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Climate and topography control variation in the tropical dry forest–rainforest ecotone

Jonathan A. Walter[1,2] | **Jeff W. Atkins**[3] | **Catherine M. Hulshof**[4]

[1]Center for Watershed Sciences, University of California, Davis, California, USA

[2]Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia, USA

[3]USDA Forest Service, Southern Research Station, New Ellenton, South Carolina, USA

[4]Department of Biology, Virginia Commonwealth University, Richmond, Virginia, USA

Correspondence
Catherine M. Hulshof
Email: cmhulshof@vcu.edu

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Abstract

Ecotones are the transition zones between ecosystems and can exhibit steep gradients in ecosystem properties controlling flows of energy and organisms between them. Ecotones are understood to be sensitive to climate and environmental changes, but the potential for spatiotemporal dynamics of ecotones to act as indicators of such changes is limited by methodological and logistical constraints. Here, we use a novel combination of satellite remote sensing and analyses of spatial synchrony to identify the tropical dry forest–rainforest ecotone in Area de Conservación Guanacaste, Costa Rica. We further examine how climate and topography influence the spatiotemporal dynamics of the ecotone, showing that ecotone is most prevalent at mid-elevations where the topography leads to moisture accumulation and that climatic moisture availability influences up and downslope interannual variation in ecotone location. We found some evidence for long-term (22 year) trends toward upslope or downslope ecotone shifts, but stronger evidence that regional climate mediates topographic controls on ecotone properties. Our findings suggest the ecotone boundary on the dry forest side may be less resilient to future precipitation reductions and that if drought frequency increases, ecotone reductions are more likely to occur along the dry forest boundary.

KEYWORDS
dry forest, ecotone, phenology, rainforest, spatial synchrony, tropics

INTRODUCTION

Ecotones are the transition zones between ecosystems and are diverse and temporally dynamic ecological communities existing as areas of discontinuity between two adjacent ecosystems (Livingston, 1903; Shugart, 1990). Ecotone locations often correspond to spatial discontinuities in ecological or geophysical properties or processes, for example, climatic, edaphic, or topographic features. In turn, these spatial discontinuities impact community composition and vegetation structure through interactions with species' physiological limits (Holland & Risser, 1991). Ecotones are vital to ecology for several reasons. Ecotones were fundamental to early ecological theory (e.g., Clements, 1905; Odum, 1971), with their conceptual development preceding the ecosystem concept (e.g., Tansley, 1935). Furthermore, contemporary ecotone research can provide insight into landscape ecology, environmental gradients, competitive dynamics and coexistence, and local- to global-scale environmental change (cf. Gosz, 1992; Schilthuizen, 2000). Well-studied examples of ecotones include the savanna–forest ecotone (Oliveras & Malhi, 2016), the forest–shrubland ecotone (Eldridge et al., 2011), and, in aquatic systems, the salt-marsh upland ecotone (Wasson et al., 2013) and the littoral zone (van der Maarel, 1990).

Importantly for this study, ecotones are sensitive indicators of the ecological consequences of regional climate variation linked to global change (di Castri et al., 1988; Smith & Goetz, 2021; Turner et al., 1991). Ecotones serve as indicators because they are temporally dynamic (Peters et al., 2006)—expanding, contracting, or shifting in one or more directions in response to climatic variability and change (Eldridge et al., 2011; Kirwan & Gedan, 2019; Kutzbach et al., 1998; Smith & Goetz, 2021). This study conceptualizes ecotones as transition zones between two adjacent systems with properties distinct from either, rather than as defined through a hierarchy of scale (Meentemeyer & Box, 1987; van der Maarel, 1976). Conceptions of ecotones may also differentially emphasize transitions in species composition versus differences in vegetation dynamics. While both perspectives are valid, they may reflect different underlying processes and have different characteristic timescales of variability. Changes in community composition are expected to accompany ecotone change, but—especially in systems like forests that are composed of long-lived, sessile species—changes in community composition may be slow (e.g., decadal) compared to changes in dynamical features like phenology or productivity (e.g., months–years) that involve plastic responses to environmental conditions. As such, an ecotone defined from dynamical properties, such as across a precipitation seasonality gradient, may not only be expected to change *faster than* community composition changes but also be subject to short-timescale (e.g., intra-annual) climate variation that is unrelated to long-term (e.g., decadal), directional climate change. Mechanisms of short-term ecotone variation may be associated with longer term ecotone changes, particularly if they reflect environmental conditions that are becoming more common with global change.

Ecotone movements are likely common in nature, yet under-detected because monitoring ecotones is cumbersome. For example, the intensity of field sampling needed to monitor ecotones limits our ability to study ecotones over larger spatiotemporal scales, and a lack of viable methods for detecting and monitoring ecotones over large spatial and temporal extents results in both a lack of necessary data and subsequent supporting theory (cf. van der Maarel, 1990). Thus, understanding of ecotone spatiotemporal dynamics is limited. However, contemporary remote sensing and quantitative techniques offer promising solutions for detecting ecotones and monitoring their spatiotemporal dynamics (Foster & D'Amato, 2015). The application of remote sensing for mapping ecotones has primarily focused on treeline expansion and contraction in alpine and montane systems (Moreno-De Las Heras et al., 2015; Ndyamboti et al., 2020), or shrub/vegetation cover changes in dryland/arid systems (Chhetri & Thai, 2019; Mohapatra et al., 2019; Oliveras & Malhi, 2016). Given the striking spectral differences between vegetation and soil as detected by passive remote sensing (e.g., Landsat, MODIS), remote sensing-enabled change detection approaches straightforwardly produce reliable results in these contexts. Detecting ecotone dynamics in more structurally complex systems (e.g., tropical forests), where differences among vegetation classes may be less obvious, requires a different approach.

