

## RESEARCH ARTICLE

# Resilience of a tropical montane pine forest to fire and severe droughts

Daniel E. B. Swann<sup>1</sup>  | Peter J. Bellingham<sup>2,3</sup>  | Patrick H. Martin<sup>1</sup> 

<sup>1</sup>Department of Biological Sciences,  
University of Denver, Denver, Colorado,  
USA

<sup>2</sup>Manaaki Whenua – Landcare Research,  
Lincoln, New Zealand

<sup>3</sup>School of Biological Sciences, University  
of Auckland, Auckland, New Zealand

## Correspondence

Daniel E. B. Swann  
Email: [danswann329@gmail.com](mailto:danswann329@gmail.com)

## Funding information

National Science Foundation, Grant/  
Award Number: 1803192

Handling Editor: Julieta Rosell

## Abstract

1. Higher temperatures, declining precipitation, changing cloud cover and increased wildfires threaten tropical montane pine forests by overriding the environmental heterogeneity that typically buffers these systems from catastrophic fires. Severe fires threaten to overwhelm forest resilience and tip this biome into alternate vegetation states.
2. This study focused on long-term dynamics of montane *Pinus occidentalis* forests in the Cordillera Central, Dominican Republic after a ~1000 km<sup>2</sup> fire in 2005, the largest since 1965. We used long-term records to investigate climate before and after the fire, and 19-year dataset of pre- and post-fire vegetation change from a network of 55 permanent plots (20 small 0.05 ha plots and 35 large 0.1 ha plots) established in 1999 to model overstorey and understorey vegetation dynamics.
3. The 2005 fire was synchronized with the most extreme drought in the region in over 60 years. The fire burned from <1600 to >3000 m a.s.l. in elevation across windward and leeward slopes, creating a mosaic of low-, moderate- and high-severity patches. Lower elevations, leeward slopes and stands with a higher proportion of smaller pine trees all burned at higher severities.
4. Growth rates of trees that survived the fire remained lower than pre-fire rates 13 years after the fire. The highest post-fire mortality rates were soon after the fire and in the census immediately following subsequent post-fire droughts. Post-fire pine seedling abundance was significantly greater in stands with higher basal area of live canopy trees and significantly reduced by increased shrub abundance in the understorey. Understorey composition recovered rapidly to pre-fire states in sites affected by low- and moderate-severity fires, but sites affected by high-severity fires remained dissimilar to pre-fire composition 13 years after the fire. Even though high-severity patches had persistently low pine regeneration, 100% of small plots and 96% of large plots had at least one pine sapling or canopy tree recruit by 2018. Shrub taxa survived the fire in higher numbers and recovered to pre-fire densities much faster than the pine, especially in high-severity burns.
5. *Synthesis.* Climate change has increased the likelihood of wildfires in tropical montane pine forests, with long-lasting effects on vegetation dynamics. However, this biome may prove resilient to increasingly severe fires in the near future, given the ongoing recovery of *Pinus occidentalis* forests in Hispaniola despite

repeated severe droughts. Nevertheless, highly drought- and fire-resistant taxa (e.g. shrubs) may form alternate stable states in drier portions of tropical montane landscapes in the future as droughts and high-severity fires become more common.

#### KEYWORDS

alternate stable states, disturbance ecology, El Niño Southern Oscillation (ENSO), fire ecology, forest dynamics, monodominance, *Pinus occidentalis*, tropical montane forest

## 1 | INTRODUCTION

Tropical montane ecosystems are highly vulnerable to rapidly altering temperature and moisture regimes caused by global climate change (Hannah, 2021; Krishnaswamy et al., 2014; Muñoz et al., 2022; Williams et al., 2007) and extreme weather events, especially severe droughts (Foster, 2001; Scholl et al., 2021). Climate change is also causing large shifts in the elevation of orographic clouds and the trade wind inversion (TWI; a synoptic subsidence inversion that traps clouds below a roughly constant elevation, Giambelluca & Nullet, 1991) on tropical mountains, both of which strongly shape climate (Cao et al., 2007; Martin & Fahey, 2014; Marzol-Jaén et al., 2011) and disturbance regimes (Crausbay & Martin, 2016; Martin et al., 2007, 2011) in these ecosystems.

Fire disturbance regimes in tropical ecosystems are changing in response to global climatic change, as well as from fire suppression, changing land use patterns and invasive species (Archibald et al., 2009; Bellingham et al., 2018; Bowman et al., 2011; Ganteaume et al., 2013; Shlisky et al., 2007; Westerling et al., 2006). Highly altered fire regimes in fire-sensitive areas of the tropics have received widespread attention (Cochrane & Schulze, 1999; Laurance, 2003). However, less attention has been paid to altered fire regimes in historically fire-maintained tropical forests (Myers & Rodríguez-Trejo, 2009). Tropical montane pine forests, in particular, have historic disturbance regimes of fire and drought (Goldammer & Peñafiel, 1990; Martin et al., 2007; Myers & Rodríguez-Trejo, 2009; Ohsawa, 1995; Santisuk, 1997), but these may be changing as temperatures rise and moisture regimes shift (Bradley et al., 2006; Pepin et al., 2015; Seddon et al., 2016). While plants in these ecosystems have co-evolved with fire (He et al., 2012; Keeley et al., 2011), the consequences of altered fire regimes interacting with intensifying droughts call into question their long-term resilience (Delettre, 2021; Seidl et al., 2016).

Resilience is most often evaluated by the rate a variable returns to its reference condition after a perturbation (Pimm, 1984; Van Meerbeek et al., 2021), that is, in a tropical montane pine ecosystem, the rate at which forest reforms after a fire or drought kills adult trees. Yet, altered disturbance regimes under climate change, particularly in fire-adapted coniferous ecosystems, may result in tipping points towards other ecosystems (Seidl et al., 2017). Therefore, it is also appropriate to evaluate resilience *sensu* Holling (per Van Meerbeek et al., 2021), that is, since ecological systems can have multiple stable

states, resilience should be evaluated whether altered states form under changing disturbance regimes (Delettre, 2021; Holling, 1973). Holling (1981, 1986) recommended evaluating resilience in fire-prone ecosystems as functions of fire intensity, fire frequency and plant biomass that define two basins of attraction: forest and grassland. In tropical mountains, warming temperatures and altered moisture patterns may produce novel fire regimes (Hemp, 2009), shifting fire-tolerant pine forests to non-forested ecosystems such as grass-, shrub- or fern-dominated communities, with many species that sprout vigorously even after severe fires and create persistent thickets that inhibit tree regeneration (Barton & Poulos, 2018; Falk et al., 2022; Martin et al., 2011; Slocum et al., 2006). Thus, tropical montane pine forest is only one possible state and resilience in this system should be evaluated in terms of the formation and persistence of altered states under fire and drought (Delettre, 2021), potentially reaching a tipping point that leads to a new equilibrium state (Paniw et al., 2021).

Ecological resilience is appropriately evaluated using plant demography (Capdevila et al., 2020; Paniw et al., 2021), ideally before, during and after the perturbation or change in state conditions. Long post-disturbance observation periods capture not only population dynamics and new tree recruitment, but also future perturbations that impede recovery mechanisms (Coop et al., 2020). Indeed, the long-term vigour of surviving trees and post-fire environmental conditions are often as important for forest recovery as the immediate effects of the disturbance. For non-serotinous species, large surviving trees are critical to post-fire resilience, providing seed source and maintaining patches of forest cover (Franklin et al., 2007). However, surviving trees are not all equivalent, as varying fire damage impairs vigour and admits pathogens in more injured stems, resulting in delayed mortality for years after a fire (Busse et al., 2000; Fajardo et al., 2007; Van Mantgem et al., 2011), with cascading effects on regeneration (Franklin et al., 2007). Likewise, climate change may cause greater post-fire stress and delayed mortality, as post-fire survivorship and fecundity is highly sensitive to environmental and climate conditions (Allen et al., 2015; Harvey et al., 2016a; Kolb et al., 2019; Littlefield, 2019). Poor post-fire regeneration in montane conifers in temperate forests most likely occurs at lower elevations and ecotone boundaries (Coop et al., 2020; Davis et al., 2019), but the importance of delayed mortality, climate and environmental heterogeneity on post-fire dynamics in tropical montane pine forests is largely unknown.

A large, high-severity fire burned through a tropical montane pine forest dominated by the endemic Hispaniolan pine, *Pinus occidentalis* Sw., in the Cordillera Central, Dominican Republic in 2005 during an ENSO event (Martin et al., 2011; Sherman et al., 2008). This provided an exceptional opportunity to quantify the resilience of tropical montane ecosystems to disturbance and climate change. Along with tropical cyclones (Gannon & Martin, 2014; Van Bloem & Martin, 2021), regular fires have disturbed these montane pine forests for millennia (Crausbay et al., 2015; Horn et al., 2000; Kennedy et al., 2006), and natural and anthropogenic fires are the most important cause of tree mortality and turnover in the system (Martin et al., 2007; Martin & Fahey, 2006; Myers et al., 2004; Sherman et al., 2005). Hispaniola has warmed slowly in recent decades (+0.25°C in mean annual temperature since 1960), but climate change is likely to accelerate (Stephenson et al., 2014). Models predict mean annual temperatures to rise 1.1–1.5°C by 2050 and mean annual precipitation to decrease 4.7%–8.5% (United States Agency for International Development (USAID), 2017), and mountains are likely to warm and dry more rapidly than the island as a whole (Longman et al., 2015; Pepin et al., 2015), with strong implications for the Cordillera Central fire regime (Martin & Fahey, 2006).

Using pre- and post-fire vegetation measurements in the Cordillera Central over 19 years, we evaluated ecosystem resilience in the context of climate variability. We asked: (1) How has climate in this system changed in recent decades and were unusual climate conditions associated with the 2005 fire? Given the link between droughts and ENSOs in the area (Martin & Fahey, 2006), we expected the 2005 ENSO triggered a drought in the region, creating the conditions for an unusually large and severe fire that helped supersede stand-scale biophysical controls (e.g. topography, stand structure and necromass fuel) on fire patterning; (2) How did temporal variation in climate and spatial variation in stand-scale fire severity and environment shape post-fire patterns of resilience (sensu Pimm, 1984)? Due to stress from fire damage and climate change, we hypothesize that post-fire pine growth rates were low and mortality rates high; (3) What were the long-term dynamics and drivers of resilience sensu Holling? We expected stand-scale variation in fire severity, environment and demographic vigour of surviving canopy trees to determine patterns in regeneration and canopy recruitment and that hotter and drier stands (on lower elevation, leeward slopes) with higher-severity burns were more likely to tip into alternate transient or stable states dominated by shrubs. Collectively, these questions address the resilience of tropical montane pine forests to high-severity fires in the face of accelerating climate change.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

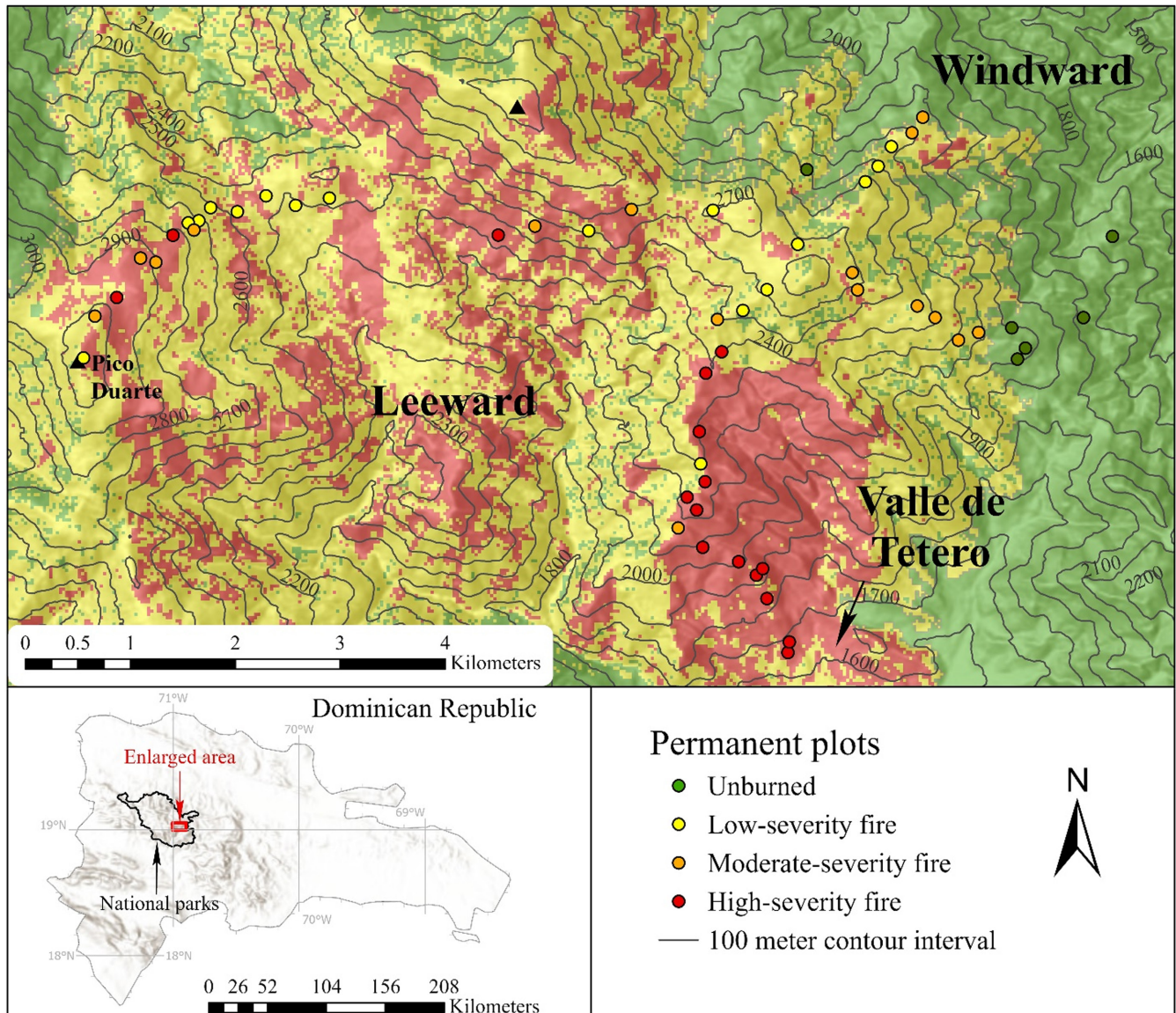
This study was conducted in two adjoining national parks, Armando Bermúdez (766 km<sup>2</sup>) and José del Carmen Ramírez (764 km<sup>2</sup>), in the Cordillera Central mountains of the Dominican Republic (Figures 1

and Figure S1). The parks, ranging in elevation from 459 to 3087 m above sea level (m a.s.l.) including Pico Duarte (the highest peak in the Caribbean), were established in the mid-1950s before any logging or clearing had occurred in the parks' interiors, forming a continuous protected area of rain, cloud and pine forests (Hoppe, 1989). Land use around the national parks is a mosaic of predominantly low-intensity agriculture in wetter areas north and east of the parks, livestock grazing on all sides of the parks (but concentrated in the drier areas to the south and west), and regrowth of secondary forests, mainly from reforestation projects. The use of fire in agriculture to clear fields has declined substantially in recent decades (F. Peralta, pers. comm.). Deforestation and illegal logging are non-existent in the areas around our study area, though sporadic logging may occur in the western extremes of the parks (F. Peralta, pers. comm.). Overall, direct and indirect land use pressures on the parks has remained very low over the last 30 years or longer, at least in the areas around the study site (PHM, pers. obs.).

