

Hierarchical drivers and ecological thresholds of shrub-to-forest transition in Mediterranean landscapes: implications for restoration

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Abstract

Context: In Mediterranean landscapes, agricultural abandonment has promoted secondary succession from shrubland to forest. However, many shrublands persist for decades without transitioning to forest, suggesting that forest recovery following land-use change is not inevitable. Understanding how landscape context and local environmental conditions shape these contrasting trajectories is essential for predicting vegetation dynamics and supporting restoration planning.

Objectives: We aimed to identify the ecological drivers, thresholds and interactions determining shrub persistence and shrub-to-forest transition across Mediterranean landscapes.

Methods: We analysed shrub persistence and shrub-to-forest transition across Catalonia (north-eastern Iberian Peninsula) over a 35-year period (1987–2022) using 600,000 shrubland pixels, 51 ecological and environmental variables, and an explainable machine learning framework based on XGBoost and SHAP.

Results: Only 27% of shrublands present in 1987 transitioned to forest by 2022, whereas 64% remained as shrubland. Vegetation productivity (NDVI), surrounding forest and shrub cover, evapotranspiration, pH and elevation were the main predictors. Forest transition was associated with high vegetation productivity, acidic soils, lower evapotranspiration and high surrounding forest cover. The contribution of surrounding forest cover increased rapidly until approximately 40%, beyond which further increases had little additional effect.

Conclusions: Our findings support a hierarchical two-stage process in which landscape context first regulates forest transition through propagule availability, while local environmental conditions determine establishment success once dispersal limitation is overcome. This framework explains contrasting successional trajectories and highlights how landscape context and environmental filtering jointly constrain forest expansion. Identifying these constraints can improve predictions of vegetation dynamics and help target restoration interventions.

1. Introduction

Land-use management is one of the main driving forces in vegetation dynamics. Over the past few decades, socioeconomic changes in the Mediterranean basin have led to landscape transformation, primarily driven by agricultural intensification and subsequent land abandonment (Rey-Benayas et al., 2010). In regions such as the Iberian Peninsula, this abandonment has triggered spontaneous secondary succession, resulting in widespread forest expansion (Vidal-Macua et al., 2018; Cervera et al., 2019). While the recovery of forest cover is often perceived positively, it may have unintended ecological consequences. Although forest expansion generally increases forest cover, many newly established forests remain in relatively early successional stages and lack structural features characteristic of mature forests (Brotons et al., 2020). Consequently, some ecosystem functions and biodiversity values associated with mature forests may require decades to fully develop. Furthermore, increasing forest

cover may contribute to a landscape homogenisation, increased fire risk, and a loss of specialist species in favour of generalists (Le Viol et al., 2012; Varela et al., 2020).

Despite the general trend of forest expansion observed across Mediterranean post-agricultural landscapes (Chauchard et al., 2007), the process is not spatially uniform. Trees do not automatically colonise all abandoned lands (San Roman Sanz et al., 2013). Following land abandonment, the establishment of a shrubland community is typically the first phase of vegetation recovery (Navarro and Pereira, 2012; Köbel et al., 2021). Historically, these post-abandonment shrublands have been viewed as intermediate, temporary stages, often assumed to be degraded areas waiting to mature into a closed-canopy forest (Cortina et al., 2006).

However, empirical observations challenge the idea of inevitable succession, as many Mediterranean shrublands persist in a shrub-dominated state for decades without transition to forest (Acácio et al., 2007; Pato et al., 2026). In Príncipe et al. (2014), even after 60 years of land abandonment in a semiarid area of south-eastern Portugal, the most extreme microclimatic zones remained dominated by shrubs. Rather than being an arrested or delayed developmental phase, these persistent shrublands often function as highly stable, climate-adapted alternative vegetation states (Eldridge et al., 2011; Meiners et al., 2015). These divergences in landscape trajectories highlight the need to understand the environmental and ecological conditions that determine whether a shrubland transitions to forest or persists over time.

Previous studies have identified a range of environmental and climatic factors that influence vegetation dynamics in Mediterranean ecosystems, including climate, soil properties and topographic conditions (McDowell et al., 2008; Sardans and Peñuelas, 2013; Nunes et al., 2019; Príncipe et al., 2019). At the same time, landscape context may influence successional trajectories by regulating the availability of nearby forest sources and opportunities for tree colonisation (Pérez-Cárdenas et al., 2021). Moreover, recent studies suggest that vegetation dynamics in Mediterranean environments are controlled by the interaction between broad-scale climatic conditions and local-scale environmental factors, rather than by single drivers acting independently (Príncipe et al., 2022). However, much less is known about how these drivers interact, whether they operate hierarchically, and whether forest transition is governed by ecological thresholds rather than gradual responses.

Although traditional statistical models provide useful insights into the effects of individual predictors, successional dynamics emerge from complex interactions among landscape and local environmental drivers (Chang and Turner, 2019; Batllori et al., 2020). Forest transition is governed by multiple constraints operating across spatial scales and can be viewed as a sequential process, where dispersal limitation determines whether seeds reach a site (Schupp et al., 2010), and environmental conditions determine whether they successfully establish (Serra et al., 2008; Vicente-Serrano et al., 2010; Lévesque et al., 2013). Capturing these interactions and non-linear dynamics requires approaches capable of representing complex relationships among drivers (Du et al., 2025; Santo et al., 2026).

Understanding how these interacting processes determine whether shrublands persist or transition to forest is essential to explain the observed variability in successional outcomes, and becomes increasingly important under climate change, as rising temperatures and altered precipitation regimes are likely to shift the environmental conditions that regulate forest transition (Peñuelas et al., 2017; Doblas-Miranda et al., 2017). Within this context, the recent adoption of the EU Nature Restoration Law (*Regulation (EU) 2024/1991*) highlights the need for large-scale ecosystem recovery across Europe including forests, while emphasising that restoration strategies must be adapted to landscape context and local ecological conditions. Therefore, identifying ecological thresholds that distinguish where passive restoration is feasible from where active intervention is required has become increasingly important for efficient restoration planning (Vallejo et al., 2012).

In our study, we aim to identify the ecological drivers, thresholds and interactions that determine whether shrublands transition to forest or persist over time. To address this objective, we combined spatial remote-sensing data with a machine learning approach based on XGBoost and SHAP interpretation, which are well suited to identifying non-linear ecological thresholds. Focusing on a complex Mediterranean landscape in the northeast of the Iberian Peninsula, our objectives are: (1) to predict the probability of transition from shrubland to forest; (2) to identify the key ecological and environmental drivers controlling this secondary succession, and to quantify their thresholds and interactions; and (3) to assess the implication of these constraints for identifying where passive recovery is likely to succeed and where active intervention may be required.

2. Methodology

2.1. Study area

Catalonia is a region in the northeast of the Iberian Peninsula (41° 51' N 1° 34' E), covering roughly 32,000 km² (Fig. 1). It is characterised by a complex topography comprising three main relief units: the Pyrenees in the north, the Mediterranean system (Coastal and Pre-coastal mountain ranges) parallel to the sea in the east, and the Central Depression inland.