We propose a framework using geographies of spatial synchrony (Walter et al., 2017) to distinguish among tropical dry forest, tropical rainforest, and ecotone areas based on similarity (correlation) in temporal patterns of the remotely sensed index of vegetation greenness, Normalized Difference Vegetation Index (NDVI). Spatial synchrony quantifies the tendency for spatially replicated variables to be temporally correlated across locations. Spatial synchrony is a ubiquitous feature of ecological systems (Liebhold et al., 2004), but can exhibit complex geographic structures due, for example, to differences in internal system dynamics or responses to environmental forcings across locations (Haynes et al., 2019; Walter et al., 2017). In the present context, we expect locations (i.e., pixels) corresponding to either dry forest or rainforest types to be highly synchronous with locations of similar forest types, but with weak synchrony between the dry and rainforest types. In our system, dry forest species are predominantly deciduous, while rainforest species are predominantly evergreen, likely creating distinct temporal signatures in NDVI variability. Locations corresponding to ecotones, as zones of transition, will have attributes of both dry and rainforest and hence will have moderate levels of synchrony with both dry forests and rainforests.

We used a spatial synchrony-based approach to map the dry forest–rainforest ecotone in an area of northwestern Costa Rica and examined spatiotemporal patterns in ecotone location and ecotone attributes including its area, its shape complexity, and the elevation it is distributed over. This region is characterized by an elevational gradient from lowland tropical dry forests to rainforests and then cloud forests. Evidence of climate change in the region includes decadal-scale declines in precipitation (Enquist & Enquist, 2011) and changes in the variation and seasonality of precipitation (Janzen & Hallwachs, 2021), as well as increases in temperature and upslope shifts in the distribution of high temperatures (Smith et al., 2023). Furthermore, the mass mortality of dry forest tree species during the extreme 2015 ENSO event (Powers et al., 2020) suggests that lowland dry forests may be at their physiological limits of drought tolerance, even though these forests experience 6 months of drought. Thus, it is plausible that both dry forest and rainforest plant species may exhibit complex responses to changing climatic conditions, thereby shifting the position or composition of the dry forest–rainforest ecotone on both interannual and decadal timescales.

Given support for the validity of our ecotone delineation (Appendix S1), we asked: (1) Does topography mediate ecotone location? (2) How has the delineated ecotone changed through time on interannual to decadal timescales? (3) Does regional climate mediate temporal variability in the delineated ecotone? We addressed these questions across the tropical dry forest–rainforest ecotone in northwestern Costa Rica. Although some ecotones are well studied (e.g., shrubland–grassland and forest–savanna ecotones), the ecotone between tropical dry and rainforests, two of the largest tropical biomes, is not. Since water availability is a major determinant of the transition between tropical dry and rainforest biomes, future precipitation regimes expected under climate change may have major impacts on the distribution of tropical dry forests, which are economically and culturally important biomes that comprise 42% of all tropical forests (Murphy & Lugo, 1986).

METHODS

Study site

Area de Conservación Guanacaste (ACG) in northwestern Costa Rica encompasses diverse forest types within a contiguous tract of protected area from sea level to ~1500 m elevation. Lowland forests are classified as seasonally dry tropical forests (Holdridge et al., 1971) with a mean annual precipitation of 1500 mm, high interannual precipitation variability, and strong seasonality, that is, a 6-month dry season from December to May during which many plant species drop their leaves (i.e., are seasonally deciduous). Upland forests include tropical moist, wet, and rainforests; premontane moist, wet, and rainforests; and lower montane moist, wet, and rainforests. These categories are based on Holdridge Life Zones which are distinguished by differences in altitude, potential evapotranspiration (PET), precipitation, and humidity (Holdridge, 1967). However, for the purpose of delineating the ecotone, we group upland forests as "rainforests." Most upland forest plant species are evergreen owing to the greater mean annual precipitation (3000–4000 mm) and a brief dry season (1–3 months).

Image acquisition and processing

To identify ecotones, we used NDVI data from the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Indices data product Version 6 (MODIS level 3 product, MOD13Q1) from the years 2000–2021. These data are generated every 16 days at 250 m spatial resolution. The MODIS algorithm chooses the best available pixel value from all the acquisitions from the 16-day period based on criteria including low cloud cover, low view angle, and the highest acquired NDVI value. NDVI is a dimensionless index of the difference between infrared and red reflectance that estimates plant greenness and is well-correlated with vegetation productivity (Myneni et al., 1995; Schloss et al., 1999). Data were acquired, queried, filtered, and processed using Google Earth Engine. First, the MODIS MOD13Q1 data were imported into the workspace. We then clipped our data to the boundaries of the country of Costa Rica using the Large-Scale International Boundary (LSIB) dataset provided by the United States Office of the Geographer. Using Google Earth Engine (Gorelick et al., 2017), all matching data for each queried year were mosaicked using median reduction and exported as an image collection by year, where each data layer was one 16-day mosaic.