The region's climate is tropical to subtropical, with a dry season in January–March, a rain shadow on slopes leeward of the main ridge (mean annual precipitation 1200–1400 mm year<sup>-1</sup>) and wetter conditions (1900–2200 mm year<sup>-1</sup>) on slopes windward (Martin & Fahey, 2014). This wet windward–dry leeward contrast in moisture patterns has a fundamental influence on the region's forests. In the dry portions of the landscape—which occur in all high elevations above the TWI and at lower elevations in the leeward rain shadow—*P. occidentalis* forms a monodominant forest overstorey (Figure 1; Cano et al., 2011; Darrow & Zanoni, 1990; Martin et al., 2007; Sherman et al., 2005). Shaped by the TWI, the shift from mesic to xeric conditions is abrupt on windward slopes and at ~2100 m a.s.l. a discrete ecotone occurs between pine forests and the cloud forests that dominate windward elevations below the TWI. Cloud forests (10–12 m tall) are comprised of tree ferns (Cyatheaceae), angiosperm and Podocarpaceae tree species.

### 2.2 | Disturbance history

Fires and tropical cyclones are the major disturbances in this ecosystem (e.g. Kennedy et al., 2006), and the return intervals of these disturbances vary widely along elevation, topographic and orographic gradients (Gannon & Martin, 2014; Martin & Fahey, 2006). The fire regime in the monodominant pine forests for the past 200 years was characterized by regular, low-intensity surface fires punctuated by infrequent and patchy crown fires (Martin & Fahey, 2006). Over this 200-year period, the mean fire return interval—a point estimate of fire frequency (Baker & Ehle, 2001)—was 31.5 ± 24.9 (SD) year for the entire study area, 42.1 ± 27.6 year on wet windward slopes and 16.7 ± 7.8 year on dry leeward slopes (Martin & Fahey, 2006). In 1965, severe fires burned across the region and the parks were put under a fire suppression policy thereafter (Kustudia, 1998), a policy that remains in effect to this day; thereafter, only a few small, low-severity fires occurred in our study area (Dirección Nacional De Parques, 1997;



**FIGURE 1** Locations of permanent plots ( $n = 55$ ) and associated fire severity classes in a tropical montane pine forest. Fire severity classes were assigned based on the percentage of stems in a plot killed by the fire: Low-severity  $\leq 25\%$ ; moderate-severity between  $25\%$ – $67\%$ ; high-severity:  $>67\%$ . All high-severity plots experienced stand-replacing fires. Fire severity map modified from Sherman et al. (2008).

Martin & Fahey, 2006). In 2005, an agricultural fire escaped into the parks and burned  $>1000\text{km}^2$  as surface and crown fires through most of the parks' monodominant pine forest (Figure 2; Sherman et al., 2008). Tropical montane forests have slow rates of decomposition (Looby & Martin, 2020; Ostertag et al., 2022), which can allow fuels and organic matter to accumulate in the absence of fire, and the long interval with few fires after 1965 likely contributed to the severity of the fire as fuels accumulated.

### 2.3 | Vegetation sampling

In 1999, 55 circular, permanent plots were established in monodominant pine forest over an elevation range of 1695–3050m a.s.l. on both windward and leeward slopes (Martin et al., 2007; Sherman

et al., 2005); twenty 0.05 ha small plots were placed in higher density stands (mean  $692 \pm 57.9$  [SEM] stems  $\text{ha}^{-1}$  in 1999) and 35 0.1 ha large plots were placed in lower density stands (mean  $282 \pm 30.9$  stems  $\text{ha}^{-1}$ ; Sherman et al., 2005). Pre-fire mean basal area was  $20.5 \pm 1.5 \text{ m}^2 \text{ ha}^{-1}$  in small plots and  $15.6 \pm 1.0 \text{ m}^2 \text{ ha}^{-1}$  in large plots. After the 2005 fire, plots were re-measured in 2007, 2010, 2015 and 2018–2019. Access to the site was granted via a series of research permits issued by the Dominican Park Service, Dirección Nacional De Parques. Excluding the high-severity fire plots (16 of the 55 plots; these plots had 98%–100% mortality), live post-fire tree density in 2007 was  $327 \pm 95.3$  stems  $\text{ha}^{-1}$  in small plots and  $160 \pm 23.1$  stems  $\text{ha}^{-1}$  in large plots, and live post-fire tree basal area in 2007 was  $14.1 \pm 2.6 \text{ m}^2 \text{ ha}^{-1}$  in small plots and  $12.6 \pm 1.2 \text{ m}^2 \text{ ha}^{-1}$  in large plots (Sherman et al., 2012). One large (0.1) and 5 small (0.05 ha) monodominant pine plots sampled in 1999 did not burn in the fire; these six

**FIGURE 2** Patterns of post-fire vegetation regeneration in the Cordillera Central, Dominican Republic. (a) MODIS image (3/2005), note the smoke from several separate fires burning simultaneously across the wider region; (b) high-severity burns (2/2006) on the Tetero slopes; (c) *Pinus occidentalis* and *Danthonia domingensis* bunchgrass regeneration (3/2008) after a high-severity burn at ~2800 m; (d) regrowth (3/2015) on the Tetero slopes; (e) pine regeneration (7/2018) at ~2600 m a.s.l. in a moderate-severity burn with high levels of delayed mortality of canopy pines; (f) pine regeneration (7/2018) at ~2700 m a.s.l. in a low-severity burn. Additional photographs of pre-fire structure are shown in Figure S1. (photographs from P.H. Martin).



plots were remeasured in 2019 (but not in 2007–2015) for comparison with burned plots. The unburned plots had a mean stem density of  $468 \pm 106$  stems  $\text{ha}^{-1}$  and a mean basal area of  $19.1 \pm 2.7$   $\text{m}^2$   $\text{ha}^{-1}$  in 1999, and  $435 \pm 86.9$  stems  $\text{ha}^{-1}$  and  $24.9 \pm 4.7$   $\text{m}^2$   $\text{ha}^{-1}$  in 2019. The number of live trees on average per plot before the fire were such that estimates of mortality had a precision of 3.5% in large plots and 2.8% in small plots. See Table S1 for full sampling details.

In 1999, all live and dead trees in a plot were identified, tagged and measured at the tag for DBH to 0.1 cm. Trees are defined in all analyses as stems  $\geq 10.0$  cm diameter at breast height (DBH). All woody understorey plants ( $< 10$  cm DBH) were identified and tallied as established tree seedlings (5–130 cm height), tree saplings ( $> 130$  cm), or shrubs in a 1-m wide strip on the plot's diameter. Shrubs were defined as non-tree woody understorey species; these species are predominately multi-stemmed and reach  $> 25$  cm in height but generally do not grow taller  $> 1.5$  m (Horn et al., 2001; Sherman et al., 2005). In ensuing censuses, existing and new trees ( $\geq 10.0$  cm DBH) were measured as above, existing tree mortality status was noted, and the understorey was remeasured. Herbaceous cover is patchy and small-statured in the monodominant pine forest, mostly the bunchgrasses *Danthonia domingensis* and *Agrostis hiemalis* above 2000 m a.s.l. elevation (Sherman et al., 2005), so pine seedlings interact primarily with other established pines and shrubs; woody taxa are hence the focus of the analyses.

Nine months after the fire in December 2005, we assessed the site. In the first post-fire census (in January–February 2007), fire damage (e.g. scorch) and time since mortality (e.g. level of decay) were used to classify trees ( $\geq 10.0$  cm DBH) as dead before or killed by fire (Sherman et al., 2008). For the understorey, charred stems dead in 2007 were assumed killed by fire and tallied as pines or shrubs. We are confident this method successfully distinguished trees killed by fire for three reasons: (1) There was no evidence of any notable dieback, disturbance, or tree mortality in and around the plots in the pre-fire period, 1999–2004 (PHM, pers. obs.); (2) We remeasured a subset of plots immediately after the 2005 fire (Sherman et al., 2008). Fire-killed trees were readily distinguished from trees dead before the fire. Fire-killed trees remained standing with dead foliage retained and bark intact in 2005 and 2007 inspections, whereas stems that were dead before the fire had often fallen, had little or no retained foliage and had usually lost their bark; (3) Background mortality rates between 1999 and 2007 in unburned monodominant pine plots (i.e. the forest type impacted by the 2005 fire) were very low: on average,  $0.4 \pm 0.1$  (SEM) % of pine trees died per year (Sherman et al., 2012). Cumulatively, over the 8 years between censuses (1999 to 2007), background, non-fire mortality rates showed 1.1 tree stems died on average in small plots and 0.8 stems in large plots, and a portion of background mortality would have occurred long enough before the fire to be separated morphologically

from stems killed by fire. Stems that died shortly before the fire may have been erroneously classified as killed by fire, but the evidence indicates this percentage was small.

Using 386 sample points and <3-m resolution imagery, Sherman et al. (2008) distinguished three fire severity classes based on intensive, fine-scale sampling. Hence, we calculated fire severity (as a % of tree basal area killed by fire) binned into three classes, as done in numerous fire severity studies (e.g. Cocks et al., 2005; Odion et al., 2010; Romme et al., 2003). These bins had similar sample sizes in each severity class (low—17 plots; moderate—16 plots; high—16 plots).

## 2.4 | Pre- and post-fire climate

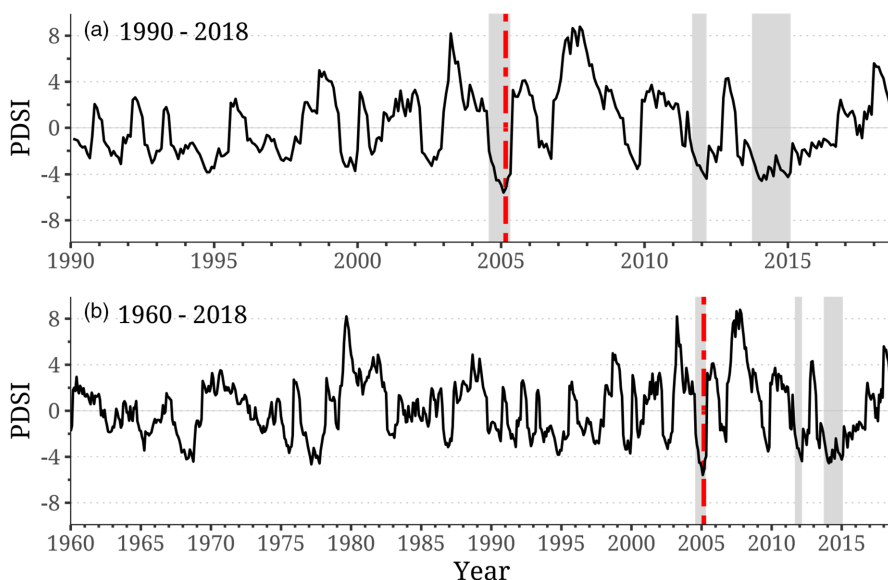
We used TerraClimate—a monthly, gridded 4-km resolution global climate dataset (Abatzoglou et al., 2018)—to compare pre- and post-fire climate in the Cordillera Central to the 1961–1990 reference period (World Meteorological Organization (WMO), 2017). We compared the deviation in monthly climate for 15 months before the fire (1/2004–3/2005) and in drought periods after the fire (2006–2019) to average monthly reference values. To distinguish between shorter dry periods versus droughts in the post-fire years, we defined periods of 6 or more consecutive months with a monthly Palmer Drought Severity Index (PDSI) of < -2.0 as a drought, the same threshold used by the National Integrated Drought Information System of the US government.

Drier and hotter conditions prevailed for 15 months before the fire, creating an extreme drought by February 2005 (PDSI = -5.59; Table S2), the site's lowest PDSI in the TerraClimate dataset (1958–2018, Figure 3). Compared with the reference period, mean monthly precipitation was 27.7% lower in the 15 months before the fire, and mean monthly maximum and minimum temperatures were 0.8% and 14.3% higher. After the fire, there were severe droughts from September 2011 to March 2012 (7 months) and October 2013 to

February 2015 (17 months), hereafter referred to as the post-fire droughts (Table S3).

## 2.5 | Patterns of fire severity

Using ordinary least squares linear regression, we modelled predictors of stand-scale fire severity patterns in burned plots only across the site using plot-scale basal area mortality from fire (%) as a continuous index of severity. We accounted for the inherent spatial autocorrelation of fire spread and severity using Moran's Eigenvector Mapping (MEM; Borcard et al., 2018; Dray et al., 2006) and we used variation partitioning to compare the importance of spatial (e.g. eigenvectors) and plot-scale environment (e.g. elevation) and vegetation (e.g. average tree DBH) variables against fire severity patterns. MEM creates a spatially explicit, distance-based connectivity matrix from plot locations, which is decomposed via ordination into eigenvectors based on Moran's *I* statistic. We used a distance-based connectivity matrix with a maximum distance of 875 meters and a concave-down geographic distance weighting function to determine spatial patterns in the plot data; their irregular spacing meant that we could not identify finer spatial structures without an extra point added directly between the two furthest plots (Borcard et al., 2018). We used double-stopping forward selection for biophysical and spatial predictors to reduce overfitting and type 1 errors that can result from traditional forward selection or multi-model selection with AIC (Bauman et al., 2018; Blanchet et al., 2008). We selected biophysical predictors without detrending the response (i.e. fire severity) but constrained the spatial eigenvector to within-site scales by detrending the response variable of any linear spatial structures larger than the study site. The final model selected six parameters: three plot-scale biophysical predictors (elevation, orography and quadratic mean diameter of tree DBH), two spatial predictors and one intercept term.