While the region is broadly shaped by a Mediterranean climate, its complex topography generates pronounced local microclimatic variations, leading some areas to differ markedly from the surrounding landscape. The Mediterranean Sea has a significant impact on pre-coastal and coastal regions, reducing extreme temperatures and providing a continuous source of humidity that often intensifies rainstorms. Inland regions, on the other hand, exhibit a continentality gradient with more pronounced day/night and summer/winter thermal contrast. Furthermore, there is an increase in rainfall, from south to north and a decrease from the coast to the central plains (Lana et al., 2004; Martin-Vide and Lopez-Bustins, 2006).

Figure 1 Study area in Catalonia (Spain). Location of the study area showing spatial variability in topography and climate, including elevation (left) (ICGC), mean annual precipitation (top right) and temperature (bottom right) (Ninyerola et al., 2005).

Land cover is highly dominated by forest and shrublands, covering approximately 60% of the territory (Generalitat de Catalunya, 2024). Its distribution follows the climatic gradients, divided into three main geographical zones. The northern mountain areas (Pyrenees and Pre-Pyrenees) are dominated by montane and subalpine forests, featuring species such as Scots pine (*Pinus sylvestris*), mountain pine (*Pinus uncinata*), and European beech (*Fagus sylvatica*). Conversely, the Coastal and Pre-coastal areas are characterized by drought-adapted Mediterranean vegetation, where Aleppo pine (*Pinus halepensis*) and evergreen Holm oak (*Quercus ilex*) are the most widespread canopy species, often interspersed with dense sclerophyllous shrublands (Cervera et al., 2019; Brotons et al., 2020). Meanwhile, the Central Depression is primarily an agricultural matrix of dryland and irrigated crops, and fragmented forest patches (Generalitat de Catalunya, 2024).

The spatial configuration of land cover in Catalonia has undergone significant historical changes. While the region previously experienced widespread agricultural expansion and deforestation (Tello et al., 2018), recent decades show an opposite trend. Today, the central plains remain an intensively managed agricultural matrix, whereas less productive mountainous and pre-coastal areas are undergoing extensive secondary succession driven by rural abandonment (Cervera et al., 2019). Consequently, there has been a progressive densification of forest cover across much of the territory (Brotons et al., 2020).

2.2. Development of environmental feature catalogue

To characterise the drivers of shrub-to-forest transition, we constructed a spatial database comprising 51 predictor variables (see Supplementary Material Table S1). These variables were selected to capture the diverse ecological, topographical, environmental and population dimensions that potentially influence successional dynamics over the 35-years period studied. The predictors were grouped into the following conceptual categories:

- Vegetation productivity (NDVI): we calculated the Normalized Difference Vegetation Index (NDVI) using Landsat 4–5 Thematic Mapper Collection 2 Level 2 satellite images (USGS, 2025). A total of eight images acquired during May from 1986 and 1987 were selected to characterise vegetation productivity during the peak growing season in the study area. Mean NDVI values were calculated for each shrubland location and used as an indicator of vegetation productivity prior to the analysed successional trajectories.
- Landscape context: to assess the role of landscape neighbourhood effects, a 500 m buffer was generated around each initial shrub observation. The percentage of each surrounding land use class within this buffer was calculated based on the 1987 landscape configuration.
- Topography: elevation and slope were extracted using the Digital Elevation Model (DEM) with a 15 m resolution from Cartographic and Geological Institute of Catalonia (ICGC, 2011). Additionally, the Topographic Wetness Index (TWI) was derived from the DEM using SAGA GIS algorithms (Conrad, 2014). Potential solar radiation with a 200 m resolution was extracted from the Digital Climate Atlas of Iberian Peninsula (Ninyerola et al., 2005).

- Bioclimate: high-resolution bioclimatic variables, including precipitation and temperature, were obtained from the Copernicus Program Climate Data Store (Wouters, 2021). Aridity index and potential evapotranspiration (ET) were derived from the Global Aridity Index and Potential Evapotranspiration Climate Database v2 (Zomer et al., 2022).
- Soil properties and lithology: soil data were obtained from European Soil Data Centre (ESDAC). Physical and chemical properties were derived from LUCAS 2009/2012 soil surveys for EU-25 and EU-26, respectively (Ballabio et al., 2016; Ballabio et al., 2019). Soil Organic Carbon was extracted from Soil Organic Carbon Maps at 90 m for peninsular Spain (Durante et al., 2024). Geology was derived from Map of lithological groups of Catalonia 1:250.000 (ICGC, 2006), which was reclassified from 39 lithological groups into 5 new classes, siliceous, carbonated, limestone, calcareous sediments, siliceous sediments, following Thuiller et al., 2003.
- Population influence: to account for human pressure, night-time lights as a proxy of human activities and population density were included in the dataset. Night-time lights were obtained from the SNPP VIIRS DNB, Monthly Cloud-Free DNB Composite for 2013, provided by the Earth Observation Group (Elvidge et al., 2017), as the earliest available high-quality proxy data. Also, population at municipality level from 2015 was taken into account (IDESCAT, 2015).

2.3. Land cover trajectories and spatial sampling

With the explanatory feature catalogue established, we defined our target response variable (successional trajectory) using 1987 and 2022 Land Use Land Cover Maps (hereafter, LULCM), developed by CREAM and provided by Generalitat de Catalunya (Generalitat de Catalunya, 2024). The LULCM, with a 30 m resolution was reclassified from its original 25 categories into 8 new classes: shrub, forest, agricultural areas, urban areas, meadow, sparse vegetation, humid vegetation, and other classes.

2.3.1. Forest balance and precursor habitats

To contextualise the precursor habitats of the regional forest expansion between 1987 and 2022, we generated a spatial layer difference between the 2022 and 1987 forest layers. The resulting layer was vectorized and overlaid onto the 1987 LULCM raster to identify the primary precursor habitats that transitioned to forest. For each polygon corresponding to new forest that appeared between 1987 and 2022, we obtained the number of pixels of every 1987 LULCM class.

2.3.2. Extraction of the shrub-to-forest transition

To isolate the specific mechanisms of shrub-to-forest succession, we converted the 1987 shrub raster layer into a point vector layer. Using QGIS Point Sampling Tool plugin (Jurgiel, 2025; *QGIS Development Team*, 2026, 2026), each point was spatially joined with its corresponding 2022 land cover class to determine its trajectory (either transition to forest, persisting as shrubland, or other). To minimise the influence of disturbance-driven transitions, we excluded points classified as burned areas in any of the

intermediate LULCM maps available at five-year intervals between 1987 and 2022. Ultimately, more than 6,000,000 points were extracted.

All the procedures for data acquisition and curation were developed via QGIS.

2.4. Machine learning framework: XGBoost Classification Model and SHAP

2.4.1. Model training and hyperparameter tuning (XGBoost)

To identify non-linear predictors of successional transition across the large spatial dataset, we used the eXtreme Gradient Boosting algorithm (XGBoost), implemented in the R package “xgboost” (Chen et al., 2025). XGBoost can efficiently handle large and imbalanced datasets while capturing complex non-linear relationships and interactions among predictors (Chen and Guestrin, 2016; Santo et al., 2026).