Delineating the dry forest–rainforest ecotone

We used analyses of geographic structures in spatial synchrony (Walter et al., 2017) in NDVI phenology to delineate the dry forest–rainforest ecotone. We delineated the ecotone using all years together, and for different temporal windows detailed below. These analyses, respectively, were used to identify the general dry forest–rainforest ecotone area and to analyze temporal changes in the ecotone. Prior to analysis, we removed NDVI observations suspected to be biased low by fog and low-lying clouds common in rainforest areas, and discarded locations missing more than 33% of observations. Locations were discarded on a year-by-year basis for analyses on individual years. We removed individual NDVI observations <0.2; this is below typical values for vegetation (Cheng et al., 2008). Additionally, the distribution of raw NDVI values was bimodal, suggesting two underlying processes. Removing observations <0.2 eliminated this low-density mode that, based on visual inspection, was primarily associated with locations in rainforests, supporting our interpretation that NDVI values below the 0.2 threshold were indicative of interference from fog and low-lying cloud cover that was not removed by standard cloud masking.

We then used an adaptation of the module decomposition algorithm of Newman (2006) suitable for correlations (Walter et al., 2021) to identify groups of pixels tending to have high within-group synchrony, but low between-group synchrony. Briefly, the algorithm uses the eigendecomposition of the adjacency matrix (i.e., the matrix of pairwise correlations among locations) to subdivide the pixels into groups. The adjacency matrix is split into groups based on its leading positive eigenvector; positive values go in one group, and negative eigenvalues in the other. If there are no positive eigenvalues, the matrix is not split, and >1 split may be made if the eigendecomposition of a sub-adjacency matrix resulting from an earlier split has a positive eigenvalue.

This algorithm was used to divide the study area into two groups, generally corresponding to dry forests and rainforests, based on similarity in NDVI phenology. We then computed the contribution of each grid cell to the total modularity of the study area, which can be interpreted as a measure of the certainty that each grid cell belongs to the group it was assigned to. Areas with low certainty (i.e., weak correspondence to either of the two forest types) were considered ecotone, as these reflect zones of transition in environmental conditions and species composition. We normalized the modularity contribution of each grid cell by the total modularity contribution of its group in that year to create a statistic that could be compared across groups and years. Although an ecotone is conceptually a continuous transition between two distinct ecosystem types, to facilitate analyses of temporal change in properties of the ecotone, we delineated discrete ecotone areas based on thresholding the normalized group membership certainty. We focus on analyses using a threshold of 0.2. Within a range of thresholds from 0.1 to 0.3, adjusting this threshold altered the number of pixels identified as ecotone but did not change the general location of the ecotone. We used this approach to delineate the ecotone using all years (2000–2021) combined and, to evaluate changes over time in the ecotone and the importance of temporal scale, we used this approach to delineate the ecotone using (1) the first 7 years (2000–2006) and last 7 years (2015–2021) of the time series, (2) all years individually, and (3) 3-year moving windows. Synchrony analyses were conducted in R version 4.1.2 (R Core Team, 2022) using the "wsyn" package (Reuman et al., 2021). Derived data products arising from this study are archived on Dryad (Walter, 2024a).

Validation of ecotone delineation

To evaluate the effectiveness of our synchrony-based delineation of dry forest, rainforest, and ecotone, we compared our maps to point locations of dry forest, rainforest, and ecotone or transitional vegetation communities obtained from the published literature, from a network of 20 × 50 m field plots in which all woody stems greater than 5 cm in diameter at breast height have been mapped, measured, and identified to species (Appendix S1: Section S1), from Holdridge Life Zone maps (Holdridge et al., 1971), from a 20-year history of field research throughout the area (e.g., Hulshof & Powers, 2020), and an even longer history (60+ years) of biodiversity inventory (Janzen & Hallwachs, 2011) and resident expertise throughout ACG.

Topographic effects on ecotone location

We next tested how topography influences ecotone location by testing whether the probability of a location being classified as ecotone based on the full 2000–2021 time series depended on elevation and topographic wetness index (TWI), a measure of the degree to which, given slope and up-slope contributing area, water tends to accumulate in an area (Sörensen et al., 2006). In this system, environmental factors including water availability, seasonality of precipitation, and temperature covary with elevation (Hulshof & Powers, 2020; Smith et al., 2023) and we consider elevation to be an indicator of these environmental gradients, as opposed to elevation being responsible for a direct, mechanistic effect on vegetation dynamics. These dependencies were tested within a generalized additive modeling (GAM) framework (Wood, 2017), which is analogous to linear regression but replaces regression coefficients with penalized regression splines, and hence performs well at describing nonlinear relationships between predictor and response variables. Given a binary response variable (ecotone or not ecotone), we used a binomial GAM with logit link function, yielding an analog of logistic regression but allowing nonlinear relationships between predictor and response. Analyses were conducted in R version 4.2.1 using the "mgcv" (Wood, 2022), "whitebox" (Lindsay, 2016), "raster" (Hijmans, 2022), and "rgdal" packages (Bivand et al., 2022).

