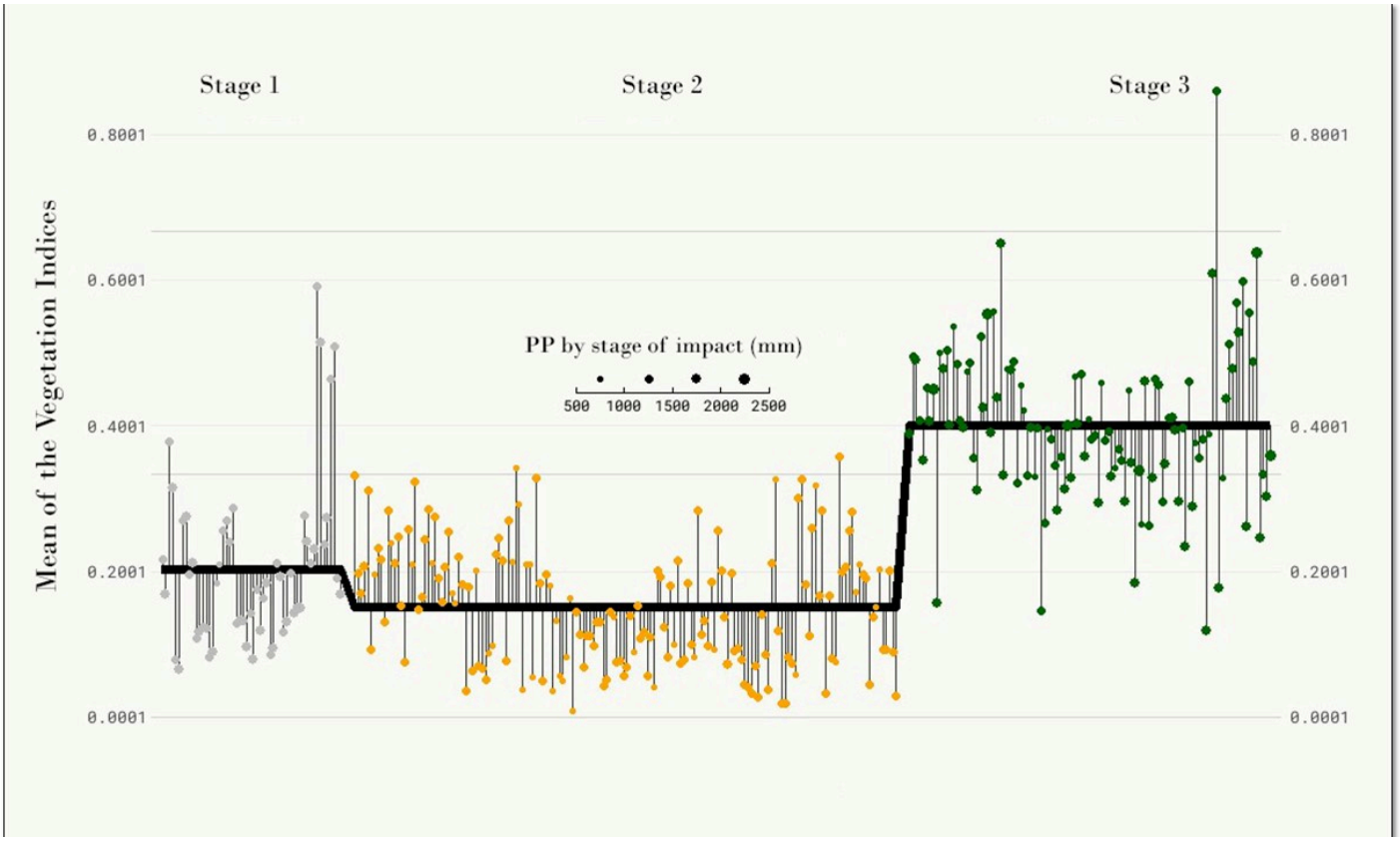


Figure 2

Mean Vegetation Indices for Sampled Plots – Stages Before, During, and After Bark Beetle Infestation (2012–2023)