Due to computational constraints, a stratified random selection of 10% of the initial data set was applied, maintaining the original class proportions. The resulting approximately 600,000 observations were randomly split into a training set (80%) to define parameters and train the model, and a testing set (20%) to evaluate performance.

An iterative hyperparameter tuning process was conducted to identify an optimal combination of parameters, to prevent overfitting and maximizing accuracy in model performance (see Supplementary Material Table S2). The optimal configuration included: learning rate (eta) of 0.08, gamma of 7, maximum tree depth 4, minimum child weight 10, column and subsampling rates of 0.6, and 3000 boosting rounds with early stopping applied. This configuration provided the best balance between model complexity, overfitting control and predictive performance.

2.4.2. Model interpretation (SHAP)

Unlike simpler models, machine learning algorithms do not directly express the relationships between predictors and the response variables through explicit coefficients. Accordingly, Shapley Additive exPlanations (SHAP) values were used to interpret the influence of the 51 predictors. SHAP quantifies both the magnitude and direction of a feature’s contribution to a specific prediction by calculating its marginal impact across all possible feature combinations. A positive SHAP value indicates a variable pushes the prediction toward forest transition, while a negative SHAP value indicates a push toward shrubland persistence (Lundberg and Lee, 2017). This analysis was performed using the “shapviz” R package (Mayer and Stando, 2025).

Finally, to determine the optimal number of key variables to isolate for ecological discussion, an elbow-point method was applied to the ranked mean absolute SHAP values (|SHAP|) (Santo et al., 2026). By plotting the decline in explanatory importance, a geometric elbow point was identified, defining the threshold where marginal gains in feature importance diminished markedly.

3. Results

3.1. Forest expansion and precursor habitats

Over the 35-year study period (1987–2022), total forest cover in Catalonia increased by 12%. Shrubland was the primary precursor habitat for this expansion, accounting for 81% of all newly developed forest. However, trajectory analysis showed that succession was not an automatic process. Of the total shrubland area present in 1987, only 27% (just over one-quarter) transitioned to forest by 2022, while 64% (nearly two-thirds) persisted in a shrub-dominated state. The remaining 9% transitioned to other classes (mainly agricultural and urbanised areas).

Geographically, shrub persistence was heavily concentrated in the western and central parts of Catalonia, corresponding to drier and more continental conditions. In contrast, successful forest transition was primarily observed in the eastern and north-eastern areas, particularly the pre-Pyrenean and coastal ranges, which are characterised by higher precipitation and milder climatic conditions (Fig. 2).

3.2. Shrub-to-forest transition drivers (XGBoost classification model)

The XGBoost classification model captured these successional dynamics, achieving an overall accuracy of 80% and a balanced accuracy of 74%. The model classified shrubland persistence with an F1 score of 86%, while achieving an F1 score of 65% for forest transition. Based on SHAP value analysis and the elbow-point criterion, the model's predictions were heavily driven by six principal variables. These dominant predictors can be categorized into three ecological dimensions: vegetation productivity (represented by NDVI), landscape context (surrounding forest and shrubland cover), and local environmental conditions (pH, ET and elevation). As a result, the model is largely driven by a limited number of key factors (Fig. 3) (see Supplementary Material Figure S1).

Vegetation productivity (NDVI) emerged as one of the strongest predictors and showed an overall positive relationship with forest transition. A breakpoint in the SHAP response was observed around an NDVI value of 0.4, above which forest transition became increasingly likely, whereas lower values were more frequently associated with shrubland persistence (Fig. 4a).

Also, pH emerged as a main predictor of shrubland to forest transition. The model showed a clear association with acidic environments, with SHAP values decreasing as pH increased. A threshold was identified at a pH around 7.5, below which transition was favoured. In contrast, alkaline environments were consistently associated with shrubland persistence (Fig. 4b).

Globally, elevation showed a negative relationship with transition likelihood, with a clear primary threshold identified around 500 m.a.s.l., above which the contribution to forest transition became increasingly negative (Fig. 4c).

Evapotranspiration also showed a strong negative relationship with forest transition. At low levels of evapotranspiration, higher forest transition likelihood was predicted. Above the threshold identified at approximately 1100 mm/year, SHAP contributions were predominantly negative, favouring shrubland persistence (Fig. 4d).

Surrounding forest cover in shrubland areas showed a nonlinear relationship to forest transition. At low percentage of surrounding forest cover, the contribution to the prediction was negative. Increasing surrounding forest cover increased its positive contribution to forest transition until approximately 40%, beyond which SHAP values stabilised and further increases had little additional effect on model predictions (Fig. 4e).

Surrounding shrub cover displayed a strong negative relationship to forest transition. At low percentages of surrounding shrub cover, transition to forest was more likely, while higher percentages increasingly reinforced shrubland persistence. A threshold was observed at approximately 50% (Fig. 4f).

While the marginal SHAP effects describe general trends, significant vertical dispersion was observed in specific variables, suggesting strong context dependency. The most notable context dependency occurred around 40% surrounding forest cover threshold. Interaction analyses revealed that at high surrounding forest cover, higher elevations were more frequently associated with positive SHAP contributions to forest transition (Fig. 5a). Similarly, lower evapotranspiration values favoured forest transition likelihood, and higher evapotranspiration values contributed towards shrubland persistence (Fig. 5b). Moreover, in this range of surrounding forest cover, acidic conditions were associated with forest transition, whereas alkaline conditions were associated with shrubland persistence (Fig. 5c).

Figure 4 SHAP dependence plots for the six main predictors controlling shrub-to-forest transition. Each panel shows the relationship between predictor values (x-axis) and SHAP values (y-axis), representing the marginal contribution of each variable to model predictions. Positive SHAP values indicate increased probability of forest transition, whereas negative values indicate shrub persistence. The red dashed line represents a SHAP value of 0. Panels correspond to: (a) NDVI, (b) pH, (c) elevation, (d) evapotranspiration, (e) surrounding forest cover, and (f) surrounding shrub cover.

Additional interaction analyses were conducted using climatic variables that were included in the model but were not retained among the main predictors according to the elbow point criterion, including mean annual temperature, maximum temperature in the warmest month, minimum temperature in the coldest month, and precipitation in the driest and wettest quarter. These showed consistent patterns supporting the role of climatic conditions as modulators of the forest cover effects (see Supplementary Material Figure S2).

Figure 5 SHAP dependence plots showing interactions between surrounding forest cover and key environmental predictors in shrub-to-forest transition. The x-axis represents surrounding forest cover in 1987, while the y-axis shows the corresponding SHAP values of surrounding forest cover. Positive SHAP values indicate increased probability of forest transition, whereas negative values indicate shrub

persistence. Points are coloured according to the interacting variable shown in each panel: (a) evapotranspiration, (b) pH, and (c) elevation. The dashed line indicates a SHAP value of 0. All three predictors respond to the breakpoint around 40%.