Long-term changes in the ecotone

To evaluate long-term changes in the ecotone, we first compared the elevation of the ecotone during 2000–2006 versus 2015–2021, focusing on whether the 0.1, 0.5, and 0.9 quantiles shifted upslope. To assess whether any upslope shifts were greater than expected by chance under a null hypothesis of no change, we constructed a resampling-based significance test. From a pool of elevations comprising pixels that were classified as ecotone in either 2000–2006 or 2015–2021, we constructed the elevations of a surrogate "early" ecotone and a surrogate "late" ecotone by sampling from the pool of elevations randomly and with replacement sets of elevations with size matching the observed number of ecotone pixels during the 2000–2006 ("early") and 2015–2021 ("late") periods. By sampling randomly and with replacement, in the ecotone surrogate differences in elevation arise from sampling variation alone. We took the difference (late–early) in the 0.1, 0.5, and 0.9 quantiles of the ecotone surrogates, repeated this procedure 9999 times to generate a distribution of surrogate ecotone elevation shifts, and compared the empirical ecotone elevation shifts to this distribution to determine a *p*-value. Ecotone elevation shifts were considered statistically significant if they were larger than 95% of surrogates (i.e., $p < 0.05$).

Next, we measured four properties of the delineated ecotone areas over time from 2000 to 2021 using 1- and 3-year increments. These included median elevation, elevation range (75th percentile–25th percentile), area, and perimeter-to-area ratio. We tested for linear temporal trends in each ecotone property using generalized least squares linear regression and accounted for temporal autocorrelation assuming model errors had second-order autoregressive (AR(2)) structure. An AR(2) structure was chosen because residual autocorrelation functions showed some evidence of cyclic behavior, and AR(2) processes are capable of reproducing stochastic cycles. Analyses were conducted in R version 4.2.1 using the "nlme" package (Pinheiro et al., 2022).

Climatic effects on ecotone properties

Using the ecotone delineations from 1- and 3-year windows, we tested for relationships among ecotone properties (i.e., median elevation, elevation range, area, and perimeter-to-area ratio) and variables describing interannual climatic variation. The climate variables were as follows: total annual precipitation, annual mean PET, dry season total precipitation, the Multivariate El Niño Index (MEI), and the 1-year lags of each variable. Precipitation, PET, and dry season length variables were computed using CHELSA monthly climate data (v2.1; spatial resolution 30 arc seconds (1 km); Karger et al., 2017, 2018). Following Guan et al. (2015), the dry season was defined as months with PET > precipitation. CHELSA data are available only through 2018, so these analyses focused on the years 2000–2018. Values of the MEI (v2) were obtained from https://psl.noaa.gov/enso/mei/ and averaged by year to produce an annual time series. For comparison with ecotone variables arising from 3-year windows of NDVI data, we averaged climate variables over the same 3-year windows. To minimize problems with multiple testing (4 ecotone variables × 8 climate variables × 2 temporal resolutions), we first computed Pearson correlation coefficients between all pairs of variables as a first-order indication of the strength of association. Then, for variable pairs with correlation coefficient >0.3 or <-0.3, we used generalized least squares linear regression with first-order autoregressive (AR(1)) correlated errors to test for statistical significance while accounting for temporal autocorrelation. Examination of model residuals indicated that an AR(1) model was sufficient to address temporal autocorrelation. Analyses were conducted in R version 4.2.1 using the "nlme" package (Pinheiro et al., 2022). Analysis code is available on Zenodo (Walter, 2024b).

RESULTS

Delineating the dry forest–rainforest ecotone

Synchrony analysis identified areas with distinct phenological patterns corresponding to dry forest, rainforest, and ecotone (Figure 1) that accorded well with vegetation patterns from independent sources (Appendix S1: Section S1). Considering the full 2000 to mid-2022 time series, the temporal pattern of NDVI in the dry forest was dominated by seasonal variability and NDVI peaks in the second half of the year when it is rainier. Rainforests showed less consistent seasonality, often exhibiting NDVI peaks early in the year when dry forests receive little rain. Rainforests also had a wider range of overall variability and interannual variability in the timing and magnitude of NDVI peaks. The ecotone showed not only more apparent seasonality than rainforests, but also substantial interannual variability, including years in which NDVI peaks early in the year.

Topographic effects on ecotone location

The location of the ecotone was partly explained (deviance explained = 29.8%) by elevation and TWI