**FIGURE 3** Palmer Drought Severity Index reproduced from a gridded 4-km resolution global climate dataset, TerraClimate (Abatzoglou et al., 2018). Positive values indicate wet periods, and negative values indicate dry periods. The red line shows the 2005 fire, and the grey bars indicate defined periods of drought from 2005–2018 (see Section 2.4 for drought criteria).

## 2.6 | Post-fire patterns in growth and mortality

We analysed spatiotemporal variation in pine demography in several ways (Table S1). First, we explored controls on cumulative post-fire demography at the individual tree level (i.e. from the first post-fire census in 2007 to the final census in 2018, ignoring variation in between). Cumulative post-fire tree growth (annual diameter growth rate [ $\text{cm year}^{-1}$ ]) was modelled with a mixed-effects linear regression and cumulative post-fire mortality was modelled with a mixed-effects logistic regression, both as functions of tree DBH, fire severity, elevation, orography (windward vs. leeward), aspect, slope and terrain (an index of plot convexity or concavity; McNab, 1989). For both models of growth and mortality, Moran's  $I$  tests of distance-based spatial autocorrelation between plots were not significant and so not incorporated. Independence between trees nested by plot was modelled with a random effect term, assessed for significance with a likelihood ratio test.

Next, we used generalized estimating equations (GEEs, see below) with the *geeglm* function in *geepack* in R (Halekoh et al., 2006) to model population averages of tree demographic rates at the individual tree level (diameter growth [ $\text{cm year}^{-1}$ ] and probability of mortality [ $\% \text{ year}^{-1}$ ]) in three comparisons: (1) pre- versus post-fire: average growth and mortality rates of surviving trees in low and moderate severity plots in the post-fire censuses were compared with pre-fire rates; (2) post-fire rates: average growth and mortality rates of surviving trees were compared among the three post-fire censuses and (3) burned versus unburned: average cumulative demographic rates from 1999 to 2018 were compared between burned versus unburned plots. Post-fire tree demography in burned plots was only measured in low and moderate fire severities, as there were no surviving trees in high severities.

First, we used GEEs to compare pre- versus post-fire population average growth and mortality, with 1999–2007 as the “pre-fire” interval. Pre-fire growth was measured in 2007 on trees that survived the fire and pre-fire mortality was calculated from stems identified in 2007 as dead before fire. After a fire, bark loss on stems of living trees can compromise the accuracy of diameter growth measurements. In the 2007 census, we noted possible bark loss and the height of scorch on all living stems, and there was no evidence of bark loss, and fire scorch was usually below the DBH datum, as surviving trees occurred exclusively in low and moderate severity burns. Nevertheless, growth measurements in the first post-fire census may have been underestimated on some stems due to bark loss. The effect of fire severity (as categorical variables) in each time interval was tested using an interaction term in both the growth and mortality GEEs. Tree DBH and elevation (both significant in the mixed effects regression above) were additional covariates included in the growth GEE models to provide sized-weighted growth rates (i.e. to account for the proportional effects of tree circumference on diameter growth) and to isolate the effect of fire severity. Annualized growth rates innately account for unequal census intervals in the GEE models of growth, but mortality GEEs—a binary response—required an offset term.

Second, we used GEE models (modelled as above) to contrast post-fire pine demography through time, comparing rates in each census with the preceding and succeeding census with contrasts between low- and moderate-severity burns. Combined with the GEE analysis of recruitment rates through time (below), these models test the effects of the post-fire droughts on the recovery of pine demography in each fire severity class.

Third, we used GEEs (as above) to contrast post-fire pine demography in burned vs. unburned plots. Since unburned plots were on average lower and elevation was a significant predictor of growth rates, we partitioned growth rates in burned plots into low- and high-elevation groups based on the elevation of the TWI (2500m; Martin & Fahey, 2014). For contrasts of post-fire mortality rates, burned plots were separated into low or moderate fire severity groups as fire severity had a significant effect on rates of post-fire survivorship.

GEEs, by specifying a correlation matrix to account for the form of within-subject responses, are robust to unbalanced, non-normal, nested and repeated measures data (Ballinger, 2004) common in long-term population census datasets. Growth and mortality rates were modelled in each GEE analysis using a Gaussian and binomial distribution, respectively, with repeated tree measurements nested by tree ID and by plot and an exchangeable correlation structure in all models. Post-hoc comparisons in burned versus unburned plots were made with Tukey's HSD and pre- versus post-fire comparisons were adjusted with a multivariate-t adjustment.

## 2.7 | Post-fire community dynamics

In each fire severity class, we used GEEs to compare change over time in plot-level tree basal area and canopy recruitment, and understorey densities of pine seedlings, pine saplings and shrubs. Tukey's HSD post-hoc tests were used for pairwise comparisons among fire-severity classes in a given census, and multivariate-t adjustments were used to compare densities across successive years. For tree basal area, we used a Gaussian distribution; for understorey and recruitment densities, we used a Poisson distribution to model count data with an offset term to account for variable plot size. We also modelled variation in cumulative post-fire recruitment in 2018 of pine (seedlings, saplings and canopy recruits) and shrub species with generalized linear regression models using a negative binomial distribution (to account for non-linear and over-dispersed count data) and offset terms to account for variable plot sizes. Recruitment was modelled as functions of elevation, orography, understorey density (pine or shrub density depending on the response variable, as an index of biotic competition) and live tree basal area in 2018 (a combined index of initial and delayed mortality). Given sample size constraints, we used no more than five predictor variables in these models; all predictors were checked for cross correlation using a VIF threshold of  $<3$ .

Finally, to model changes through time in post-fire understorey woody composition, we calculated mean changes in understorey

community composition using the *multivariate\_change* function in the *CODYN* package in R (Avolio et al., 2019), and we used non-metric multidimensional scaling (NMDS) with relativized Bray–Curtis dissimilarities (in R package *VEGAN*; Oksanen et al., 2013) for the years 1999, 2007 and 2018. To test for differences between each census relative to its pre-fire composition, we used relativized Bray–Curtis dissimilarity matrices in pairwise PERMANOVA tests (in *pairwiseAdonis*; Martinez Arbizu, 2020) along with a “Benjamin–Holm” multiple comparisons *p*-value adjustment to control for a false discovery rate of 0.05. To test the effect of elevation and orography on post-fire compositional recovery, we used a linear regression to model mean dissimilarity values of each plot in 2018 vs 1999 (using a relativized Bray–Curtis dissimilarity matrix similar to NMDS and PERMANOVA tests) against elevation, orography and an interaction term. Lastly, rank abundance clocks (Hallett et al., 2016) were calculated for the six most abundant species for each fire severity class to visualize change in understory dominance over time.

All statistical analyses were done in R version 4.0.2 (R Core Team, 2018). Logistic (*glmer* in package *LME4*; Bates et al., 2015) and negative binomial regression models (*glm.nb* in package *MASS*; Venables & Ripley, 2002) were checked for over and under dispersion and spatial autocorrelation using *DHARMA* (Hartig, 2020). Residuals in all linear models were checked for normality and heteroscedasticity; growth in mixed effects regression required log transformation. To assess goodness-of-fit in GEEs, demographic rates in each census interval (i.e. the observed population averages) were checked to ensure they were within 95% confidence intervals of the predicted marginal means (estimated with *emmeans*; Lenth, 2020). Predictor variables were checked for multicollinearity and post-hoc marginal means were estimated with *emmeans*. Data used in this study are archived in the Dryad Digital Repository (Swann et al., 2022; <https://doi.org/10.5061/dryad.qnk98sfm3>).

## 3 | RESULTS

### 3.1 | Patterns of fire severity

Fire severity calculated as a percentage of tree basal area killed by fire binned into low ( $\leq 25\%$ ), moderate (25%–67%) or high severity ( $> 67\%$ ) classes. Patterns of fire severity were spatially structured with significant biophysical and spatial eigenvectors (Figure S2). The total model (summing all sections) had an  $R^2_{\text{adj}} = 52.8\%$  ( $F_{5,43} = 11.74$ ,  $p < 0.001$ ). Three plot-level biophysical variables were related to patterns of fire severity: orography (leeward slopes burned most severely,  $R^2_{\text{part}} = 23.8\%$ ,  $p < 0.001$ ), elevation (a negative relationship,  $R^2_{\text{part}} = 18.5\%$ ,  $p = 0.003$ ) and stand structure (a negative relationship with quadratic mean diameter of tree DBH,  $R^2_{\text{part}} = 12.7\%$ ,  $p = 0.016$ ). Moran's eigenvectors explained the remainder of the variance in the model ( $R^2_{\text{adj}} = 7.5\%$ ,  $p = 0.049$ ); the discrepancy in the sum of the partial  $R^2$  values in the spatial

model and the  $R^2_{\text{adj}}$  of the total model is a common result using variation partitioning with partial regression (see Figure S2). The other biophysical predictors evaluated (see Tables S4 and S5 for full list) were not selected during double-stopping forward selection, including large woody fuels (i.e. necromass from recently dead, snapped and tipped trees).

### 3.2 | Resilience of pine forests to fire: Rate of return to pre-fire demographic rates

#### 3.2.1 | Growth

After accounting for declining average annual pine diameter growth rates with increasing tree size (marginal  $R^2 = 7.1\%$ ,  $p < 0.001$ , 2007–2018), we found cumulative growth rates declined with elevation (marginal  $R^2 = 9.0\%$ ,  $p = 0.004$ ) and were marginally lower on windward (marginal  $R^2 = 2.7\%$ ,  $p = 0.046$ ; Table 1) than leeward slopes. Fire severity had no significant effect on overall cumulative post-fire growth rates (Table 1). However, 13 years after the fire, population-averaged growth rates were still significantly lower than pre-fire rates in both low- ( $p < 0.001$ ) and moderate- ( $p = 0.005$ ) fire severity classes. In the GEE analysis of burned vs unburned rates from 1999 to 2018, pines in low-elevation burned plots (2175–2500 m a.s.l.) and high-elevation burned plots (2533–3094 m a.s.l.) grew 46% ( $0.17 \pm 0.02 \text{ cm year}^{-1}$ ;  $p = 0.008$ ) and 73% more slowly ( $0.08 \pm 0.02 \text{ cm year}^{-1}$ ;  $p < 0.001$ ), respectively, than those in unburned plots ( $0.30 \pm 0.04 \text{ cm year}^{-1}$ ).

#### 3.2.2 | Mortality

Pine mortality rates over the full post-fire period (2007–2018) of trees that initially survived the fire (i.e. delayed mortality) were higher as fire severity increased ( $p = 0.002$ ; Table 1; Figure S3), but were not significantly related to tree size (DBH) or geographic variables. There was a large pulse of delayed mortality in stands affected by both low- (257% mean increase,  $p = 0.006$ ) and moderate- (200% mean increase,  $p = 0.021$ ) severity fires between the initial post-fire census in 2007 and the second post-fire census in 2010 (Figure 4). After this pulse, mortality rates declined but remained significantly higher than pre-fire rates in both low- ( $p = 0.012$ ) and moderate- ( $p = 0.045$ ) severity fires. Average mortality rates in 1999–2018 in unburned plots ( $1.0 \pm 0.5\% \text{ year}^{-1}$ ) did not differ significantly from low-severity fire plots ( $2.0 \pm 0.3\% \text{ year}^{-1}$ ;  $p = 0.187$ ), but were lower than in moderate-severity fire plots ( $3.1 \pm 0.6\% \text{ year}^{-1}$ ;  $p = 0.023$ ).

#### 3.2.3 | Recruitment

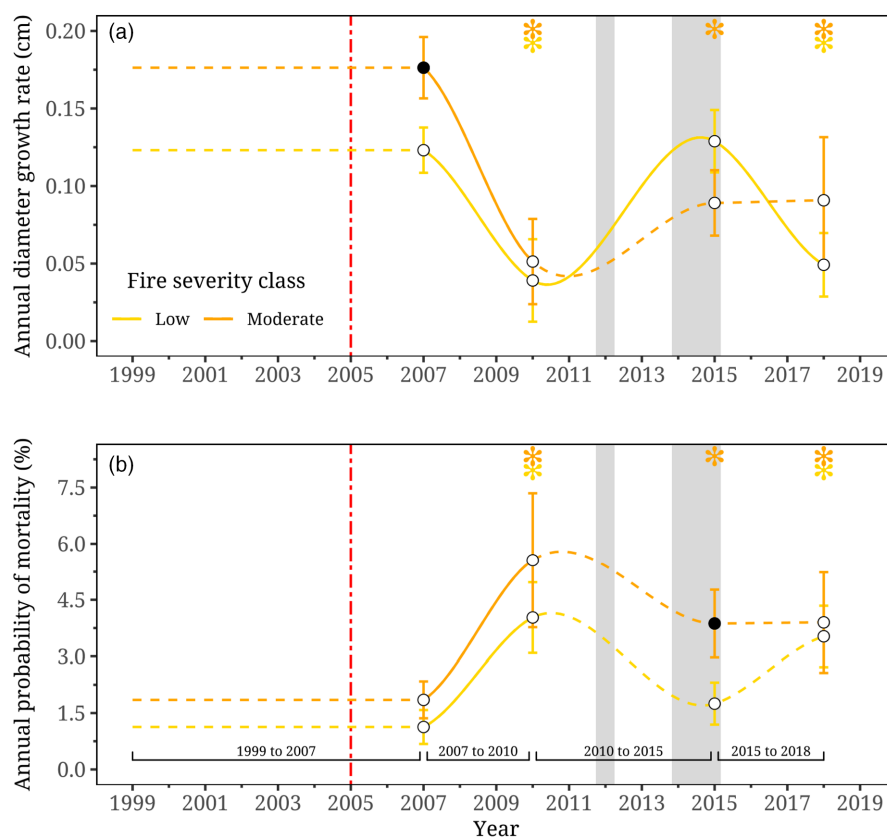
Post-fire patterns of pine recruitment began at effectively zero across all burn severities, as 100% of pine seedlings and 96%–100% of pine



**TABLE 1** Factors driving variation in cumulative post-fire (2007–2018) tree growth and mortality of trees that survived the fire (i.e. in low-severity and moderate-severity fires,  $n = 33$  plots). Linear and logistic mixed regression models were used for growth and mortality, respectively. Bolded values indicate significant predictors at the 0.05 level, and  $n =$  total number of stems included in each model. For mortality, positive coefficients indicate higher probability of death. Unlike for growth, mortality models had a higher sample sizes as stems which died before a census could still be measured. Orography refers to leeward (0) versus windward (1), and TSI is a terrain shape index adapted from McNab (1989)