4. Discussion

Over the 35-year study period, just over one-quarter of the shrubland changed to forest, while nearly two-thirds persisted as shrubland. These results demonstrate that forest transition is a conditional process rather than a guaranteed outcome. More important, the identified drivers support a hierarchical framework in which landscape connectivity regulates propagule availability, while local environmental conditions determine establishment success once dispersal limitation is overcome (Caspersen and Saprunoff, 2005; Vidal-Macua et al., 2017). This framework helps to explain why shrublands exposed to similar regional climatic conditions may follow contrasting successional trajectories.

4.1. Hierarchical drivers of forest transition

Landscape context strongly influences shrub-to-forest transition by regulating propagule pressure. Proximity to surrounding forest cover acts as the primary trigger, with a minimum threshold required to initiate transition (Herrera and Garcia, 2010). At low levels of surrounding forest cover, systems are likely to be dispersal-limited. Increasing surrounding forest cover rapidly increases transition probability until the effect stabilises, suggesting that a minimum level of surrounding forest cover is required to overcome dispersal limitation and ensure sufficient seed availability and propagule pressure (Caspersen and Saprunoff, 2005; Acevedo-Limón et al., 2026).

In addition, surrounding forest cover may indirectly reflect favourable environmental conditions, as the presence of nearby forest suggests sites that have historically supported tree establishment and persistence. On the other hand, high surrounding forest cover is known to improve microclimatic conditions by decreasing temperature and increasing moisture (Grilo et al., 2020), which subsequently favours seedling establishment (von Arx et al., 2013).

However, overcoming dispersal limitation alone does not guarantee forest transition. Once propagule availability is sufficient, the likelihood of successful forest establishment depends on both the overall favourability of the site and local environmental constraints.

Beyond dispersal processes, vegetation productivity (NDVI) emerged as an important indicator of the environmental context in which succession occurs. Although NDVI was the most influential predictor in the model, it does not represent a direct successional mechanism. Instead, it reflects the overall environmental favourability of a site for forest transition, integrating characteristics associated with vegetation development, including biomass accumulation, water availability, and favourable soil and climatic conditions (Kerr and Ostrovsky, 2003; Cabello et al., 2012; Jorge et al., 2019). Consequently, high NDVI values are associated with conditions that favour forest establishment, whereas low-productivity sites are often linked to resource-poor or drought-stressed environments, resulting in abiotic conditions

insufficient to support a structurally complex forest regardless of seed availability (Pettorelli et al., 2005; Karnieli et al., 2010). While NDVI captures broad differences in environmental favourability, the interaction analyses indicate that specific local abiotic conditions ultimately determine whether establishment succeeds once dispersal limitation is overcome.

At high levels of surrounding forest cover, local abiotic conditions become the primary determinants of establishment success. This is consistent with studies in Mediterranean drylands showing that local-scale factors, such as soil properties and microclimatic conditions, can exert stronger controls on tree establishment than broad-scale climatic variables once dispersal limitation is overcome (Príncipe et al., 2022). In our study, pH and evapotranspiration emerged as the strongest environmental filters regulating shrub-to-forest transition. Acidic soils were consistently associated with forest transition, whereas alkaline soils were associated with shrubland persistence, supporting previous work highlighting the importance of local edaphic conditions in Mediterranean vegetation dynamics (Nunes et al., 2019). Likewise, lower evapotranspiration values were associated with forest transition, whereas high atmospheric water demand was associated with shrubland persistence.

Together, these results suggest that successful forest establishment requires both favourable soil conditions and reduced water stress. This interpretation aligns with studies identifying drought and water limitation as major constraints on forest dynamics in Mediterranean ecosystems (Vidal-Macua et al., 2017; Doblas-Miranda et al., 2017). Furthermore, specific edaphic conditions may be required to support the higher nutrient demands of establishing forest species compared to persistent shrublands (Sardans and Peñuelas, 2013).

Elevation showed a more context-dependent response. This apparent contrast reflects the difference between the overall marginal effect of elevation and its conditional effect once dispersal limitation is reduced. Marginal effects suggested higher transition probability at lower elevations, likely reflecting the historical legacy of land abandonment in Catalonia. (Olarieta et al., 2008; Vidal-Macua et al., 2018; Cervera et al., 2019). Lowlands were cultivated intensively until recent decades, and their recent abandonment falls within our 35-year window, capturing a highly visible wave of rapid forest transition.

However, once dispersal limitation was reduced, higher elevations became more strongly associated with forest transition. This pattern likely reflects the close relationship between elevation and climate in Mediterranean regions, where higher altitudes generally experience lower temperatures and higher precipitation due to orographic effects, resulting in improved water availability and reduced drought stress (Vidal-Macua et al., 2017). By providing a more favourable hydric balance through increased precipitation, lower evapotranspiration, improving moisture conditions, higher elevations enhance tree establishment and survival (Sánchez-Salguero et al., 2015). In contrast, lower elevations are often exposed to intense summer drought and high irradiance, which can limit seedling survival (Sánchez-Gómez et al., 2006). This indicates that elevation acts not as a direct driver but as a proxy for climatic gradients that regulate water availability and establishment success (Körner, 2007; Améztegui et al., 2010).

Overall, these dynamics support a hierarchical model of shrub-to-forest transition in which propagule availability constrains colonisation opportunities and local environmental conditions regulate establishment success. Consequently, shrublands exposed to similar regional climates may follow contrasting trajectories depending on landscape connectivity and local site conditions.

4.2. Shrubland persistence

Our findings suggest that shrubland persistence may reflect long-term or slow successional dynamics maintained by distinct ecological and environmental conditions, rather than simply representing a delayed successional stage. Persistent shrublands were linked to low vegetation productivity, high evapotranspiration, basic pH, high surrounding shrub cover and low surrounding forest cover. Together, these factors indicate two complementary constraints on forest transition: limited propagule availability due to low forest connectivity and strong environmental filtering imposed by drought stress and edaphic conditions. Previous studies have similarly shown that high atmospheric water demand and basic pH favour drought-resistant shrub communities while limiting forest establishment and seedling survival (Vidal-Macua et al., 2017; Nunes et al., 2019; Príncipe et al., 2019). Recent evidence further suggests that increases in shrub cover can exert a strong influence on ecosystem water balance through elevated evapotranspiration, potentially reinforcing water-limited conditions in Mediterranean ecosystems (Sánchez-Dávila et al., 2026)

For the nearly two-thirds of persistent shrublands, their long-term trajectory remains uncertain. With a longer temporal window, some of these areas may eventually undergo forest recovery, whereas others may represent sites whose ecological potential is to persist as shrubland even over extended timescales. A similar pattern has been reported in south-facing Mediterranean shrublands in southern Portugal, where shrub-dominated communities persisted for more than 60 years following abandonment (Príncipe et al., 2014).

Although shrubs may act as ecosystem engineers that improve soil conditions and create favourable microclimates for seedling establishment (Gómez-Aparicio et al., 2004; Köbel et al., 2023; Acácio et al., 2024), this facilitative effect alone appears insufficient to guarantee forest transition. Without sufficient propagule availability or under severe abiotic stress, shrublands may be unable to overcome key successional thresholds within the observed timeframe, resulting in prolonged persistence.