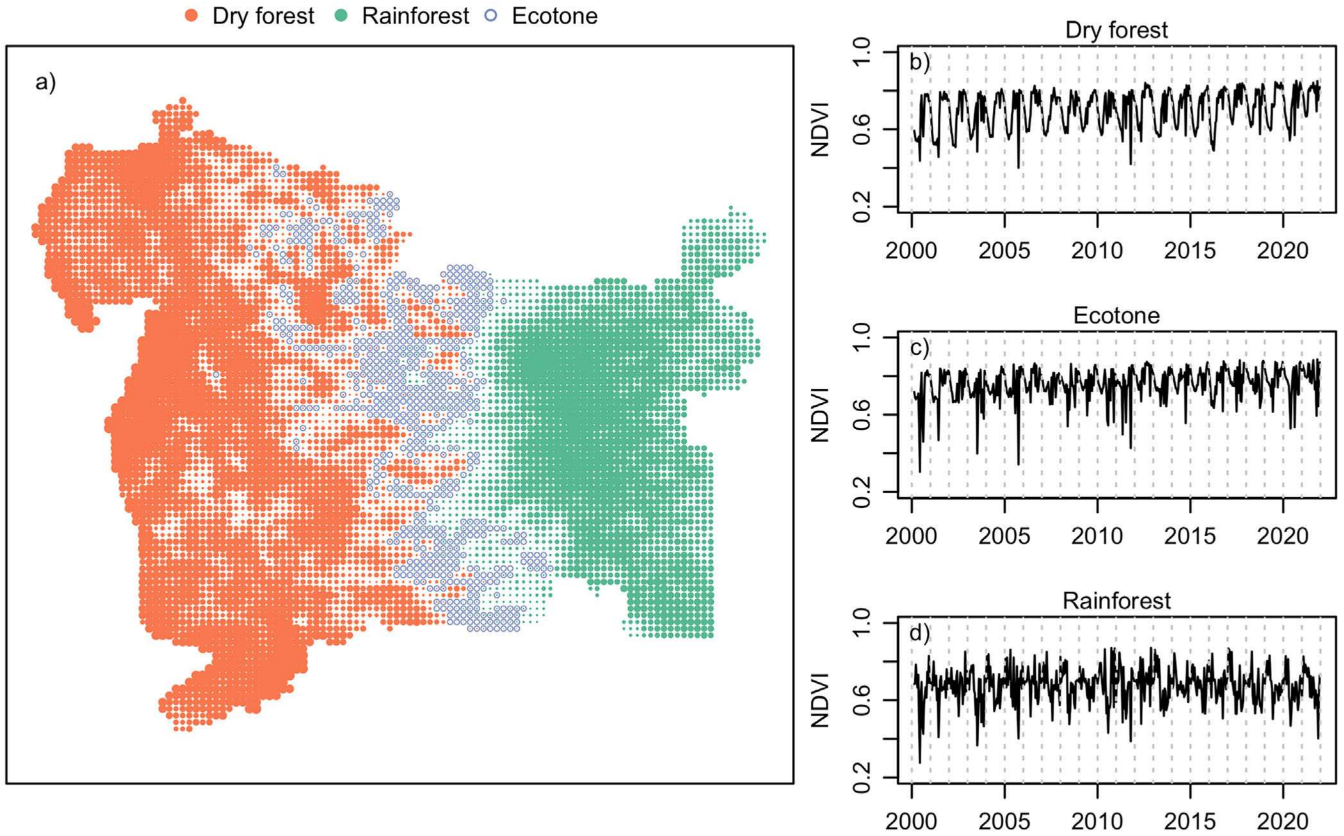

FIGURE 1 (a) Delineation of Area de Conservación Guanacaste into dry forest, ecotone, and rainforest, considering the full 2000–2021 time series. Pixel size indicates strength of association with the dry forest and rainforest classes. (b–d) Mean time series for pixels identified as dry forest, ecotone, and rainforest. NDVI, Normalized Difference Vegetation Index.

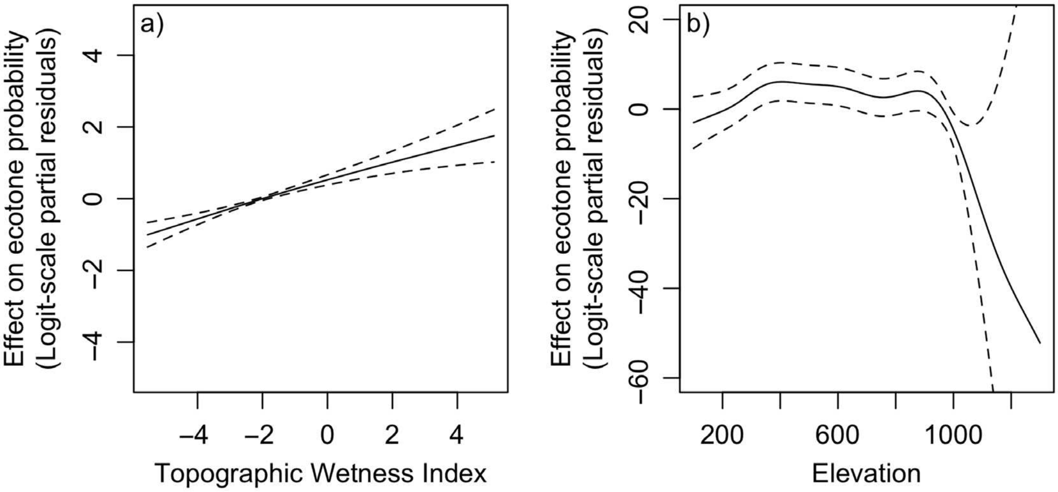

FIGURE 2 Generalized additive model effects of (a) topographic wetness index and (b) elevation on the probability of a location being classified as ecotone; $n = 5926$ pixels, deviance explained = 28%. Dotted lines indicate ±2 SE.

(Figure 2). The probability of a location being classified as ecotone was greatest at mid-elevations and increased with increasing TWI, and the effects of both variables were significant ($p < 0.001$). Hence, topographic variation partly explained the more complex and dendritic shape of the ecotone (Figure 1a). Maps of elevation and TWI are shown for reference in Appendix S1: Figure S2.

Long-term changes in the ecotone

When comparing the early (2000–2006) versus late (2015–2021) periods, the ecotone shifted modestly upslope. Respectively, the 10th percentile, 50th percentile, and 90th percentile of elevations of ecotone pixels shifted from 299.6 to 305.7 m ($p = 0.099$), from 403.0 to 416.0 m ($p = 0.041$), and from 627.0 to 627.3 m ($p = 0.487$). In the later period, the ecotone covered a larger area (early: 43.1 km^2; late: 48.8 km^2) and had a less complex shape (perimeter: area early: 5.35; late: 4.15). However, when we examined linear temporal trends using ecotones delineated using 1- and 3-year windows, no trend was statistically significant (Appendix S1: Table S2). Time series plots of ecotone properties for 1- and 3-year windows are shown in Appendix S1: Figures S3 and S4.