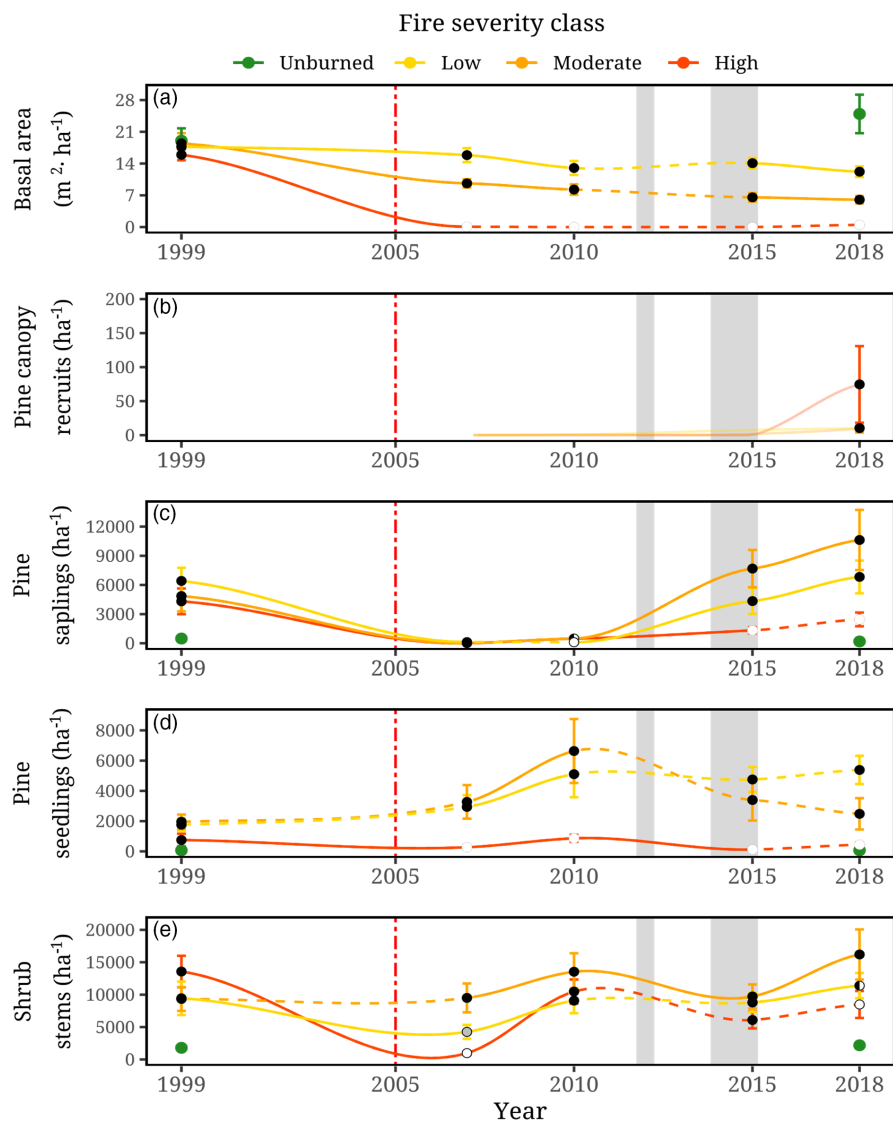
	Predictor	Standardized $\beta$	SE	Z-value	$p$
Growth rates ( $n = 352$ )	Intercept	0.077	0.010	7.53	<b>&lt;0.001</b>
	DBH (2007)	-0.044	0.008	-5.84	<b>&lt;0.001</b>
	Elevation	-0.043	0.013	-3.20	<b>0.004</b>
	Orography (1)	-0.028	0.013	-2.10	<b>0.046</b>
	Aspect	0.016	0.014	1.16	0.258
	Slope	-0.008	0.011	-0.71	0.486
	TSI	-0.006	0.012	-0.49	0.625
	Fire severity	0.010	0.010	1.11	0.276
Mortality rates ( $n = 509$ )	Intercept	-0.888	0.154	-5.76	<b>&lt;0.001</b>
	DBH (2007)	0.058	0.119	0.48	0.628
	Elevation	-0.098	0.189	-0.52	0.604
	Orography (1)	0.120	0.197	0.61	0.542
	Aspect	-0.039	0.196	-0.20	0.841
	Slope	0.088	0.166	0.53	0.595
	TSI	0.016	0.170	0.10	0.923
	Fire severity	0.436	0.139	3.14	<b>0.002</b>

**FIGURE 4** Twenty years of post-fire tree demography in monodominant *Pinus occidentalis* forests in the Cordillera Central, Dominican Republic. Points show marginal means ( $\pm 1$  SEM) from generalized estimating equations in each census interval for (a) annual growth and (b) annual probability of mortality, on trees that survived the fire in plots affected by low- and moderate-severity fires. Different coloured points (black vs white) indicate significant differences between fire severity classes within a census interval; lines indicate significant (solid) or non-significant (dashed) differences between census intervals for a given fire severity. Asterisks denote significant differences ( $<0.05$ ) compared with 1999–2007 rates. The dashed red line shows the 2005 fire, and the shaded grey zones indicate periods of post-fire drought.



saplings were killed in the fire, irrespective of severity (Figure 5). By 2018, all burned plots had at least one pine seedling or sapling, but post-fire pine sapling densities were low across all fire severities for at least the first 5 years (Figure 5). Pine sapling densities increased markedly after 2010 in low- and moderate-severity burns, matching pre-fire levels by 2015 and exceeding them by 2018, but sapling densities in high-severity burns did not begin to approach pre-fire

levels until 2018 (Figure 5). Likewise, pine seedlings rapidly regenerated after the fire in low- and moderate-severity burns, attaining densities markedly higher than pre-fire levels by 2010. Thereafter, seedling densities remained high and relatively constant from year to year (Figure 5). In contrast, seedlings densities in high-severity burn plots were persistently low irrespective of elevation. Shrub taxa in the understorey survived the fire in higher numbers than the pine,



**FIGURE 5** Results of a post-hoc analysis of 20 years of change in overstorey and understorey structure in monodominant pine forests of the Cordillera Central, Dominican Republic. The fire severity classes used in the panels are the percentage of tree basal area killed by the fire: low-severity ( $\leq 25\%$ ), moderate-severity ( $25\%–67\%$ ) or high-severity ( $>67\%$ ). In all panels, points show average plot-level densities ( $\pm$ SEM) and different coloured points (black, grey and/or white) indicate significant differences between fire severity classes within a census interval; semi-circles indicate statistical similarity with other points that are significantly different from one another; lines indicate significant (solid) or non-significant (dashed) differences between census intervals for a given fire severity; transparent lines, used only in panel (b), indicate no statistical comparisons between censuses (due excessive zero counts). In panels (c) and (d),  $\geq 96\%$  of pine saplings and 100% of pine seedlings were killed in the 2005 fire across all severities; hence, nearly all understorey pine stems tallied in 2007 and later germinated post-fire. In all panels, the dashed red line shows the 2005 fire, and the shaded grey zones indicate periods of post-fire drought.

either with above-ground tissues surviving or by resprouting: 34.4% ( $\pm 4.5\%$  SEM) living shrub stems in 2007 were resprouts. In 2007, live shrub stem density was on average 45.1% of pre-fire densities in low severity, 101.7% in moderate severity and 7.2% in high-severity burns. By 2010, densities of shrub species recovered to pre-fire levels in high-severity burns (Figure 5).

### 3.2.4 | Stand structure

In 2018, pine seedling densities were positively correlated with live tree basal area ( $\beta = 0.90$ ,  $p < 0.001$ ) and elevation ( $\beta = 0.31$ ,  $p = 0.062$ ), and negatively correlated with live shrub density in 2007 ( $\beta = -0.52$ ,  $p = 0.023$ ; Table 2). Pine sapling densities were positively correlated with elevation ( $\beta = 0.43$ ,  $p = 0.012$ ). Shrub stem densities were higher on windward slopes ( $\beta = 0.23$ ,  $p = 0.023$ ) and positively correlated with live tree basal area ( $\beta = 0.33$ ,  $p = 0.001$ ), and negatively correlated with elevation ( $\beta = -0.64$ ,  $p < 0.001$ ). Cumulative

post-fire pine canopy recruitment (i.e. the density of new stems that reached  $\geq 10$  cm DBH by 2018) was highly localized and variable: by 2018, mean canopy recruitment in all burned plots was  $21.8 \pm 11.2$  stems  $\text{ha}^{-1}$ , but 27 of 42 burned plots still had zero pine canopy recruits. A single high-severity fire plot had the highest canopy recruitment ( $464$  new stems  $\text{ha}^{-1}$  by 2018). Cumulative post-fire pine canopy recruitment by 2018 was not significantly related to any predictor (Table 2). Over the study, understorey densities in unburned plots were stable and low, with pines slightly decreasing and shrubs slightly increasing, but tree basal area in unburned plots grew by 25% from  $19.9 (\pm 2.78)$   $\text{m}^2 \text{ha}^{-1}$  in 1999 to  $24.9 (\pm 4.25)$   $\text{m}^2 \text{ha}^{-1}$  in 2018 (Figure 5).

### 3.2.5 | Droughts

The post-fire droughts reduced pine growth rates in plots affected by low-severity fires by 162% compared with the period

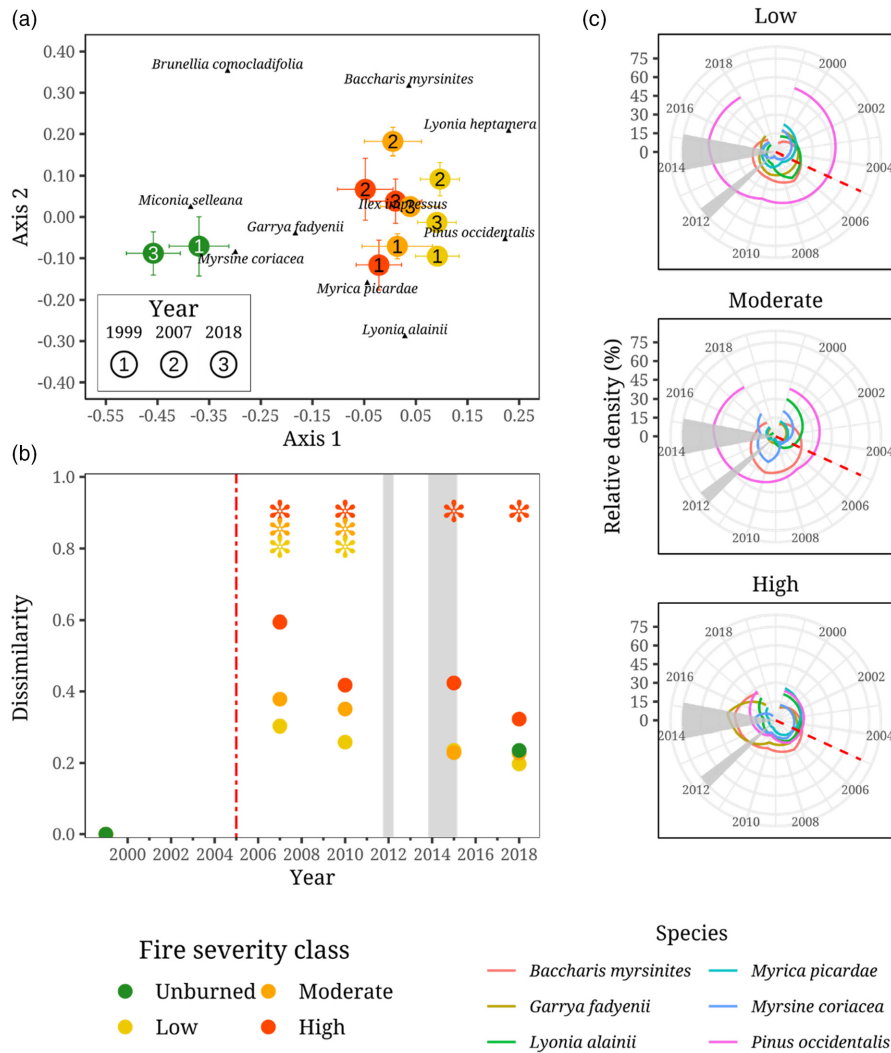
**TABLE 2** Predictors of post-fire regeneration patterns (stem densities,  $n = 40$  in all classes) in 2018 as a function of plot-scale environmental variables and stand structure. Orography refers to leeward (0) versus windward (1). Pine and shrub predictors are their respective plot-level density for the year used in the model (noted in parentheses). Live shrub taxa had resprouted by 2007, and hence, was used to model pine densities. Live tree basal area in 2018 combines both initial fire-caused and delayed tree mortality. Bolded values indicate significant predictors  $<0.05$

Response	Predictor	Standardized $\beta$	SE	Z-score	$p$
Pine canopy recruits	Intercept	-2.61	0.36	-7.20	<b>&lt;0.001</b>
	Shrubs (2007)	0.11	0.52	0.22	0.826
	Elevation	-0.58	0.44	-1.31	0.190
	Orography (1)	-0.45	0.48	-0.95	0.345
	Live tree basal area (2018)	-0.34	0.38	-0.88	0.380
Pine saplings	Intercept	-0.40	0.14	-2.81	<b>0.005</b>
	Shrubs (2007)	-0.19	0.21	-0.90	0.370
	Elevation	0.43	0.17	2.51	<b>0.012</b>
	Orography (1)	0.09	0.18	0.49	0.621
	Live tree basal area (2018)	0.09	0.15	0.60	0.549
Pine seedlings	Intercept	-1.56	0.14	-11.3	<b>&lt;0.001</b>
	Shrubs (2007)	-0.52	0.23	-2.27	<b>0.023</b>
	Elevation	0.31	0.17	1.86	0.062
	Orography (1)	0.09	0.16	0.60	0.551
	Live tree basal area (2018)	0.90	0.14	6.49	<b>&lt;0.001</b>
Shrub stems	Intercept	-0.02	0.10	-0.24	0.809
	Pine saplings (2018)	-0.01	0.11	-0.06	0.954
	Elevation	-0.64	0.12	-5.54	<b>&lt;0.001</b>
	Orography (1)	0.23	0.10	2.27	<b>0.023</b>
	Live tree basal area (2018)	0.33	0.10	3.19	<b>0.001</b>

beforehand ( $p < 0.001$ ) but there was no significant reduction in plots affected by moderate-severity fires (Figure 4a). The droughts had no significant effects on pine mortality rates (Figure 4b). Pine sapling densities continued to increase significantly across all fire severities during and after the droughts (Figure 5c). Pine seedling densities did not change significantly in plots affected by low- or moderate-severity fires during or after the post-fire droughts compared with the 2007–2010 census ( $p = 0.99$  and  $0.24$ , respectively), but decreased significantly (mean 862 seedlings  $\text{ha}^{-1}$  in 2010 vs. mean 118 seedlings  $\text{ha}^{-1}$  in 2015) during the post-fire droughts in plots affected by high-severity fires ( $p < 0.001$ ; Figure 5d). Overall, after the post-fire droughts, seedling densities remained greatest in plots affected by low-severity fires and lowest in those affected by high-severity fires ( $p < 0.001$ ; Figure 5d). Shrub densities declined significantly during the droughts (2010–2015,  $p < 0.001$ ) in plots affected by moderate-severity fires and increased significantly after the droughts in plots affected by low- and moderate-severity fires ( $p < 0.002$  and  $p < 0.007$ , respectively; Figure 5e). There were no significant changes in shrub densities in plots affected by high-severity fires during the post-fire droughts or the census afterwards, but by 2018 mean shrub densities in plots affected by high-severity fires were lower than those in moderate-severity fires ( $p < 0.039$ ).