Rather than representing an arrested or delayed stage of succession, these persistent shrublands may represent long-lasting or potentially stable vegetation states adapted to local environmental conditions (Meiners et al., 2015). In the Mediterranean context, shrub communities represent a natural stage of secondary succession following land abandonment (Pugnaire et al., 2006), and transitions to forest can take several decades to centuries depending on environmental conditions and land-use history (Meiners et al., 2015; Cervera et al., 2019; Pato et al., 2026).

However, several limitations should be considered when interpreting these results. Shrublands were analysed as a common starting state regardless of their age, origin, or time since abandonment.

Consequently, the 35-year study period may capture both shrublands progressing slowly toward forest and communities constrained by long-term environmental limitations. Some shrublands classified as persistent may therefore represent relatively early or intermediate successional stages, whereas others may reflect genuinely long-lasting vegetation states. Nevertheless, the analysis identified consistent relationships between shrub-to-forest transition and ecological drivers across 600,000 shrubland locations, suggesting that the observed patterns are robust at the regional scale. Incorporating historical land-use information and estimates of abandonment age would help disentangle the relative importance of successional time and environmental constraints in determining forest expansion dynamics.

4.3. Implications for restoration: passive and active restoration

The hierarchical framework identified in this study provides a practical basis for identifying the dominant bottleneck limiting forest recovery and selecting restoration actions accordingly. In the context of the newly adopted EU Nature Restoration Law (*Regulation (EU) 2024/1991*) which sets targets for large-scale ecosystem recovery, identifying the most ecologically appropriate and cost-effective interventions is critical. We argue that forest restoration efforts should be specifically adapted to the particular successional environmental constraints that the site is facing.

Our findings suggest that passive restoration could provide a cost-effective and ecologically appropriate approach at large scales where favourable environmental and landscape conditions are already in place. In contexts with high baseline productivity, enough propagule availability, favourable moisture conditions and suitable soil properties, natural regeneration is more likely to succeed. In this specific scenario, forest transition may therefore occur without direct intervention (Vallejo et al., 2012).

In contrast, areas where some of these successional constraints are present may require targeted active restoration efforts to overcome specific limitations. For instance, highly productive sites with suitable edaphic conditions but lacking surrounding forest cover are likely to be dispersal-limited. In this situation, active restoration should be focused on assisted seeding or seedling plantations to promote forest establishment (González-Rodríguez et al., 2011; Gutiérrez et al., 2025).

Conversely, where propagule availability is not a limitation but local environmental conditions prevent seedling survival, the site is establishment limited. In these areas, adding seeds may be insufficient, and more advanced techniques should be applied such as artificial shading, soil amendments or planting mature saplings to improve micro-site conditions and facilitate woody species survival (Cortina et al., 2011; Oliet and Jacobs 2012).

Nonetheless, shrubland areas should not necessarily be viewed as a degraded ecosystem requiring intervention. Our model highlights that shrubland persistence is often an environmentally driven, highly stable state where forcing forest expansion may be ecologically unviable and economically inefficient. Shrubland areas may represent stable and ecologically valuable systems adapted to local environmental conditions (Barnaud et al., 2021). In fact, regional nature reports warn that uncontrolled forest expansion

following land abandonment, may lead to a decrease in open-habitat biodiversity (Brotons et al., 2020). Maintaining shrubland areas may also enhance landscape heterogeneity, specific biodiversity and overall ecosystem resilience in the face of a fire-prone Mediterranean climate by preserving a patchy mosaic of vegetation types (Vallecillo et al., 2008; Rey-Benayas et al., 2010).

4.4. Climate change implications for forest transition

The hierarchical framework identified here also provides a useful perspective for anticipating future shrub-to-forest dynamics under climate change. In Mediterranean regions, warming rates significantly exceed global averages, with regional temperatures projected to rise by up to 2 °C within the next two decades (Zittis et al., 2019). This rapid warming, alongside increasing temperatures and evapotranspiration are expected to intensify summer drought stress, which may further limit tree establishment and seedling survival (Peñuelas et al., 2017; Yi et al., 2022). Under these conditions, environmental constraints are likely to become even more important, particularly in low-elevation and water-limited areas (Peñuelas et al., 2007; Peñuelas and Sardans, 2021). In this context, the thresholds identified in our framework may represent approximate ecological limits under current environmental conditions, beyond which successful forest establishment becomes increasingly unlikely.

Climate change may shift these limits by altering key predictors such as site productivity and evapotranspiration. Reduced vegetation productivity under increasing climatic stress may prevent some sites from reaching the minimum conditions required for forest development. At the same time, higher evapotranspiration will increase water demand, further constraining seedling establishment (McDowell et al., 2008; Hallett et al., 2011). Under these conditions, passive forest recovery may become less effective, especially in already marginal environments (Prach and Hobbs, 2008; Vallejo et al., 2012). At the landscape scale, continued forest expansion and land abandonment may still increase surrounding forest cover, facilitating seed dispersal into shrublands. However, increased propagule pressure alone may not be sufficient to drive transition if environmental constraints intensify. This reinforces the importance of environmental filtering in determining forest establishment under future conditions (Gómez-Aparicio et al., 2004).

5. Conclusions

This study demonstrates that shrub-to-forest transition in Mediterranean landscapes is not an automatic process, but a conditional outcome governed by a hierarchical, two-stage dynamic. Landscape context emerged as a primary constraint, with a critical threshold of surrounding forest cover required to overcome dispersal limitation and ensure seed availability. Once this landscape-level constraint filter is overcome, local environmental filtering (driven by soil properties, topographic gradients and water demand) controls tree seedling establishment and dictates the final successional outcome. Together, these results challenge the assumption of uniform forest recovery following land-use change and abandonment, and reveal a hierarchical linkage between landscape context and local ecological processes, explaining why shrublands within the same regional landscape may follow contrasting successional trajectories and highlighting the importance of context-dependent ecological processes.

These findings have direct implications for ecosystem management and restoration. Rather than applying generalised afforestation strategies, interventions should account for landscape context and local environmental constraints. Passive restoration may be effective in areas where both propagule availability and environmental conditions are favourable, while active interventions should be targeted to overcome specific limitations, such as limited propagule availability or harsh abiotic conditions.

Under accelerating climate change, these contemporary successional limits are highly vulnerable. Rising regional temperatures and increasing water stress may reduce the environmental space suitable for forest development, potentially making passive recovery less viable in marginal areas and reinforcing long-term shrubland persistence. Future shrub-to-forest dynamics will therefore depend on the interaction between landscape context and increasingly restrictive environmental conditions. As environmental stress increases, many shrublands may remain in a shrub-dominated state for extended periods, functioning as stable or semi-stable systems under conditions that increasingly limit forest expansion.

Future research should integrate historical land-use legacies and time since abandonment to clarify how landscape history interacts with contemporary environmental constraints. Incorporating temporal changes in landscape context and climate, particularly changes in water availability, would further improve predictions of shrub-to-forest transition under changing environmental conditions.

Declarations

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

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Author Contribution

M.G.C. contributed to formal analysis, data curation, visualization, writing of the original draft, and review and editing of the manuscript. M.V.M. contributed to conceptualization, methodology, data curation, supervision, and review and editing of the manuscript. M.E.S. contributed to methodology, software, and review and editing of the manuscript. A.N. contributed to conceptualization, methodology, and review

and editing of the manuscript. C.B. contributed to conceptualization, methodology, supervision, and review and editing of the manuscript. All authors reviewed and approved the final manuscript.