Climatic effects on ecotone properties

Variability in ecotone characteristics over time was related to climatic variation (Figures 3 and 4; Appendix S1: Figure S5). We focus here on results for 1-year windows; for 3-year windows, correlation directions were generally similar, though some magnitudes increased, likely because aggregation over a longer time period increased the signal-to-noise ratio. Appendix S1: Figure S5 matches Figure 3 for 3-year time windows. Ecotone area was significantly negatively related to MEI and 1-year lagged mean PET and significantly positively related to 1-year lagged annual total precipitation (Figure 4a–c). Ecotone median elevation was significantly positively related to 1-year lagged mean PET (Figure 4d). Ecotone elevation range was significantly positively related to mean PET (Figure 4e). For reference, climate variable time series are shown in Appendix S1: Figure S6.

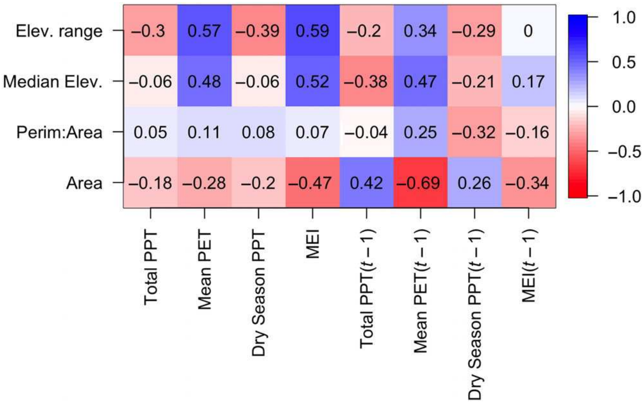

FIGURE 3 Correlations between ecotone characteristic and climate variables for 1-year windows. Text indicates Pearson correlation coefficient. MEI, Multivariate El Nino Index; PET, potential evapotranspiration; PPT, precipitation.

DISCUSSION

Using a novel combination of remotely sensed imagery and spatial synchrony analyses, we quantified spatiotemporal patterns in the tropical dry forest–rainforest ecotone, overcoming long-standing challenges for studying spatiotemporal dynamics of ecotones in response to environmental change and regional climate. We found that topographic and climatic variables related to moisture availability explained spatial and temporal patterns in ecotone characteristics. However, over our two-decade study period, evidence for long-term trends in the size, shape, or elevation of the ecotone was equivocal. Ecotone locations predominated at mid-elevations and in topographic depressions with higher moisture accumulation. Additionally, in wet years the ecotone tended to move downslope and be more spatially contiguous, whereas in dry years the ecotone tended to shift upslope and become more fragmented (Appendix S1: Figure S7). Given our understanding of differences in composition and productivity between dry forests and rainforests, this finding supports ecological theory that topography-induced soil water heterogeneity controls plant productivity and forest composition, especially in dry forests (Borchert, 1994; Comita & Engelbrecht, 2009). It also supports a role for regional climate in mediating the topographic distribution of microhabitats (Axelrod, 1967; Stebbins, 1952), suggesting further that tropical dry forests are sensitive to future drought, and possibly shrinking ecotone areas along the dry forest boundary.

Our synchrony-based method of ecotone delineation leveraged the substantial differences in seasonality between dry forests and rainforests in our study area. Pronounced seasonality in rainfall, and consequently vegetation productivity, is a defining feature of dry forests (Allen et al., 2017; Schwartz et al., 2020), which we observed in our data based on changes and patterns in NDVI (Figure 1). Productivity variability in the rainforest—inferred from NDVI—had weaker seasonality, yet stronger interannual variability, even though both dry forests and rainforests experienced wet and dry years, and total annual precipitation was strongly positively correlated across the study area. Rainforest productivity has been shown to be highly responsive to interannual precipitation variability (Gurgel & Ferreira, 2003; Jiang et al., 2022), partly due to a high degree of phenological plasticity and variation in leaf turnover in rainforests (Frankie et al., 1974).