### 3.3 | Resilience and alternate states

A total of 22 shrub species occurred in the plots (Table S6). Pre-fire understorey composition was similar between plots except at the highest elevations ( $>2900\text{m}$ ) and in lower elevation windward plots below the ecotone, which contained some taxa absent above the ecotone. Understorey composition in unburned plots had only modest variation across the site (Figure 6a). In the first 2 years after the fire, understorey community composition was altered across all fire severities (low-,  $p = 0.027$ ; moderate-,  $p = 0.007$ ; high-severity,  $p = 0.009$ ; Figure 6b). Ten years after the fire, dissimilarity in understorey composition in low- and moderate-severity fires was not significantly dissimilar from pre-fire composition ( $p = 0.079$  and  $0.124$ , respectively), indicating recovery to pre-fire composition. In high-severity fires, however, compositional dissimilarity to pre-fire levels remained significantly different 13 years after the fire ( $p = 0.037$ ; Figure 6b). Understorey composition in unburned plots showed no significant change over 19 years (1999 vs. 2018,  $p = 0.645$ ). Elevation was negatively correlated with compositional dissimilarity between 2018 and 1999 on leeward ( $p = 0.010$ ) and windward slopes ( $p < 0.001$ ); windward slopes were also more dissimilar on average to their pre-fire compositions than leeward slopes ( $p = 0.006$ ; Table S7).



**FIGURE 6** (a) Non-metric multidimensional scaling (NMDS) of understory woody species community composition by fire severity and time (model stress: 0.195). NMDS scores for each ordination axis and each fire severity class were averaged ( $\pm 1$  SEM) into centroids and plotted pre-fire (1999), immediately post-fire (2007) and 13 years post-fire (2018). Displayed species were the 10 most abundant; their distances indicate affinities with other species, and their relative direction with regards to the general upward shift after the fire indicates association with census year and fire severity class (e.g. *Pinus occidentalis* was more associated with pre-fire community compositions, *Baccharis myrsinites* was more associated with post-fire years). Fire severity classes were assigned per the percentage of tree basal killed by the fire: Low-severity ( $\leq 25\%$ ), moderate-severity (25%–67%) or high-severity ( $> 67\%$ ). (b) Change in time and fire severity in understory woody community composition compared with pre-fire composition. Compositional change (from 0 to 1; 0 = identical composition overlap, 1 = no composition overlap) was calculated for each fire severity class based on Euclidean distances between NMDS centroids using a Bray–Curtis dissimilarity matrix and principal coordinates analysis. Asterisks denote significant differences (<0.05) compared with pre-fire composition and are colour-coded according to fire severity class. (c) Rank clocks of change over time in relative stem density for the six most abundant understory woody species by fire severity class. The dashed red line demarks the 2005 fire, and the shaded grey zones indicate periods of post-fire drought.

## 4 | DISCUSSION

Recent fires in the tropics have raised concerns on the resilience and the formation of alternate stable states in the tropical forest biome in general (Hirota et al., 2011) and the tropical montane pine forest biome in particular (Sherman et al., 2008). The tropical montane pine forests of the Cordillera Central, Dominican Republic, were affected by the most extensive and severe fire in over 40 years coincident with unusually severe droughts and this biome has so far proven

resilient, with an ongoing recovery of *P. occidentalis* forest communities. Fire-maintained tropical ecosystems such as the pine forests in our study are well adapted to a fire regime spanning millennia (Crausbay et al., 2015; Horn et al., 2000; Kennedy & Horn, 2008); however, warming temperatures and altered moisture patterns may produce novel fire regimes with severities or frequencies outside the adaptations of *P. occidentalis* and associated flora (Martin et al., 2011). As precipitation patterns change across the tropics (e.g. Corlett, 2016), the same pressures of increasing droughts and fire

severity are likely to apply to fire-maintained forests across the montane tropics and subtropics, especially those dominated by *Pinus*; in particular, montane forests dominated by the closely related *Pinus cubensis* in south-eastern Cuba, which have a natural disturbance regime similar to *P. occidentalis* forests (Pérez-Pereda et al., 2012; Reyes & Acosta Cantillo, 2012), the monodominant montane *Pinus canariensis* forests of the Canary Islands (Fernández-Palacios & de Nicolás, 1995), the fire-maintained montane *Pinus kesiya* forests of the Philippines (Kowal, 1966) and the fire-maintained montane pine forests of Mexico and the Central American highlands (e.g. Rodríguez-Trejo et al., 2011).

#### 4.1 | Shifting fire regimes

In many tropical forests, droughts and large fires are closely linked to ENSO events (e.g. Cerano-Paredes et al., 2021; Crausbay & Martin, 2016). Despite the weak and short-lived ENSO anomaly of 2004–2005 (Null, 2020), the study site's drought index (PDSI) was its lowest in 60 years (Abatzoglou et al., 2018). Since severe droughts diminish the influence of local vegetation structure and terrain on fire patterns (i.e. biophysical factors; Collins et al., 2019), we expected fire severity patterns would be shaped primarily by stochastic factors, which should increase spatial autocorrelation among plots (Bessie & Johnson, 1995). Instead, we found fire patterns were primarily associated with biophysical factors, including a strong signal of higher-severity burns at lower elevations. The combination of high-density stands in the hotter, drier conditions on lower elevation, leeward slopes of the Cordillera Central made *P. occidentalis* forests in this setting prone to high-severity fires, especially after the long, mostly fire-free interval from 1965 to 2005. The large patch of high-severity fire on low-elevation, leeward slopes (c. 525 ha; Figure 2), however, could have been created in part by stochastic influences (such as wind direction and speed; Sullivan, 2009) which reinforced the biophysical patterns in our model, as this area is reported to have burned rapidly while fanned by a strong south-easterly wind (F. Peralta, Dominican Park Service, pers. comm.).

We cannot compare spatial variation in fire severity with other tropical montane forests, as this is the first analysis in such systems, but studies in temperate coniferous forests with steep climate gradients (e.g. montane ecosystems) report a similar range of stochastic and biophysical influences on fire patterns (Harvey et al., 2016b; Perry et al., 2011). Many montane coniferous forests in western North America typically display a positive relationship between fire severity and elevation, with frequent, low-severity fires in drier, low elevations and infrequent, high-severity, stand-replacing fires in wetter, high elevations (e.g. Schoennagel et al., 2004; Veblen, 2000); in our study, these patterns were inverted, with fire severity negatively correlated with elevation. In recent years, a series of high-severity fires have occurred in North American forests that typically experience low-severity fires (e.g. *Pinus ponderosa* forests), sparking a debate whether such fires are novel (e.g. Fulé et al., 2014) and

suggesting the 'inverted' severity patterns in our study may become more widespread across systems with ongoing climate change.

Tropical cyclones also influence forest dynamics in our study system (Crausbay & Martin, 2016; Sherman et al., 2012), differentiating them from many temperate forests affected by fire (e.g. Rocky Mountains). The most recent cyclone to hit the study site was Hurricane Georges in 1998 and pre-fire storm damage likely contributed to the patterns of fire severity in 2005 (Sherman et al., 2008). However, Georges damaged trees at detectable levels in only 10 of the 49 burned plots in this study (Gannon & Martin, 2014), so we did not include plot-level cyclone damage as a covariate. The small influence of cyclone damage in the data also likely contributed to the low variation in standing dead, snapped, or tipped trees (necromass) among plots (Table S4), leaving no detectable effect of necromass on the patterns of fire severity. Instead, the ~40-year interval with few and small fires (Martin & Fahey, 2006) likely contributed far more to the severity of the 2005 fires than cyclones. Prior cyclone damage can even increase forest resilience to severe fire by creating discontinuity in fuel loads (Cannon et al., 2019) and promoting landscape heterogeneity (Schoennagel et al., 2008). Nevertheless, quantifying cyclone effects on fuel loads and addressing cyclone–fire interactions should be a priority for future research in our study site as well across tropical montane pine forests – including those in Cuba (Reyes & Acosta Cantillo, 2012) where cyclone frequency is similar to the Dominican Republic, and the Philippines (Doyog et al., 2021) where cyclones are very frequent—since their interactions can be complex and nonlinear (Ibanez et al., 2022).

#### 4.2 | Tropical montane pine forest resilience to fire and drought disturbance

Our 19-year study has found the *P. occidentalis* forests of the Cordillera Central were resilient (sensu Pimm, 1984) to an unusually large and severe fire, despite a severe multi-year drought after the fire and ongoing climate change. Trees that initially survived the fire had a large pulse of delayed mortality in both low- and moderate-severity burns, a common pattern caused by severe stem char, crown scorch and fine root damage that weaken the tree and increase pathogen susceptibility (Busse et al., 2000; Fajardo et al., 2007; Hood et al., 2018; Slack et al., 2016; Varner et al., 2009, 2021; Woolley et al., 2012). Yet, 13 years post fire, pine regeneration was evident across all fire severities, and recruitment of new pine trees (i.e.  $\geq 10$  cm DBH) had occurred even in areas with high-severity burns. By 2018, 98% of plots had at least one pine sapling, despite the wide range in conditions (fire severity, tree stand structure and shrub density) and landscape context (patch size, environment) across the study. A wet period immediately after the fire (Figure 3)—when new regeneration from the *Pinaceae* is generally most sensitive to climate conditions (Andrus et al., 2018; Carroll et al., 2017, 2021; Copenhagen-Parry et al., 2020; Foster et al., 2020; Goke & Martin, 2022; Harvey et al., 2016a; Kemp et al., 2019; Urza & Sibold, 2017)—may have enhanced pine regeneration across

the study and contributed to the ecosystem's ensuing resilience. Increasing temperatures, however, may reduce soil moisture and thus limit pine regeneration (e.g., of *Pinus hartwegii* on sites exposed to high solar radiation near treelines in tropical Mexico; Astudillo-Sánchez et al., 2019), potentially reducing the resilience of these ecosystems across much of the tropics.

Robust resilience in these forests (sensu Pimm, 1984) was most evident in the post-fire recovery of surviving trees in low-severity burns, which were on track to return to pre-fire mortality and growth rates approximately a decade after the fire. The two periods of intense post-fire drought, however, slowed this rapid recovery of pines in low-severity patches through reduced growth rates, as in found other ecosystems (Allen et al., 2010; Anderson-Teixeira et al., 2013) and demonstrate why multiple disturbance interactions need to be considered in evaluations of ecosystem resilience (Buma & Wessman, 2011). In stands affected by low-severity fires, it is likely that the rapid return to pre-fire growth rates in the census before effects of the post-fire droughts were manifest (Figure 4) was caused in part by reduced interspecific competition for resources above- and below-ground as a result of direct and delayed mortality caused by the fire, as shown in other studies of tree growth responses in monodominant stands affected by disturbance (Coomes & Allen, 2007). In contrast, the droughts had no significant effect on pine demography in stands affected by moderate-severity fires: a decade later the severity of the fire remained the predominant influence on recovery in these patches, slowing their recovery such that any additional impacts of drought therein were below detection. By 2018, the combined effects of fire and drought left growth and mortality rates on average across fire severities c. 50% lower and c. 230% higher, respectively, than before the 2005 fire (Figure 4). Future measurements will reveal whether demography in these forests remain altered; if so, a reappraisal of their resilience may be necessary. Overall, saplings were the life-history stage of *P. occidentalis* most resilient to drought, with more or less linear increases in recruitment across all fire-severities during and after the post-fire droughts (Figure 5c), a pattern consistent with effects of drought on some pine species (Madrigal-González et al., 2017), but not others (Herrero & Zamora, 2014).

A study shorter than ours may have reached a different conclusion about the resilience of these forests. Consistent with a 2-year post-fire study in the eastern Cordillera Central (Horn et al., 2001), there was little indication that the pine populations across our study were resilient in the first 5 years after the fire: 14.3% of large (DBH  $\geq 25.0$  cm) pine trees that survived the fire died over the 2–5 years after the fire, recruitment of pine seedlings was low, especially in high-severity burns due to the loss of nearly all seed trees, and the post-fire recovery of shrubs (across elevations) and the native bunchgrass *Danthonia domingensis* (at high elevations) was vigorous. As in subtropical pine forests (Barton & Poulos, 2018; Fulé et al., 2000), this initially suggested an alternate stable state dominated by shrubs might develop, but 13 years later it is evident the shrub community formed an alternative transient state (Falk et al., 2022; Fukami & Nakajima, 2011), despite high shrub abundance initially inhibiting

pine regeneration and the impact of the droughts on the demography of the pine.

The rapid recovery of the shrub community across all fire severities is consistent with a view of the Hispaniolan montane ecosystems as resilient sensu Holling, that is, that they may alternate between pine forests and shrublands, with the latter a probable alternate stable state (Kennedy & Horn, 2008). Pine forests affected by high-severity fires on leeward slopes at low elevations, which are hotter and drier, showed significantly slower compositional and structural recovery to their pre-fire state and a longer period of shrubland species dominance than those at other sites. Low-elevation sites on windward slopes were also slow to recover community composition to their pre-fire states. These results are consistent with an emerging view that forests at lower elevations are especially vulnerable to state shifts (Davis et al., 2019). Further enhancement of a state shift on leeward slopes could result from increased frequency of ignition caused by agricultural activities on adjacent land, as might invasions by flammable non-native plant species. For example, in 2018, we noted for the first time low levels of invasion of low-elevation leeward slopes by a non-native C4 grass (*Melinis minutiflora*) that is spread by livestock and is known to increase fire frequency and spread in other tropical montane ecosystems (D'Antonio et al., 2001); its role in the 2005 fire is unknown. Future measurements will determine whether the shrubs that currently dominate the sites where pine regeneration is sparse represent a new equilibrium state (Falk et al., 2022; Paniw et al., 2021).