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Data Availability

The datasets generated during the current study are available from the corresponding author upon reasonable request. The data sources used in this study are described in the Methodology section.

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Figures

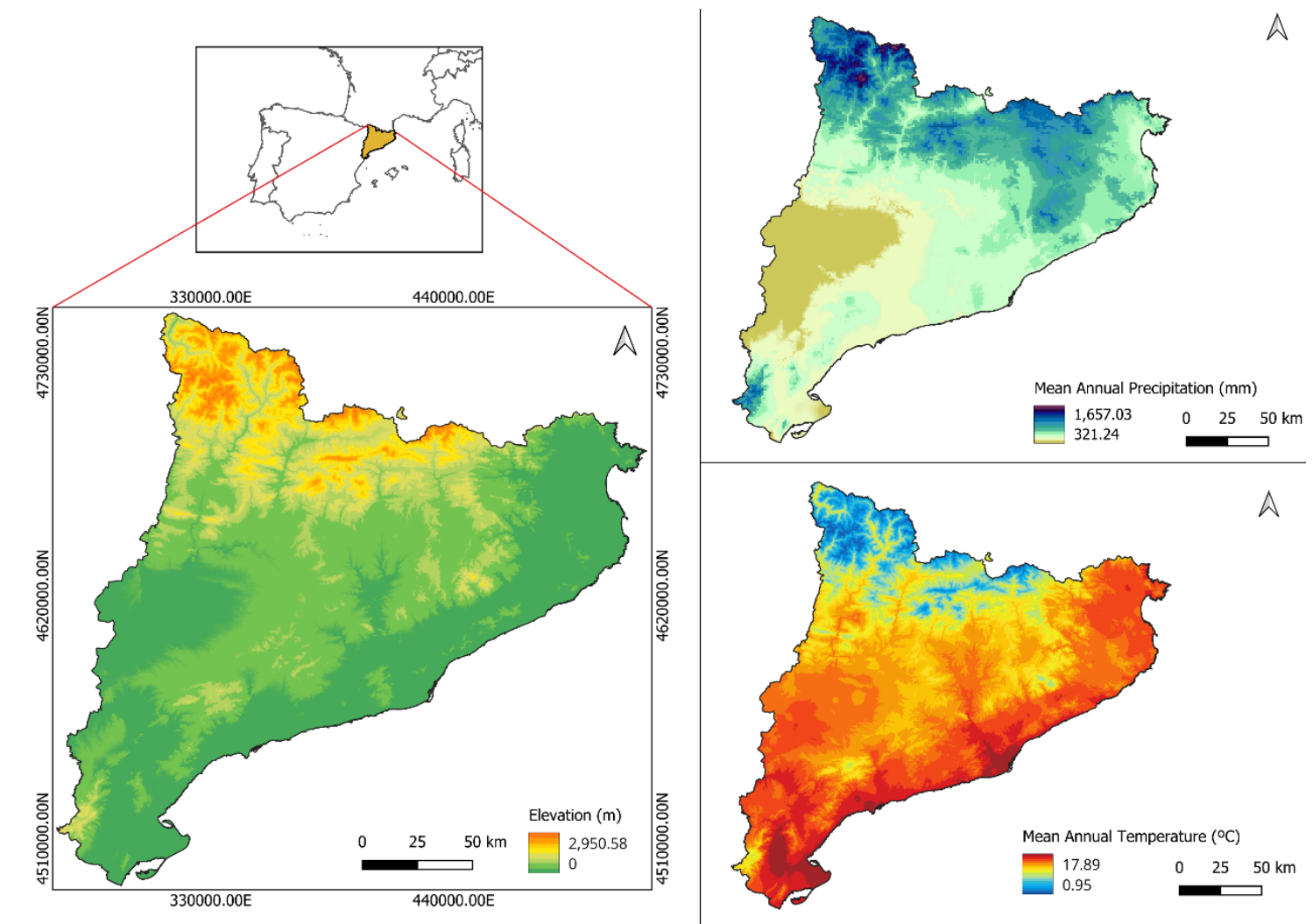


Figure 1

Study area in Catalonia (Spain). Location of the study area showing spatial variability in topography and climate, including elevation (left) (ICGC), mean annual precipitation (top right) and temperature (bottom right) (Ninyerola et al., 2005).