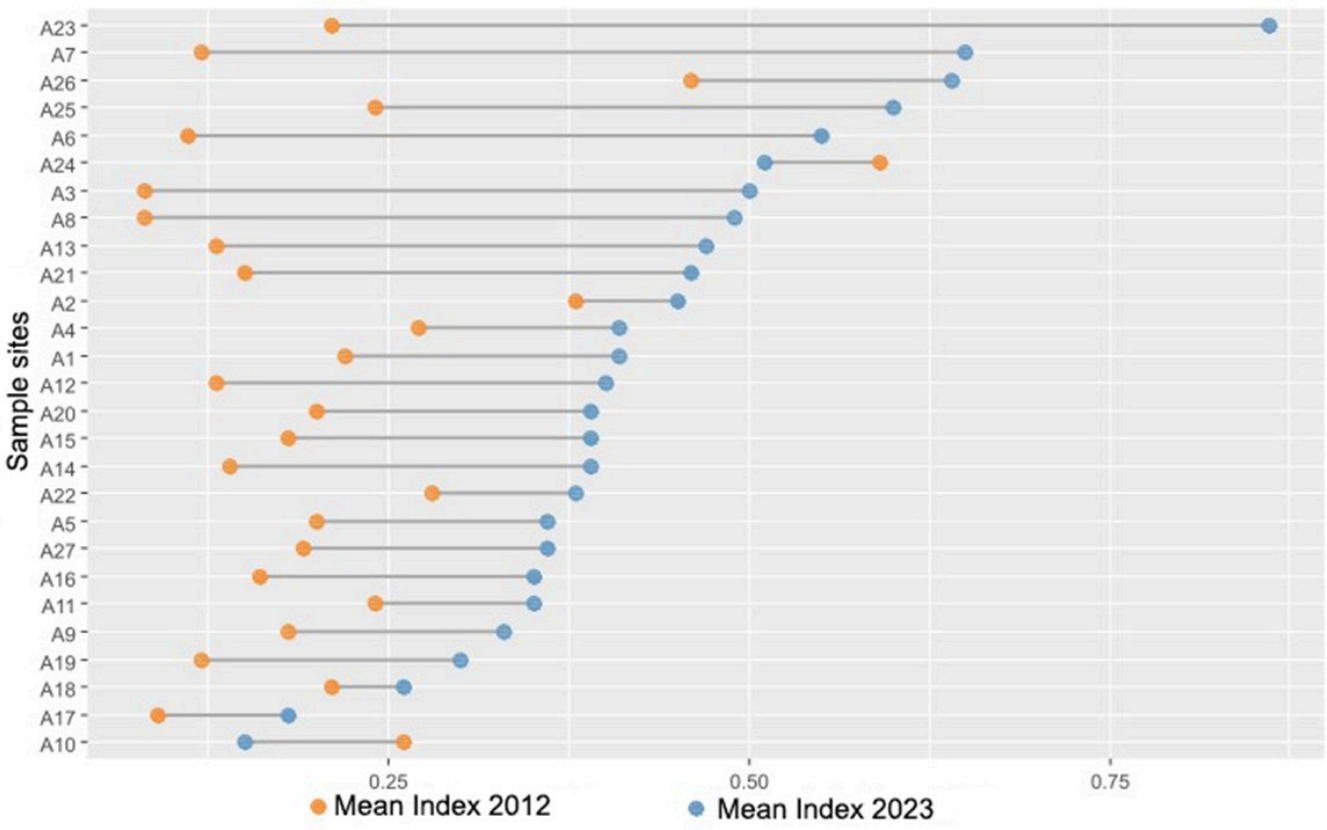


Figure 3

Difference in the mean of vegetation indices (NDVI, ARVI, and GCI) for points affected by the bark beetle from 2012 to 2023.