### 4.3 | Future directions

As temperatures rise and droughts increase across large regions (e.g. Salley et al., 2016), fire regimes are changing in both fire-maintained and fire-sensitive biomes. Tropical montane forests are no exception, raising questions about their long-term resilience that a large fire in the montane pine forests of the Cordillera Central put to the test. The fire initiated widespread loss of canopy and understory pines, but under the current conditions, the pine forest is resilient. Based on the low rates of canopy recruitment 13 years after the fire, the return to pre-fire pine forest structure across the Cordillera Central will take at least two more decades, probably longer in sites affected by high-severity fires, and resilience of the ecosystems thus affected involve transient state shifts from forest to shrubland. Shrubland states may be more persistent in future if additional perturbations occur, especially short-cycle perturbations frequent enough to impede recovery processes (Coop et al., 2020; Falk et al., 2022).

Under current conditions, *P. occidentalis* is likely to remain the dominant species even in the hottest and driest areas of the Cordillera Central. To allow an equilibrium to develop in future climate-necromass cycles (i.e. preventing a large accumulation of fuels under fire suppression policies), forest management could consider a 'let burn' or a prescribed burn policy for fires in the monodominant pine forest, as suggested for tropical montane pine forests in Mexico (Rodríguez Trejo, 2008). However, as climate

change continues to affect tropical montane forests, portions of this landscape may eventually tip into an alternate stable shrubland or grassland state if subjected to repeated fires, droughts and higher temperatures, all of which are predicted to increase in tropical mountains (Martin & Bellingham, 2016), and management will have to balance these potentially conflicting dynamics. Furthermore, canonically weak ENSOs, like the one in 2004–2005, are increasingly generating strong teleconnections (Ashok et al., 2007; Capotondi et al., 2015), with potentially profound consequences for fire susceptibility across the globe (Schoennagel et al., 2007). More climate monitoring is needed, as little long-term, high-resolution climate data exist in tropical montane forests (Martin & Bellingham, 2016), so it is unknown how climate change affects these ecosystems, and most warming and drying anticipated in these systems has yet to occur.

#### AUTHOR CONTRIBUTIONS

Patrick Martin conceived the overall research idea and all authors designed the study and methodology; Daniel Swann, Peter Bellingham and Patrick Martin collected the data; Daniel Swann analysed the data; all authors led the writing of the manuscript, contributed critically to the drafts and gave final approval for publication.

#### ACKNOWLEDGEMENTS

We are grateful for all those who participated in the establishment and remeasurement of the permanent vegetation plots over the past 20 years, including Tim Fahey, Ruth Sherman, Francisco Peralta and teams Cuava, Guapo, Carbón, Cyclone, Ratón and Muñequito. We thank the Dominican Park Service for their support and the people of La Ciénaga de Manabao for their warm hospitality, Dr. Julissa Rojas-Sandoval for help translating the abstract into Spanish, and Dr. Catherine Durso (University of Denver) for assistance with the statistical analyses. We also thank the editors and four anonymous reviewers for their helpful input and guidance in improving this manuscript. This research was supported by a National Science Foundation grant from the Division of Environmental Biology (DEB)-1803192 and the NSF-sponsored research coordination network *CloudNet* (<http://ducloudnet.wpengine.com>).

#### CONFLICT OF INTEREST

None of the authors have any conflict of interest in this study nor its publication. Peter Bellingham is an Associate Editor for *Journal of Ecology* but took no part in the peer review or decision-making process for this paper.

#### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.14017>.

#### DATA AVAILABILITY STATEMENT

All data used in this study are available online in the Dryad Digital Repository <https://doi.org/10.5061/dryad.qnk98fm3> (Swann et al., 2022).

#### ORCID

Daniel E. B. Swann  <https://orcid.org/0000-0001-6566-0710>

Peter J. Bellingham  <https://orcid.org/0000-0001-9646-4819>

Patrick H. Martin  <https://orcid.org/0000-0003-2025-4289>

#### REFERENCES

- Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific Data*, 5, 170191. <https://doi.org/10.1038/sdata.2017.191>
- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8), 1–55. <https://doi.org/10.1890/ES15-00203.1>
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. T., & Gonzalez, P. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4), 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Anderson-Teixeira, K. J., Miller, A. D., Mohan, J. E., Hudiburg, T. W., Duval, B. D., & DeLucia, E. H. (2013). Altered dynamics of forest recovery under a changing climate. *Global Change Biology*, 19(7), 2001–2021. <https://doi.org/10.1111/gcb.12194>
- Andrus, R. A., Harvey, B. J., Rodman, K. C., Hart, S. J., & Veblen, T. T. (2018). Moisture availability limits subalpine tree establishment. *Ecology*, 99(3), 567–575. <https://doi.org/10.1002/ecy.2134>
- Archibald, S., Roy, D. P., van Wilgen, B. W., & Scholes, R. J. (2009). What limits fire? An examination of drivers of burnt area in southern Africa. *Global Change Biology*, 15(3), 613–630. <https://doi.org/10.1111/j.1365-2486.2008.01754.x>
- Ashok, K., Behera, S. K., Rao, S. A., Weng, H., & Yamagata, T. (2007). El Niño Modoki and its possible teleconnection. *Journal of Geophysical Research: Oceans*, 112, C11007. <https://doi.org/10.1029/2006JC003798>
- Astudillo-Sánchez, C. C., Fowler, M. S., Villanueva-Díaz, J., Endara-Agramont, A. R., & Soria-Díaz, L. (2019). Recruitment and facilitation in *Pinus hartwegii*, a Mexican alpine treeline ecotone, with potential responses to climate warming. *Trees*, 33(4), 1087–1100. <https://doi.org/10.1007/s00468-019-01844-3>
- Avolio, M. L., Carroll, I. T., Collins, S. L., Houseman, G. R., Hallett, L. M., Isbell, F., Koerner, S. E., Komatsu, K. J., Smith, M. D., & Wilcox, K. R. (2019). A comprehensive approach to analyzing community dynamics using rank abundance curves. *Ecosphere*, 10(10), e02881. <https://doi.org/10.1002/ecs2.2881>
- Baker, W. L., & Ehle, D. (2001). Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. *Canadian Journal of Forest Research*, 31(7), 1205–1226. <https://doi.org/10.1139/x01046>
- Ballinger, G. A. (2004). Using generalized estimating equations for longitudinal data analysis. *Organizational Research Methods*, 7(2), 127–150. <https://doi.org/10.1177/1094428104263672>
- Barton, A. M., & Poulos, H. M. (2018). Pine vs. oaks revisited: Conversion of Madrean pine-oak forest to oak shrubland after high-severity wildfire in the Sky Islands of Arizona. *Forest Ecology and Management*, 414, 28–40. <https://doi.org/10.1016/j.foreco.2018.02.011>
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://arxiv.org/abs/1406.5823>
- Bauman, D., Drouet, T., Dray, S., & Vleminckx, J. (2018). Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography*, 41(10), 1638–1649. <https://doi.org/10.1111/ecog.03380>

- Bellingham, P. J., Tanner, E. V., Martin, P. H., Healey, J. R., & Burge, O. R. (2018). Endemic trees in a tropical biodiversity hotspot imperilled by an invasive tree. *Biological Conservation*, 217, 47–53. <https://doi.org/10.1016/j.biocon.2017.10.028>
- Bessie, W. C., & Johnson, E. A. (1995). The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology*, 76(3), 747–762. <https://doi.org/10.2307/1939341>
- Blanchet, F. G., Legendre, P., & Borcard, D. (2008). Forward selection of explanatory variables. *Ecology*, 89(9), 2623–2632. <https://doi.org/10.1890/07-0986.1>
- Borcard, D., Gillet, F., & Legendre, P. (2018). Spatial analysis of ecological data. In D. Borcard, F. Gillet, & P. Legendre (Eds.), *Numerical ecology with R* (2nd ed., pp. 299–367). Springer.
- Bowman, D. M. J. S., Balch, J., Artaxo, P., Bond, W. J., Cochrane, M. A., D'Antonio, C. M., Defries, R., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Mack, M., Moritz, M. A., Pyne, S., Roos, C. I., Scott, A. C., Sodhi, N. S., & Swetnam, T. W. (2011). The human dimension of fire regimes on earth. *Journal of Biogeography*, 38(12), 2223–2236. <https://doi.org/10.1111/j.1365-2699.2011.02595.x>
- Bradley, R. S., Vuille, M., Diaz, H. F., & Vergara, W. (2006). Threats to water supplies in the tropical Andes. *Science*, 312(5781), 1755–1756. <https://doi.org/10.1126/science.1128087>
- Buma, B., & Wessman, C. A. (2011). Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere*, 2, art64. <https://doi.org/10.1890/ES11-00038.1>
- Busse, M. D., Simon, S. A., & Riegel, G. M. (2000). Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of Central Oregon. *Forest Science*, 46(2), 11–22. <https://doi.org/10.1093/forests/46.2.258>
- Cannon, J. B., Henderson, S. K., Bailey, M. H., & Peterson, C. J. (2019). Interactions between wind and fire disturbance in forests: Competing amplifying and buffering effects. *Forest Ecology and Management*, 436, 117–128. <https://doi.org/10.1016/j.foreco.2019.01.015>
- Cano, E., Velóz Ramírez, E., & Cano Ortiz, A. (2011). Phytosociological study of the *Pinus occidentalis* forests in The Dominican Republic. *Plant Biosystems*, 145, 286–297. <https://doi.org/10.1080/11263504.2010.547685>
- Cao, G., Giambelluca, T. W., Stevens, D. E., & Schroeder, T. A. (2007). Inversion variability in the Hawaiian trade wind regime. *Journal of Climate*, 20(7), 1145–1160. <https://doi.org/10.1175/JCLI4033.1>
- Capdevila, P., Stott, I., Beger, M., & Salguero-Gómez, R. (2020). Towards a comparative framework of demographic resilience. *Trends in Ecology & Evolution*, 35, 776–786. <https://doi.org/10.1016/j.tree.2020.05.001>
- Capotondi, A., Wittenberg, A. T., Newman, M., Di Lorenzo, E., Yu, J. Y., Braconnot, P., Cole, J., Dewitte, B., Giese, B., Guilyardi, E., Jin, F. F., Karnauskas, K., Kirtman, B., Lee, T., Schneider, N., Xue, Y., & Yeh, S. W. (2015). Understanding ENSO diversity. *Bulletin of the American Meteorological Society*, 96(6), 921–938. <https://doi.org/10.1175/BAMS-D-13-00117.1>
- Carroll, C. J. W., Knapp, A. K., & Martin, P. H. (2017). Dominant tree species of the Colorado Rockies have divergent physiological and morphological responses to warming. *Forest Ecology and Management*, 402, 234–240. <https://doi.org/10.1016/j.foreco.2017.07.048>
- Carroll, C. J. W., Knapp, A. K., & Martin, P. H. (2021). Higher temperatures increase growth rates of Rocky Mountain montane tree seedlings. *Ecosphere*, 12, e03414. <https://doi.org/10.1002/ecs2.3414>
- Cerano-Paredes, J., Iniguez, J. M., Villanueva-Díaz, J., Vázquez-Selem, L., Cervantes-Martínez, R., Esquivel-Arriaga, G., Franco-Ramos, O., & Rodríguez-Trejo, D. A. (2021). Effects of climate on historical fire regimes (1451–2013) in *Pinus hartwegii* forests of Cofre de Perote National Park, Veracruz, Mexico. *Dendrochronologia*, 65, 125784. <https://doi.org/10.1016/j.dendro.2020.125784>
- Cochrane, M. A., & Schulze, M. D. (1999). Fire as a recurrent event in tropical forests of the eastern Amazon: Effects on forest structure, biomass, and species composition. *Biotropica*, 31(1), 2–16. <https://doi.org/10.1111/j.1744-7429.1999.tb00112.x>
- Cocke, A. E., Fulé, P. Z., & Crouse, J. E. (2005). Comparison of burn severity assessments using differenced normalized burn ratio and ground data. *International Journal of Wildland Fire*, 14(2), 189–198. <https://doi.org/10.1071/WF04010>
- Collins, L., Bennett, A. F., Leonard, S. W. J., & Penman, T. D. (2019). Wildfire refugia in forests: Severe fire weather and drought mute the influence of topography and fuel age. *Global Change Biology*, 25(11), 3829–3843. <https://doi.org/10.1111/gcb.14735>
- Coomes, D. A., & Allen, R. B. (2007). Effects of size, competition and altitude on tree growth. *Journal of Ecology*, 95(5), 1084–1097. <https://doi.org/10.1111/j.1365-2745.2007.01280.x>
- Coop, J. D., Parks, S. A., Stevens-Rumann, C. S., Crausbay, S. D., Higuera, P. E., Hurteau, M. D., Tepley, A., Whitman, E., Assal, T., Collins, B. M., Davis, K. T., Dobrowski, S., Falk, D. A., Fornwalt, P. J., Fulé, P. Z., Harvey, B. J., Kane, V. R., Littlefield, C. E., Margolis, E. Q., ... Rodman, K. C. (2020). Wildfire-driven forest conversion in western north American landscapes. *Bioscience*, 70(8), 659–673. <https://doi.org/10.1093/biosci/biaa061>
- Copenhaver-Parry, P. E., Carroll, C. J. W., Martin, P. H., & Talluto, M. V. (2020). Multi-scale integration of tree recruitment and range dynamics in a changing climate. *Global Ecology and Biogeography*, 29, 102–116. <https://doi.org/10.1111/geb.13012>
- Corlett, R. T. (2016). The impacts of droughts in tropical forests. *Trends in Plant Science*, 21(7), 584–593. <https://doi.org/10.1016/j.tplants.2016.02.003>
- Crausbay, S. D., & Martin, P. H. (2016). Natural disturbance, vegetation patterns and ecological dynamics in tropical montane forests. *Journal of Tropical Ecology*, 32(5), 384–403. <https://doi.org/10.1017/S0266467416000328>
- Crausbay, S. D., Martin, P. H., & Kelly, E. F. (2015). Tropical montane vegetation dynamics near the upper cloud belt strongly associated with a shifting ITCZ and fire. *Journal of Ecology*, 103(4), 891–903. <https://doi.org/10.1111/1365-2745.12423>
- D'Antonio, C. M., Hughes, R. F., & Vitousek, P. M. (2001). Factors influencing dynamics of two invasive C4 grasses in seasonally dry Hawaiian woodlands. *Ecology*, 82(1), 89–104. [https://doi.org/10.1890/0012-9658\(2001\)082\[0089:FIDOTI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0089:FIDOTI]2.0.CO;2)
- Darrow, W. K., & Zandoni, T. (1990). Hispaniolan pine (*Pinus occidentalis* Swartz) a little known sub-tropical pine of economic potential. *Commonwealth Forestry Review*, 69(2), 133–146. <https://www.jstor.org/stable/43737717>
- Davis, K. T., Dobrowski, S. Z., Higuera, P. E., Holden, Z. A., Veblen, T. T., Rother, M. T., Parks, S. A., Sala, A., & Maneta, M. P. (2019). Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences of the United States of America*, 116(13), 6193–6198. <https://doi.org/10.1073/pnas.1815107116>
- Delettre, O. (2021). Identity of ecological systems and the meaning of resilience. *Journal of Ecology*, 109, 3147–3156. <https://doi.org/10.1111/1365-2745.13655>
- Dirección Nacional De Parques. (1997). *Plan de manejo y conservación del parque nacional Armando Bermúdez*. Estudios y Diseños en Ingeniería Hiraualica, S.A.
- Doyog, N. D., Lin, C., Lee, Y. J., Lumbres, R. I. C., Daipan, B. P. O., Bayer, D. C., & Parian, C. P. (2021). Diagnosing pristine pine forest development through pansharpened-surface-reflectance Landsat image derived aboveground biomass productivity. *Forest Ecology and Management*, 487, 119011. <https://doi.org/10.1016/j.foreco.2021.119011>
- Dray, S., Legendre, P., & Peres-Neto, P. R. (2006). Spatial modelling: A comprehensive framework for principal coordinate analysis of