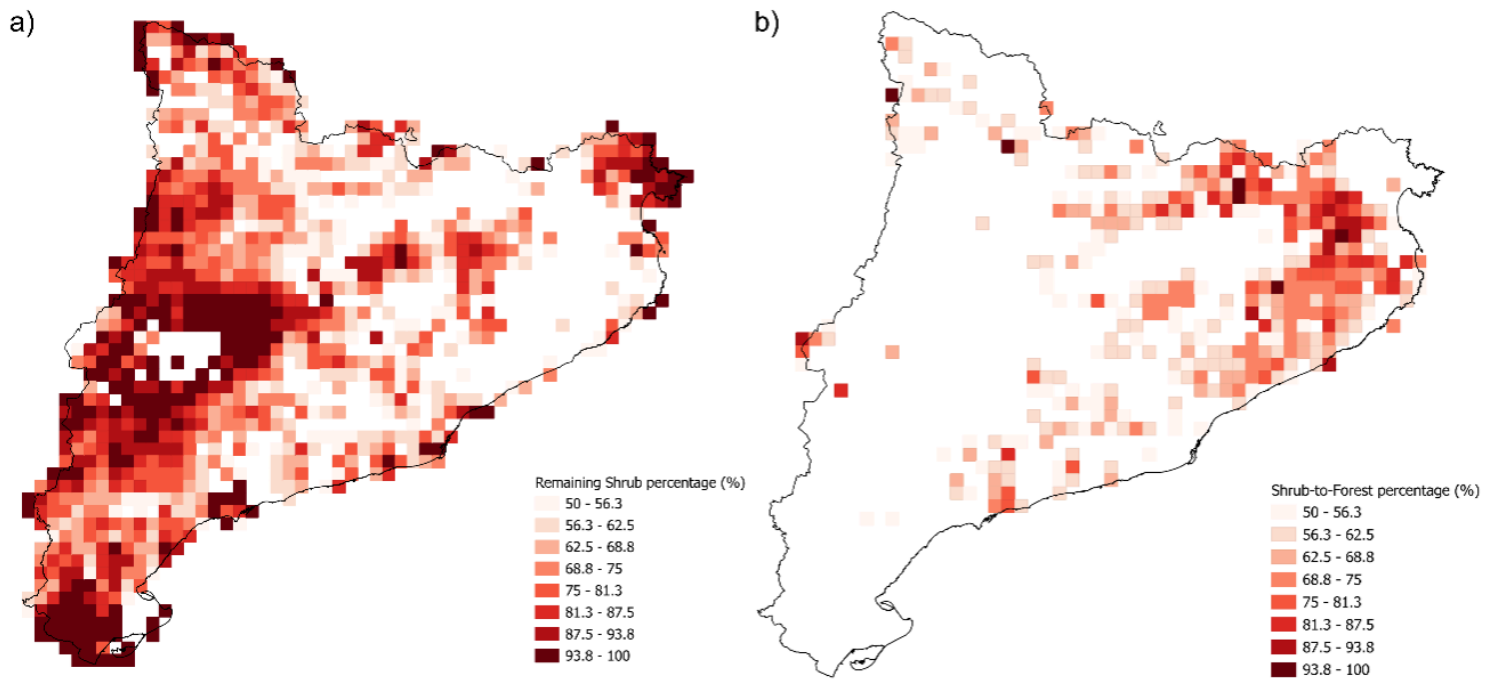


Figure 2

Spatial dominance of shrub persistence (a) and shrub-to-forest transition (b) in Catalonia from 1987 to 2022. Percentages were calculated within 5 x 5 km grid cells using 30 x 30 m shrubland pixels classified as either persistent shrubland or shrub-to-forest transition. Only grid cells where each trajectory represented the dominant shrubland dynamic are displayed.

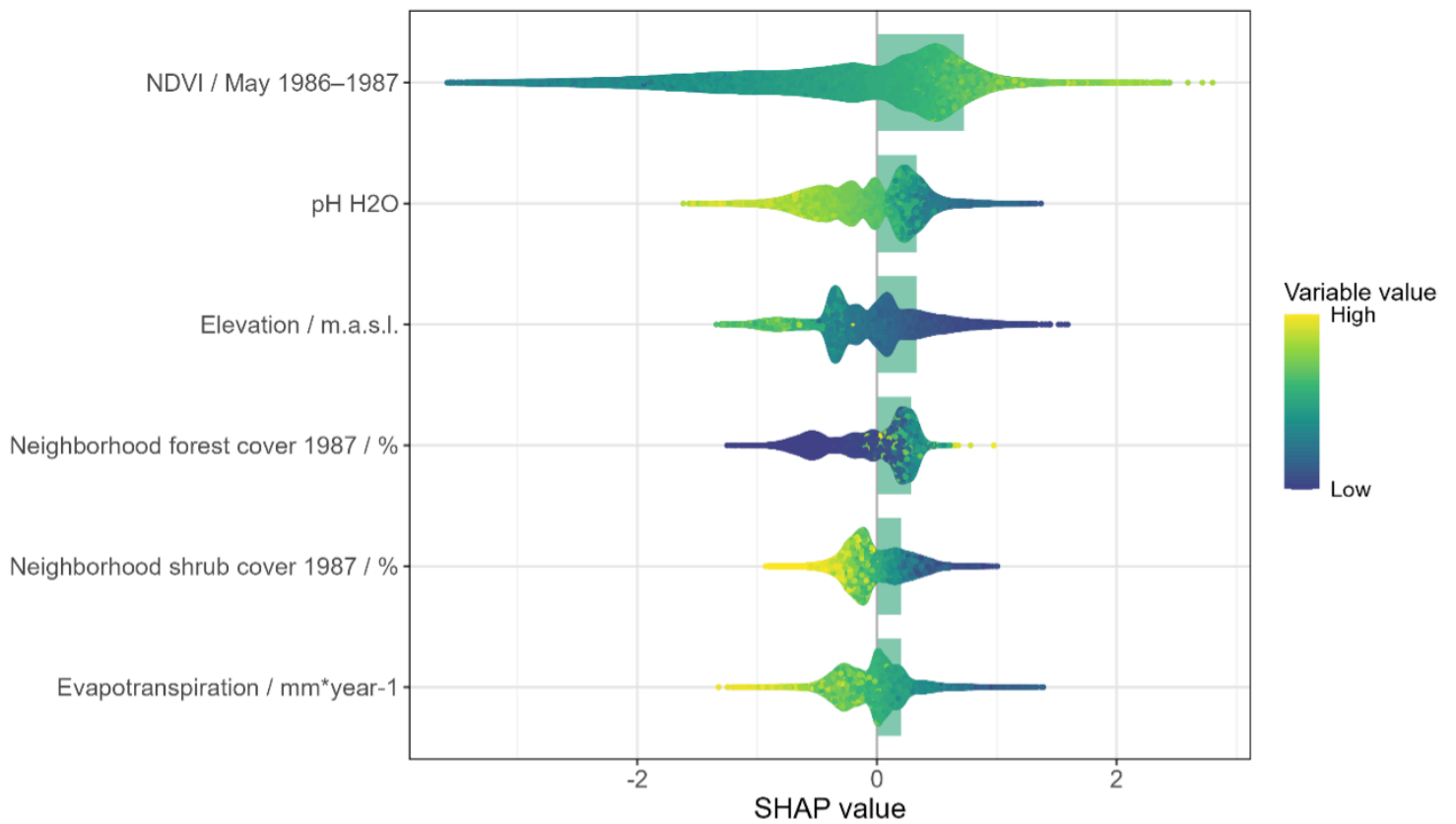


Figure 3

SHAP (Shapley Additive Explanations) beeswarm plot showing the six most influential predictors in the XGBoost classification model. Variables are ordered vertically by decreasing mean absolute SHAP value. Each point represents one observation, coloured according to the original feature value from low (blue) to high (yellow). Positive SHAP values increase the probability of shrub-to-forest transition, whereas negative values favour shrub persistence. The green bar plot below represents mean absolute SHAP importance.