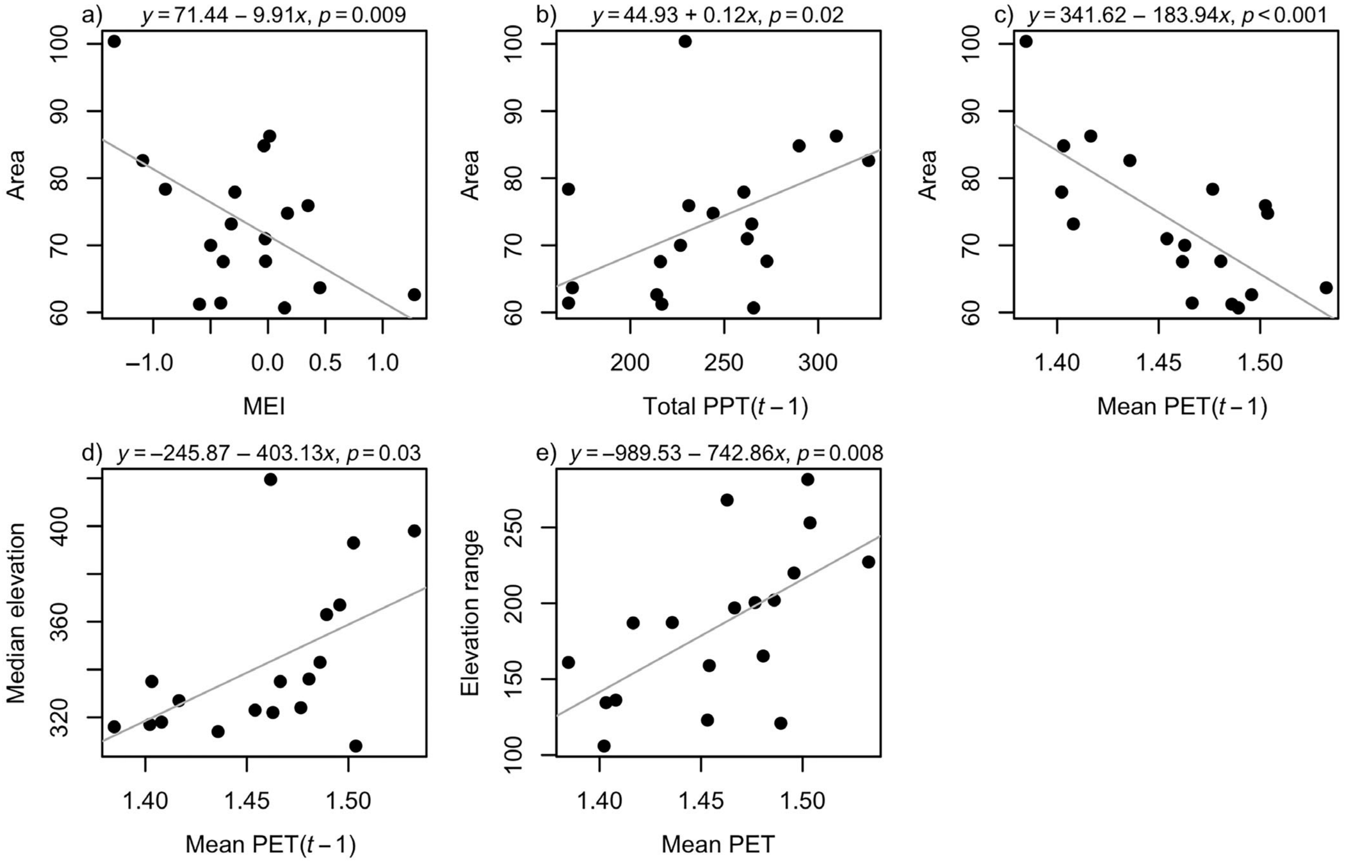

FIGURE 4 Scatterplots of statistically significant effects of climate on interannual variation in ecotone characteristics. The significance tests account for first-order temporal autocorrelation. MEI, Multivariate El Nino Index; PET, potential evapotranspiration; PPT, precipitation.

Our approach was well suited to detecting these differences among dry forest, rainforest, and ecotone even though other vegetation indices (e.g., Enhanced Vegetation Index [EVI]) tend to perform better in rainforests due to NDVI saturation in dense forests (Heute et al., 1999). Some dips in the greenness of the rainforest and ecotone areas could also result from interference by fog and low-lying clouds; however, our pretreatment of the data, in which we omitted observations apparently influenced by such interference (i.e., NDVI < 0.2), minimized impacts on our analysis. Other studies applying satellite remote sensing to ecotones have focused on the alpine treeline (Singh et al., 2012), shrubland–grassland interface (Moreno-De Las Heras et al., 2015), mangrove range boundaries (Cavanaugh et al., 2014, 2018; Rodriguez et al., 2016), and the tropical forest–savanna transition zone (Oliveras & Malhi, 2016). In these systems, spectral differences are starker on opposite sides of the ecotone, making it tractable to track shifts in ecotone boundaries solely using simple change approaches applied to remotely sensed vegetation indices.

Here, we leveraged spatial synchrony to delineate ecotone boundaries between forested biomes with subtle spectral differences in vegetation, making this a potentially useful approach for similar systems where simple spectral difference methods are insufficient. Our study was also simplified by focusing on a region with minimal interference from nonforest land cover types or land cover change; nonetheless, our approach can likely be adapted to other, more complex regions. The clustering algorithm we used can identify an arbitrary number of clusters, so assuming nonfocal land cover classes had their own temporal signature, these areas could be identified and treated according to study objectives. For systems featuring narrower transition zones between vegetation types, our general statistical approach could be applied to satellite imagery with finer spatial resolution, such as Landsat or Sentinel. While our study benefited from the near continuity of MODIS composite images, the approach can be applied to less temporally dense or somewhat irregular time series, provided sampling is sufficient to capture differences in dynamics. Similarly, our statistical approach could be used with spectral information other than NDVI, or even with other sorts of measurements entirely, provided they are dense enough to effectively characterize changes in ecosystem state across the ecotone.