- neighbour matrices (PCNM). *Ecological Modelling*, 196(3–4), 483–493. <https://doi.org/10.1016/j.ecolmodel.2006.02.015>
- Fajardo, A., Graham, J. M., Goodburn, J. M., & Fiedler, C. E. (2007). Ten-year responses of ponderosa pine growth, vigor, and recruitment to restoration treatments in the Bitterroot Mountains, Montana, USA. *Forest Ecology and Management*, 243(1), 50–60. <https://doi.org/10.1016/j.foreco.2007.02.006>
- Falk, D. A., van Mantgem, P. J., Keeley, J. E., Gregg, R. M., Guiterman, C. H., Tepley, A. J., Young, D. J. N., & Marshall, L. A. (2022). Mechanisms of forest resilience. *Forest Ecology and Management*, 512, 120129. <https://doi.org/10.1016/j.foreco.2022.120129>
- Fernández-Palacios, J. M., & de Nicolás, J. P. (1995). Altitudinal pattern of vegetation variation on Tenerife. *Journal of Vegetation Science*, 6(2), 183–190. <https://doi.org/10.2307/3236213>
- Foster, A. C., Martin, P. H., & Redmond, M. D. (2020). Soil moisture strongly limits Douglas-fir seedling establishment near its upper elevational limit in the southern Rocky Mountains. *Canadian Journal of Forest Research*, 50, 837–842. <https://doi.org/10.1139/cjfr-2019-0296>
- Foster, P. (2001). The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews*, 55, 73–106. [https://doi.org/10.1016/S0012-8252\(01\)00056-3](https://doi.org/10.1016/S0012-8252(01)00056-3)
- Franklin, J. F., Mitchell, R. J., & Palik, B. J. (2007). Natural disturbance and stand development principles for ecological forestry. In *General Technical Report NRS-19*. (p. 44). U.S. Department of Agriculture, Forest Service, Northern Research Station.
- Fukami, T., & Nakajima, M. (2011). Community assembly: Alternative stable states or alternative transient states? *Ecology Letters*, 14(10), 973–984. <https://doi.org/10.1111/j.1461-0248.2011.01663.x>
- Fulé, P. Z., García-Arévalo, A., & Covington, W. W. (2000). Effects of an intense wildfire in a Mexican oak-pine forest. *Forest Science*, 46(1), 52–61. <https://doi.org/10.1093/forestscience/46.1.52>
- Fulé, P. Z., Swetnam, T. W., Brown, P. M., Falk, D. A., Peterson, D. L., Allen, C. D., Aplet, G. H., Battaglia, M. A., Binkley, D., Farris, C., Keane, R. E., Margolis, E. Q., Grissino-Mayer, H., Miller, C., Sieg, C. H., Skinner, C., Stephens, S. L., & Taylor, A. (2014). Unsupported inferences of high-severity fire in historical dry forests of the western United States: Response to Williams and Baker. *Global Ecology and Biogeography*, 23(7), 825–830. <https://doi.org/10.1111/geb.12136>
- Gannon, B. M., & Martin, P. H. (2014). Reconstructing hurricane disturbance in a tropical montane forest landscape in the cordillera central, Dominican Republic: Implications for vegetation patterns and dynamics. *Arctic, Antarctic, and Alpine Research*, 46(4), 767–776. <https://doi.org/10.1657/1938-4246-46.4.767>
- Ganteaume, A., Camia, A., Jappiot, M., San-Miguel-Ayanz, J., Long-Fournel, M., & Lampin, C. (2013). A review of the main driving factors of forest fire ignition over Europe. *Environmental Management*, 51(3), 651–662. <https://doi.org/10.1007/s00267-012-9961-z>
- Giambelluca, T. W., & Nullet, D. (1991). Influence of the trade-wind inversion on the climate of a leeward mountain slope in Hawaii. *Climate Research*, 1(3), 207–216. <https://www.jstor.org/stable/24863349>
- Goke, A., & Martin, P. H. (2022). Poor acclimation to experimental field drought in subalpine forest tree seedlings. *AoB Plants*, 14, plab077. <https://doi.org/10.1093/aobpla/plab077>
- Goldammer, J. G., & Peñafiel, S. R. (1990). Fire in the pine-grassland biomes of tropical and subtropical Asia. In J. G. Goldammer (Ed.), *Fire in the tropical biota* (pp. 45–62). Springer.
- Halekoh, U., Højsgaard, S., & Yan, J. (2006). The R package geepack for generalized estimating equations. *Journal of Statistical Software*, 15(2), 1–11. <https://doi.org/10.18637/jss.v015.i02>
- Hallett, L. M., Jones, S. K., MacDonald, A. A. M., Jones, M. B., Flynn, D. F., Ripplinger, J., Slaughter, P., Gries, C., & Collins, S. L. (2016). Codyn: An R package of community dynamics metrics. *Methods in Ecology and Evolution*, 7(10), 1146–1151. <https://doi.org/10.1111/2041-210X.12569>
- Hannah, L. (2021). *Climate change biology* (3rd ed.). Academic Press.
- Hartig, F. (2020). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.2.0. <https://CRAN.R-project.org/package=DHARMA>
- Harvey, B. J., Donato, D. C., & Turner, M. G. (2016a). High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Global Ecology and Biogeography*, 25(6), 655–669. <https://doi.org/10.1111/geb.12443>
- Harvey, B. J., Donato, D. C., & Turner, M. G. (2016b). Drivers and trends in landscape patterns of stand-replacing fire in forests of the US northern Rocky Mountains (1984–2010). *Landscape Ecology*, 31(10), 2367–2383. <https://doi.org/10.1007/s10980-016-0408-4>
- He, T., Pausas, J. G., Belcher, C. M., Schwilk, D. W., & Lamont, B. B. (2012). Fire-adapted traits of *Pinus* arose in the fiery cretaceous. *New Phytologist*, 194, 751–759. <https://doi.org/10.1111/j.1469-8137.2012.04079.x>
- Hemp, A. (2009). Climate change and its impact on the forests of Kilimanjaro. *African Journal of Ecology*, 47, 3–10. <https://doi.org/10.1111/j.1365-2028.2008.01043.x>
- Herrero, A., & Zamora, R. (2014). Plant responses to extreme climatic events: A field test of resilience capacity at the southern range edge. *PLoS ONE*, 9, e87842. <https://doi.org/10.1371/journal.pone.0087842>
- Hirota, M., Holmgren, M., Van Nes, E. H., & Scheffer, M. (2011). Global resilience of tropical forest and savanna to critical transitions. *Science*, 334(6053), 232–235. <https://doi.org/10.1126/science.1210657>
- Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4, 1–23. <https://doi.org/10.1146/annurev.ecolsys.04.110173.000245>
- Holling, C. S. (1981). Forest insects, forest fires, and resilience. In H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, & W. A. Reiners (Eds.), *Proceedings of the conference fire regimes and ecosystem properties*, 11–15 December, 1978 (pp. 445–464). USDA Forest Service General Technical Report WO-26.
- Holling, C. S. (1986). The resilience of terrestrial ecosystems: Local surprise and global change. In W. C. Clark & R. E. Munn (Eds.), *Sustainable development of the biosphere* (pp. 292–320). Cambridge University Press.
- Hood, S. M., Varner, J. M., Van Mantgem, P., & Cansler, C. A. (2018). Fire and tree death: Understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters*, 13(11), 113004. <https://doi.org/10.1088/1748-9326/aae934>
- Hoppe, J. (1989). *Los Parques Nacionales de la Republica Dominicana*. Editora Corripio.
- Horn, S. P., Kennedy, L. M., & Orvis, K. H. (2001). Vegetation recovery following a high elevation fire in The Dominican Republic. *Biotropica*, 33(4), 701–708. <https://www.jstor.org/stable/3593173>
- Horn, S. P., Orvis, K. H., Kennedy, L. M., & Clark, G. M. (2000). Prehistoric fires in the highlands of The Dominican Republic: Evidence from charcoal in soils and sediments. *Caribbean Journal of Science*, 36(1–2), 10–18.
- Ibanez, T., Platt, W. J., Bellingham, P. J., Vieilledent, G., Franklin, J., Martin, P. H., Menkes, C., Pérez Salicrup, D. R., Russell-Smith, J., & Keppel, G. (2022). Altered cyclone–fire interactions are changing ecosystems. *Trends in Plant Science* in press. <https://doi.org/10.1016/j.tplants.2022.08.005>
- Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16(8), 406–411. <https://doi.org/10.1016/j.tplants.2011.04.002>
- Kemp, K. B., Higuera, P. E., Morgan, P., & Abatzoglou, J. T. (2019). Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, northern Rockies, USA. *Ecosphere*, 10(1), e02568. <https://doi.org/10.1002/ecs2.2568>