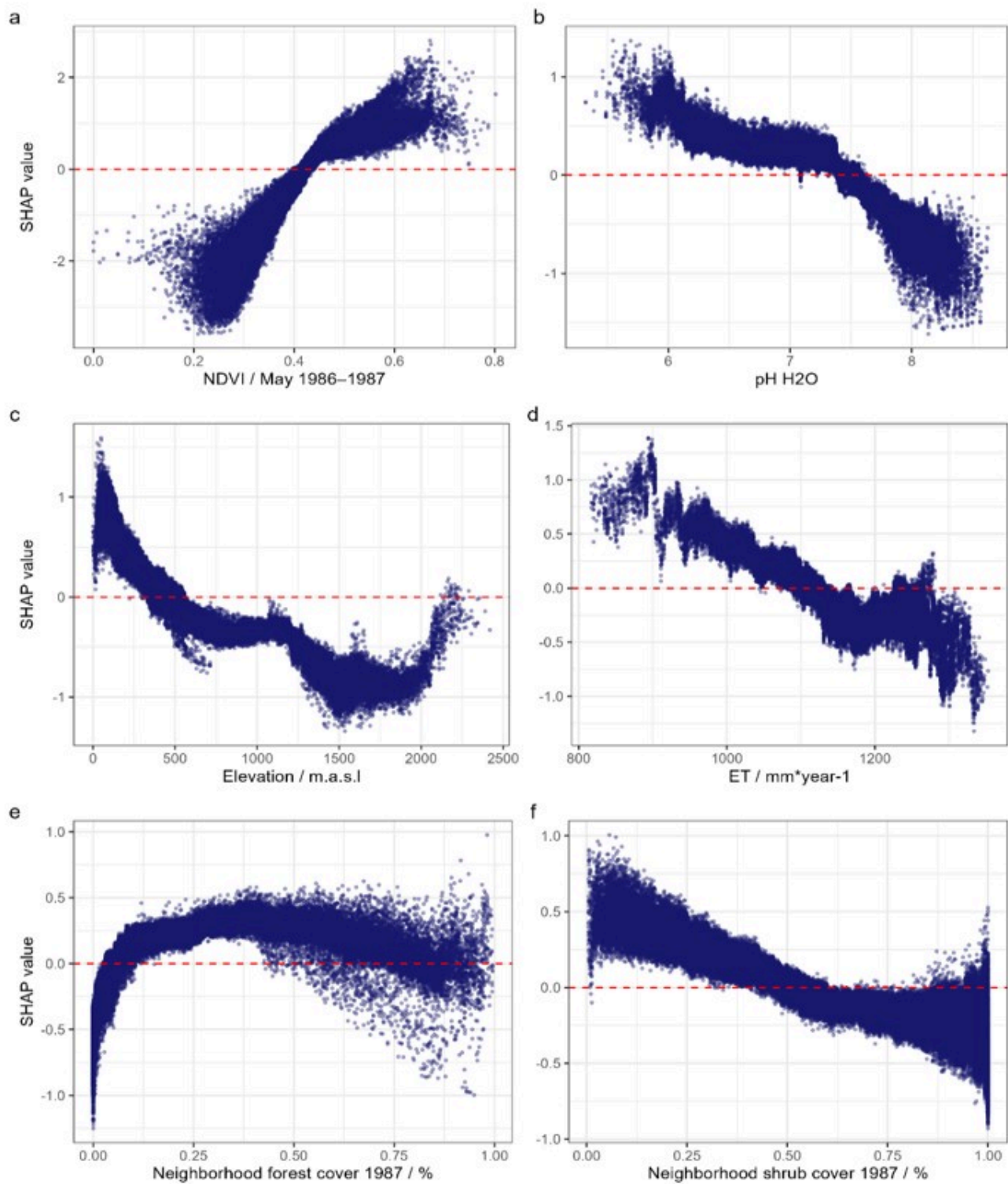


Figure 4

SHAP dependence plots for the six main predictors controlling shrub-to-forest transition. Each panel shows the relationship between predictor values (x-axis) and SHAP values (y-axis), representing the marginal contribution of each variable to model predictions. Positive SHAP values indicate increased probability of forest transition, whereas negative values indicate shrub persistence. The red dashed line

represents a SHAP value of 0. Panels correspond to: (a) NDVI, (b) pH, (c) elevation, (d) evapotranspiration, (e) surrounding forest cover, and (f) surrounding shrub cover.

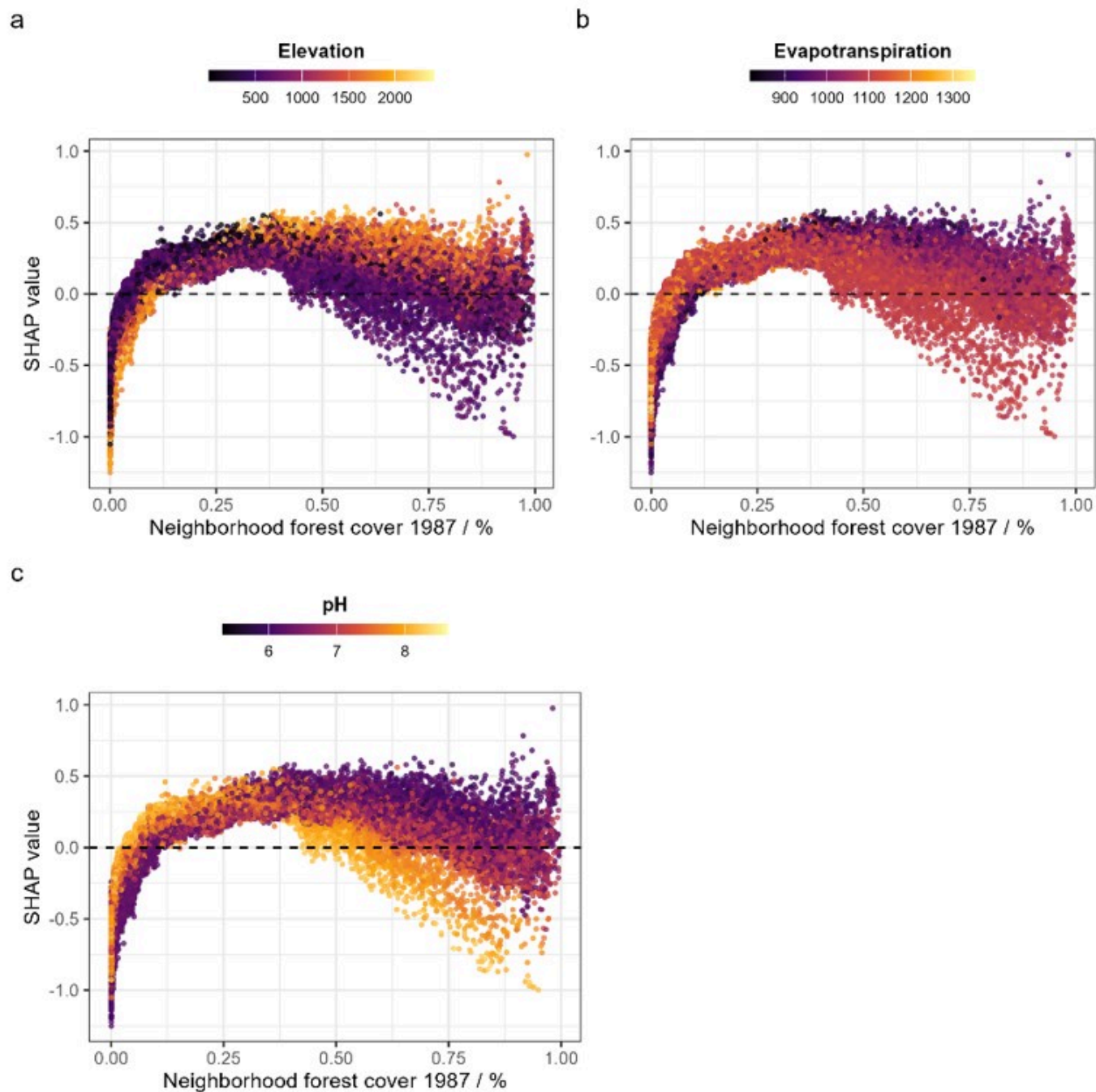


Figure 5

SHAP dependence plots showing interactions between surrounding forest cover and key environmental predictors in shrub-to-forest transition. The x-axis represents surrounding forest cover in 1987, while the y-axis shows the corresponding SHAP values of surrounding forest cover. Positive SHAP values indicate increased probability of forest transition, whereas negative values indicate shrub persistence. Points are coloured according to the interacting variable shown in each panel: (a) evapotranspiration, (b) pH, and

(c) elevation. The dashed line indicates a SHAP value of 0. All three predictors respond to the breakpoint around 40%.

Supplementary Files

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