One interesting feature of the ecotone was its complex, somewhat dendritic shape; although the ecotone was primarily found in an elevation band between 300 and 600 m above sea level, particularly on the downslope (dry forest) side it could be fragmented with strips of ecotone meandering through zones of predominantly dry forest (Figure 1), presumably following intermittent streams or valleys where water is available for longer periods (Borchert, 1994; Borchert et al., 2004). Indeed, we found that topography partly explained the probability of a pixel being identified as ecotone; the higher the TWI value, the greater the probability of ecotone occurrence at a given elevation (Figure 2). The greater apparent smoothness of the ecotone–rainforest boundary and its greater temporal stability could indicate greater resistance of rainforest vegetation to temporary reductions in precipitation. On the other hand, the dry forest–ecotone boundary was more geometrically complex and temporally dynamic. The dry forest–ecotone boundary could be more sensitive to anticipated future precipitation reductions (AlMutairi et al., 2019; Castillo & Amador, 2020; Hidalgo et al., 2013), shrinking the ecotone from the dry forest side, possibly through the loss of evergreen rainforest species in lower elevation portions of the ecotone. Major drought events are already shifting dry forest composition in this region due to differential recruitment of drought-tolerant deciduous species (Enquist & Enquist, 2011; Huang et al., 2021; Swenson et al., 2020; Wu et al., 2022).

The ecotone changes we observed may be due to changes in species composition, phenotypic plasticity, or both. The documented tree mortality event caused by the 2015 ENSO (Powers et al., 2020), combined with warming temperatures and shifts in the amount and timing of precipitation in this region (Janzen & Hallwachs, 2021), suggests that rapid canopy tree mortality and shifts in ecotone composition are plausible. Changing ecotone position due to changing species composition, however, may involve time lags (Morellato et al., 2000; Pau et al., 2010). Phenotypic plasticity can also explain the patterns we observed. That the ecotone tended to have a higher median elevation and reduced area during drier periods suggests that deciduous species on the dry forest edge of the ecotone shed leaves earlier or for longer periods and, as a result, become spatially synchronous with core dry forests during drier periods. For dry forest species, phenology is primarily determined by environmental water availability and species' ability to store water (Reich & Borchert, 1984). Thus, dry forest species occurring in the ecotone may be those normally restricted to moist microenvironments in dry forests, unable to store water, and, when stressed, exhibit a greater degree or earlier onset of deciduousness. That isolated areas typically identified as rainforests took on ecotone properties during drier periods further points to phenological plasticity playing some role in the patterns detected here. Studying climate-induced phenotypic plasticity in these regions may be key for disentangling shifts in species composition from shifts in phenology in the dry forest–rainforest ecotone and for detecting upslope migration of the ecotone.

Despite the observed effects of climate on interannual variation in the shape, area, and elevation of the ecotone, and the regional drying trend induced by climate change (Castillo & Amador, 2020), we observed equivocal evidence of long-term (2 decades) trends in ecotone properties. Although ecotone elevation, area, and shape changed between the early (2000–2006) and late (2016–2021) periods, analyses of temporal trends using shorter (1 and 3 year) time windows did not corroborate the statistical significance of these changes. Over the study period, interannual variation in rainfall and PET was far greater than any long-term trends (Appendix S1: Figure S6), likely explaining this apparent mismatch. Alternatively, noise introduced by analyzing shorter time windows could have masked real underlying trends. Our finding that moisture availability mediates the location and shape of the ecotone implies that if drying continues with climate change as predicted, the ecotone could shift to higher elevations, which we observed equivocal evidence of, but the ecotone could also become more dendritic in shape. Whether or not dry forest species will displace rainforest species remains an open question, and mechanisms controlling these shifts require greater focus. Shrubland encroachment into grasslands typically follows sustained periods of drought, resulting in a state shift thought to be irreversible, reinforced by positive feedback loops favoring shrublands (Moreno-de las Heras et al., 2015). We, however, lack a similar theory for dry and rainforest dynamics. Within the system studied here, major drying could result in a regime shift with unpredictable consequences. Because fragmentation is thought to govern thresholds in dispersal, connectivity, and species persistence (Pardini et al., 2010), an increasingly fragmented and dendritic ecotone may bode negatively for both dry and rainforest species. This may be especially true for wind-dispersed dry forest species owing to the downslope direction of trade winds.

Our approach revealed new insights into the dynamics of the tropical dry forest–rainforest ecotone and raises new questions for the ecology of this system and the transfer of our approach to other regions. Dry and rainforests make up roughly 70% of tropical forest cover in the Americas (Murphy & Lugo, 1986; Song et al., 2018), so it stands to reason that there are thousands of hectares of ecotone this approach could potentially be applied to. Our satellite imagery-based method detects differences in vegetation phenology, which likely reflects a combination of phenological plasticity and differences in performance among the species comprising the community on interannual timescales. Over longer timescales, possibly exceeding the duration of this study, major changes in species composition could also manifest. Field-based studies are needed to resolve the degree to which satellite-detected changes in phenology reflect each of these mechanisms. Using transferable quantitative ecotone definitions such as we have demonstrated here stands to further our understanding of ecotones and how they are shifting in response to global change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Walter, 2024a) are available on Dryad at https://doi.org/10.25338/B80642. Code (Walter, 2024b) is available on Zenodo at https://doi.org/10.5281/zenodo.12723979.

ORCID

Jonathan A. Walter https://orcid.org/0000-0003-2983-751X
Jeff W. Atkins https://orcid.org/0000-0002-2295-3131
Catherine M. Hulshof https://orcid.org/0000-0002-2200-8076

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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