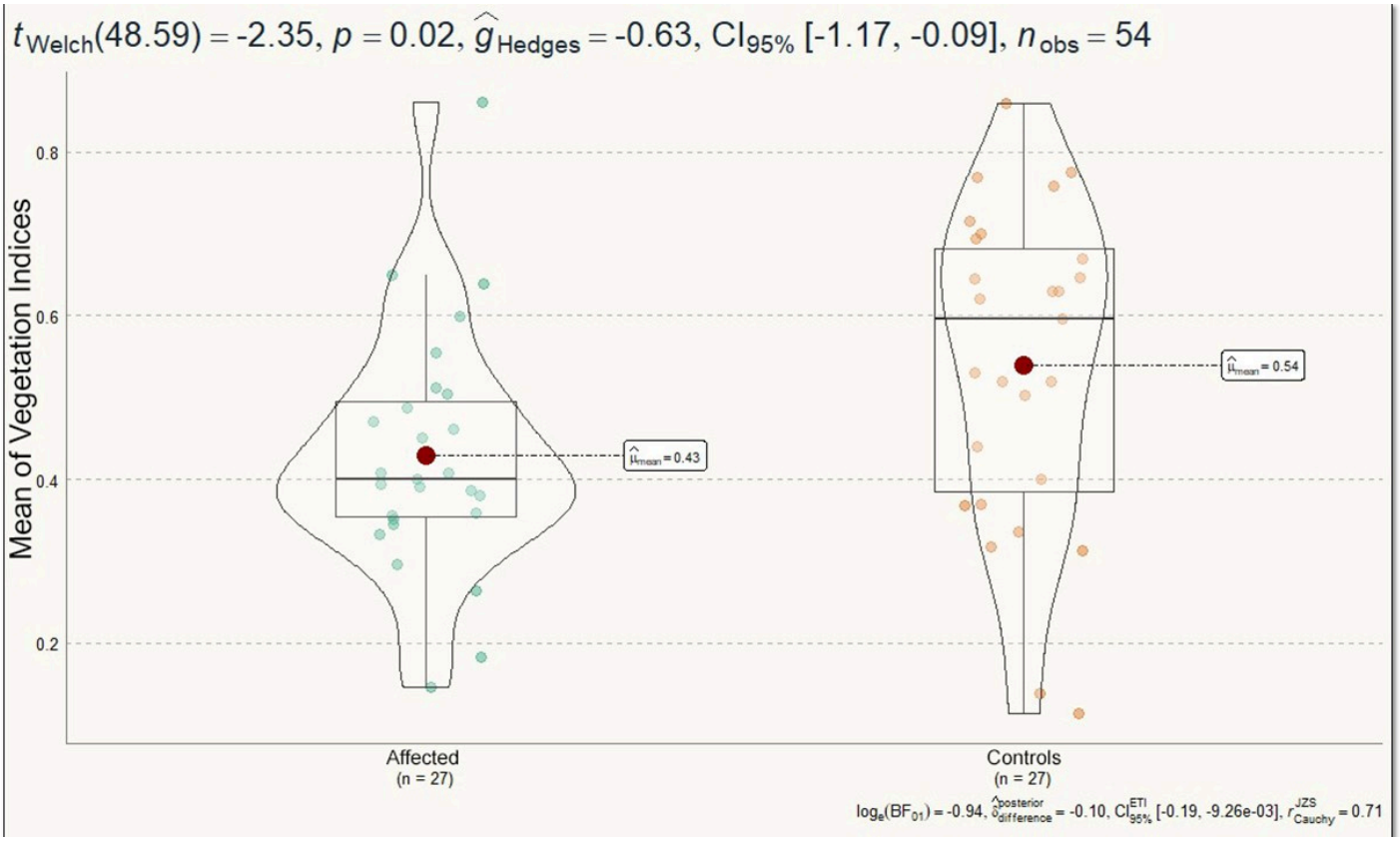


Figure 4

Mean Vegetation Indices as an Indicator of Current Forest Health in Sampling Plots for Bark Beetle-Affected and Unaffected Sites (A = affected sites, T = unaffected sites)

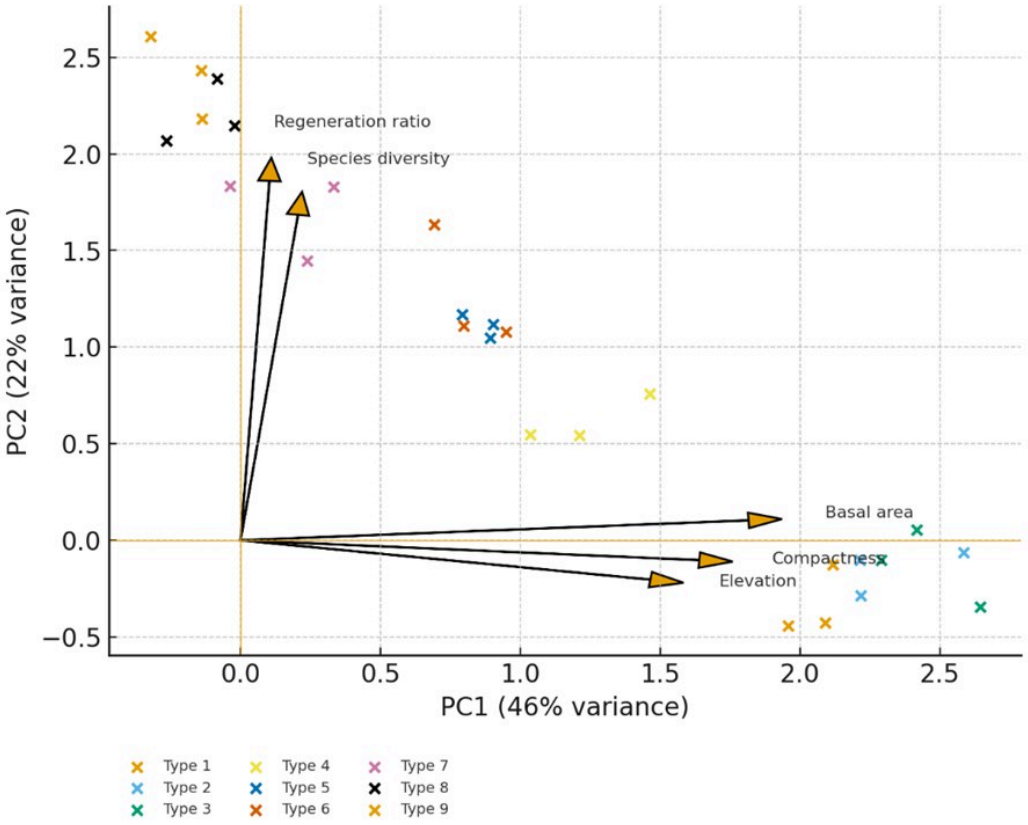


Figure 5

PCA biplot showing the distribution of nine forest patch types (n = 27) according to structural and compositional attributes.