- Kennedy, L. M., & Horn, S. P. (2008). Postfire vegetation recovery in highland pine forests of The Dominican Republic. *Biotropica*, 40(4), 412–421. <https://doi.org/10.1111/j.1744-7429.2007.00394.x>
- Kennedy, L. M., Horn, S. P., & Orvis, K. H. (2006). A 4000-year record of fire and forest history from Valle de bao, cordillera central, Dominican Republic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 231(3–4), 279–290. <https://doi.org/10.1016/j.palaeo.2005.08.002>
- Kolb, T., Keefover-Ring, K., Burr, S. J., Hofstetter, R., Gaylord, M., & Raffa, K. F. (2019). Drought-mediated changes in tree physiological processes weaken tree defenses to bark beetle attack. *Journal of Chemical Ecology*, 45(10), 888–900. <https://doi.org/10.1007/s10886-019-01105-0>
- Kowal, E. K. (1966). Shifting cultivation, fire, and pine forest in the cordillera central, Luzon, Philippines. *Ecological Monographs*, 36, 389–419. <https://doi.org/10.2307/1942374>
- Krishnaswamy, J., John, R., & Joseph, S. (2014). Consistent response of vegetation dynamics to recent climate change in tropical mountain regions. *Global Change Biology*, 20, 203–215. <https://doi.org/10.1111/gcb.12362>
- Kustudia, M. (1998). Conucos, campesinos and the contested cordillera: Grassroots perspectives in a Dominican watershed. *Forests, Trees and People Newsletter*, 36/37, 26–32.
- Laurance, W. F. (2003). Slow burn: The insidious effects of surface fires on tropical forests. *Trends in Ecology & Evolution*, 18(5), 209–212. [https://doi.org/10.1016/S0169-5347\(03\)00064-8](https://doi.org/10.1016/S0169-5347(03)00064-8)
- Lenth, R. (2020). Emmeans: Estimated marginal means, aka least-squares means. R package version 1.4.8. <https://cran.r-project.org/package=emmeans>
- Littlefield, C. E. (2019). Topography and post-fire climatic conditions shape spatio-temporal patterns of conifer establishment and growth. *Fire Ecology*, 15(1), 34. <https://doi.org/10.1186/s42408-019-0047-7>
- Longman, R. J., Diaz, H. F., & Giambelluca, T. W. (2015). Sustained increases in lower-tropospheric subsidence over the central tropical North Pacific drive a decline in high-elevation rainfall in Hawaii. *Journal of Climate*, 28(22), 8743–8759. <https://doi.org/10.1175/JCLI-D-15-0006.1>
- Looby, C. I., & Martin, P. H. (2020). Diversity and function of soil microbes on montane gradients: The state of knowledge in a changing world. *FEMS Microbiology Ecology*, 96, 1–13. <https://doi.org/10.1093/femsec/fiaa122>
- Madrigal-González, J., Herrero, A., Ruiz-Benito, P., & Zavala, M. A. (2017). Resilience to drought in a dry forest: Insights from demographic rates. *Forest Ecology and Management*, 389, 167–175. <https://doi.org/10.1016/j.foreco.2016.12.012>
- Martin, P. H., & Bellingham, P. J. (2016). Towards integrated ecological research in tropical montane cloud forests. *Journal of Tropical Ecology*, 32(5), 345–354. <https://doi.org/10.1017/S0266467416000432>
- Martin, P. H., & Fahey, T. J. (2006). Fire history along environmental gradients in the subtropical pine forests of the cordillera central, Dominican Republic. *Journal of Tropical Ecology*, 22(3), 289–302. <https://doi.org/10.1017/S0266467406003178>
- Martin, P. H., & Fahey, T. J. (2014). Mesoclimatic patterns shape the striking vegetation mosaic in the cordillera central, Dominican Republic. *Arctic, Antarctic, and Alpine Research*, 46(4), 755–765. <https://doi.org/10.1657/1938-4246-46.4.755>
- Martin, P. H., Fahey, T. J., & Sherman, R. E. (2011). Vegetation zonation in a neotropical montane forest: Environment, disturbance and ecotones. *Biotropica*, 43(5), 533–543. <https://doi.org/10.1111/j.1744-7429.2010.00735.x>
- Martin, P. H., Sherman, R. E., & Fahey, T. J. (2007). Tropical montane forest ecotones: Climate gradients, natural disturbance, and vegetation zonation in the cordillera central, Dominican Republic. *Journal of Biogeography*, 34(10), 1792–1806. <https://doi.org/10.1111/j.1365-2699.2007.01726.x>
- Martinez Arbizu, P. (2020). pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4.
- Marzol-Jaén, M. V., Sanchez-Megía, J., & García-Santos, G. (2011). Effects of fog on climatic conditions at a sub-tropical montane cloud forest site in northern Tenerife (Canary Islands, Spain). In L. A. Brujinzeel, F. N. Scatena, & L. S. Hamilton (Eds.), *Tropical montane cloud forests: Science for conservation and management* (pp. 359–364). Cambridge University Press.
- McNab, W. H. (1989). Terrain shape index: Quantifying effect of minor landforms on tree height. *Forest Science*, 35(1), 91–104. <https://doi.org/10.1093/forestscience/35.1.91>
- Muñoz, M. M., Feeley, K. J., Martin, P. H., & Farallo, V. R. (2022). The multidimensional (and contrasting) effects of environmental warming on a group of montane tropical lizards. *Functional Ecology*, 36(2), 419–432. <https://doi.org/10.1111/1365-2435.13950>
- Myers, R., & Rodríguez-Trejo, D. (2009). Fire in tropical pine ecosystems. In M. Cochrane (Ed.), *Fire in the tropics* (pp. 557–605). Springer.
- Myers, R. L., O'Brien, J., Mehlman, D., & Bergh, C. (2004). *Fire management assessment of the Highland ecosystems of The Dominican Republic*. GFI publication no. 2004-2a. The Nature Conservancy.
- Null, J. (2020). El Niño and La Niña years and intensities. *Golden Gate Weather Services*. <https://ggweather.com/enso/oni.htm>
- Odion, D. C., Moritz, M. A., & DellaSala, D. A. (2010). Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology*, 98(1), 96–105. <https://doi.org/10.1111/j.1365-2745.2009.01597.x>
- Ohsawa, M. (1995). The montane cloud forest and its gradational changes in Southeast Asia. In L. S. Hamilton, J. O. Juvik, & F. N. Scatena (Eds.), *Tropical montane cloud forests* (pp. 254–265). Springer.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2013). *Vegan: Community ecology package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>
- Ostertag, R., Restrepo, C., Dalling, J. W., Martin, P. H., Abiem, I., Aiba, S. I., Alvarez-Dávila, E., Aragón, R., Ataroff, M., Chapman, H., Cueva-Agila, A. Y., Fadrique, B., Fernández, R. D., González, G., Gotsch, S. G., Häger, A., Homeier, J., Iñiguez-Armijos, C., Llambí, L. D., ... Williams, C. B. (2022). Litter decomposition rates across tropical montane and lowland forests are controlled foremost by climate. *Biotropica*, 54(2), 309–326. <https://doi.org/10.1111/btp.13044>
- Paniw, M., de la Riva, E. G., & Lloret, F. (2021). Demographic traits improve predictions of spatiotemporal changes in community resilience to drought. *Journal of Ecology*, 109, 3233–3245. <https://doi.org/10.1111/1365-2745.13597>
- Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M. B., ... Yang, D. Q. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5(5), 424–430. <https://doi.org/10.1038/nclimate2563>
- Pérez-Pereda, E., Durán-Manual, F., Martínez-Becerra, L. W., Ramos-Rodríguez, M. P., & Tamayo-Echevarría, W. (2012). Regeneración natural de *Pinus cubensis* Griseb. en Guantánamo al aplicar quemadas prescritas. *Revista Forestal Baracoa*, 31(2), 15–22.
- Perry, D. A., Hessburg, P. F., Skinner, C. N., Spies, T. A., Stephens, S. L., Taylor, A. H., Franklin, J. F., McComb, B., & Riegel, G. (2011). The ecology of mixed severity fire regimes in Washington, Oregon, and northern California. *Forest Ecology and Management*, 262(5), 703–717. <https://doi.org/10.1016/j.foreco.2011.05.004>
- Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326. <https://doi.org/10.1038/307321a0>

- R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reyes, O. J., & Acosta Cantillo, F. (2012). Sintáxones de los pinares de *Pinus cubensis* de la zona nororiental de Cuba. *Lazaroa*, 33, 111–169.
- Rodríguez Trejo, D. A. (2008). Fire regimes, fire ecology, and fire management in Mexico. *Ambio*, 37(7), 548–556. <https://doi.org/10.1579/0044-7447-37.7.548>
- Rodríguez-Trejo, D. A., Martínez-Hernández, P. A., Ortiz-Contla, H., Chavarría-Sánchez, M. R., & Hernández-Santiago, F. (2011). The present status of fire ecology, traditional use of fire, and fire management in Mexico and Central America. *Fire Ecology*, 7, 40–56. <https://doi.org/10.4996/fireecology.0701040>
- Romme, W. H., Kaufmann, M., Veblen, T. T., Sherriff, R., & Regan, C. (2003). Ecological effects of the Hayman fire. Part 2: Historical (pre-1860) and current (1860–2002) forest and landscape structure. In R. T. Graham (Ed.), *Hayman fire case study* (pp. 196–203). Gen. Tech. Rep. RMRS-GTR-114. US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Salley, S. W., Sleezer, R. O., Bergstrom, R. M., Martin, P. H., & Kelly, E. F. (2016). A long-term analysis of the historical dry boundary for the Great Plains of North America: Implications of climatic variability and climatic change on temporal and spatial patterns in soil moisture. *Geoderma*, 274, 104–113. <https://doi.org/10.1016/j.geoderma.2016.03.020>
- Santisuk, T. (1997). Geographical and ecological distributions of the two tropical pines, *Pinus kesiya* and *Pinus merkusii*, in Southeast Asia. *Thai Forest Bulletin (Botany)*, 25, 102–123. <https://li01.tci-thaijo.org/index.php/ThaiForestBulletin/article/view/25016>
- Schoennagel, T., Smithwick, E. A., & Turner, M. G. (2008). Landscape heterogeneity following large fires: Insights from Yellowstone National Park, USA. *International Journal of Wildland Fire*, 17(6), 742–753. <https://doi.org/10.1071/WF07146>
- Schoennagel, T., Veblen, T. T., Kulakowski, D., & Holz, A. (2007). Multidecadal climate variability and climate interactions affect subalpine fire occurrence, Western Colorado (USA). *Ecology*, 88(11), 2891–2902. <https://doi.org/10.1890/06-1860.1>
- Schoennagel, T., Veblen, T. T., & Romme, W. H. (2004). The interaction of fire, fuels, and climate across Rocky Mountain forests. *Bioscience*, 54(7), 661–676. [https://doi.org/10.1641/0006-3568\(2004\)054\[0661:TIOFFA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2)
- Scholl, M. A., Bassiouni, M., & Torres-Sánchez, A. J. (2021). Drought stress and hurricane defoliation influence mountain clouds and moisture recycling in a tropical forest. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2021646118. <https://doi.org/10.1073/pnas.2021646118>
- Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, 531(7593), 229–232. <https://doi.org/10.1038/nature16986>
- Seidl, R., Spies, T. A., Peterson, D. L., Stephens, S. L., & Hicke, J. A. (2016). Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology*, 53, 120–129. <https://doi.org/10.1111/1365-2664.12511>
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., & Lexer, M. J. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7, 395–402. <https://doi.org/10.1038/nclimate3303>
- Sherman, R. E., Fahey, T. J., Martin, P. H., & Battles, J. J. (2012). Patterns of growth, recruitment, mortality and biomass across an altitudinal gradient in a neotropical montane forest, Dominican Republic. *Journal of Tropical Ecology*, 28(5), 483–495. <https://doi.org/10.1017/S0266467412000478>
- Sherman, R. E., Martin, P. H., & Fahey, T. J. (2005). Vegetation-environment relationships in forest ecosystems of the cordillera central, Dominican Republic. *Journal of the Torrey Botanical Society*, 132(2), 293–310. [https://doi.org/10.3159/1095-5674\(2005\)132\[293:VRIFE0\]2.0.CO;2](https://doi.org/10.3159/1095-5674(2005)132[293:VRIFE0]2.0.CO;2)
- Sherman, R. E., Martin, P. H., Fahey, T. J., & Degloria, S. D. (2008). Fire and vegetation dynamics in high-elevation neotropical montane forests of The Dominican Republic. *Ambio*, 37(7–8), 535–541. <https://www.jstor.org/stable/25547945>
- Shlisky, A., Waugh, J., Gonzalez, P., Gonzalez, M., Manta, M., Santoso, H., Alvarado, E., Ainuddin, A., Rodríguez-Trejo, D. A., Swaty, R., Schmidt, D., Kaufmann, M., Myers, R., Alencar, A., Kearns, F., Johnson, D., Smith, J., & Zollner, D. (2007). Fire, ecosystems and people: Threats and strategies for global biodiversity conservation. *The Nature Conservancy Global Fire Initiative Technical Report*, 17.
- Slack, A. W., Zeibig-Kichas, N. E., Kane, J. M., & Varner, J. M. (2016). Contingent resistance in longleaf pine (*Pinus palustris*) growth and defense 10 years following smoldering fires. *Forest Ecology and Management*, 364, 130–138. <https://doi.org/10.1016/j.foreco.2016.01.014>
- Slocum, M. G., Aide, T. M., Zimmerman, J. K., & Navarro, L. (2006). A strategy for restoration of montane forest in anthropogenic fern thickets in The Dominican Republic. *Restoration Ecology*, 14(4), 526–536. <https://doi.org/10.1111/j.1526-100X.2006.00164.x>
- Stephenson, T. S., Vincent, L. A., Allen, T., Van Meerbeek, C. J., McLean, N., Peterson, T. C., Taylor, M. A., Aaron-Morrison, A. P., Auguste, T., Bernard, D., Boekhoudt, J. R. I., Blenman, R. C., Braithwaite, G. C., Brown, G., Butler, M., Cumberbatch, C. J. M., Etienne-Leblanc, S., Lake, D. E., Martin, D. E., ... Trotman, A. R. (2014). Changes in extreme temperature and precipitation in the Caribbean region, 1961–2010. *International Journal of Climatology*, 34(9), 2957–2971. <https://doi.org/10.1002/joc.3889>
- Sullivan, A. L. (2009). Wildland surface fire spread modelling, 1990–2007. 2: Empirical and quasi-empirical models. *International Journal of Wildland Fire*, 18, 369–386. <https://doi.org/10.1071/WF06142>
- Swann, D. E. B., Bellingham, P. J., & Martin, P. H. (2022). Data from: Resilience of a tropical montane pine forest to fire and severe droughts. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.qnk98sfm3>
- United States Agency for International Development (USAID). (2017). *Climate Risk Profile: Dominican Republic*. [https://www.climateinlinks.org/sites/default/files/asset/document/2017\\_USAID%20CCIS\\_Climate%20Risk%20Dominican%20Republic.pdf](https://www.climateinlinks.org/sites/default/files/asset/document/2017_USAID%20CCIS_Climate%20Risk%20Dominican%20Republic.pdf)
- Urza, A. K., & Sibold, J. S. (2017). Climate and seed availability initiate alternate post-fire trajectories in a lower subalpine forest. *Journal of Vegetation Science*, 28(1), 43–56. <https://doi.org/10.1111/jvs.12465>
- Van Bloem, S. J., & Martin, P. H. (2021). Socio-ecological lessons from the multiple landfalls of hurricane Georges. *Ecosphere*, 12(2), e03373. <https://doi.org/10.1002/ecs2.3373>
- Van Mantgem, P. J., Stephenson, N. L., Knapp, E., Battles, J., & Keeley, J. E. (2011). Long-term effects of prescribed fire on mixed conifer forest structure in the Sierra Nevada, California. *Forest Ecology and Management*, 261(6), 989–994. <https://doi.org/10.1016/j.foreco.2010.12.013>
- Van Meerbeek, K., Jucker, T., & Svenning, J.-C. (2021). Unifying the concepts of stability and resilience in ecology. *Journal of Ecology*, 109, 3114–3132. <https://doi.org/10.1111/1365-2745.13651>
- Varner, J. M., Hood, S. M., Aubrey, D. P., Yedinak, K., Hiers, J. K., Jolly, W. M., Shearman, T. M., McDaniel, J. K., O'Brien, J. J., & Rowell, E. M. (2021). Tree crown injury from wildland fires: Causes, measurement and ecological and physiological consequences. *New Phytologist*, 231, 1676–1685. <https://doi.org/10.1111/nph.17539>
- Varner, J. M., Putz, F. E., O'Brien, J. J., Hiers, J. K., Mitchell, R. J., & Gordon, D. R. (2009). Post-fire tree stress and growth following smoldering duff fires. *Forest Ecology and Management*, 258(11), 2467–2474. <https://doi.org/10.1016/j.foreco.2009.08.028>
- Veblen, T. T. (2000). Disturbance patterns in southern Rocky Mountain forests. In R. L. Knight, F. W. Smith, S. W. Buskirk, W. H. Romme, & W. L. Baker (Eds.), *Forest fragmentation in the southern Rocky Mountains* (pp. 31–54). University Press of Colorado.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer ISBN 0-387-95457-0.

- Westerling, A. L., Hidalgo, H. G., Cayan, D. R., & Swetnam, T. W. (2006). Warming and earlier spring increase Western U.S. forest wildfire activity. *Science*, 313(5789), 940–943. <https://doi.org/10.1126/science.1128834>
- Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 5738–5742. <https://doi.org/10.1073/pnas.0606292104>
- Woolley, T., Shaw, D. C., Ganio, L. M., & Fitzgerald, S. (2012). A review of logistic regression models used to predict post-fire tree mortality of western north American conifers. *International Journal of Wildland Fire*, 21(1), 1–35. <https://doi.org/10.1071/WF09039>
- World Meteorological Organization (WMO). (2017). Guidelines on the calculation of climate Normals. WMO-No. 1203. [https://library.wmo.int/doc\\_num.php?explnum\\_id=4166](https://library.wmo.int/doc_num.php?explnum_id=4166)

## SUPPORTING INFORMATION

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

**How to cite this article:** Swann, D. E. B., Bellingham, P. J., & Martin, P. H. (2022). Resilience of a tropical montane pine forest to fire and severe droughts. *Journal of Ecology*, 00, 1–20. <https://doi.org/10.1111/1365-2745.14017>

## Supporting Information

**Table S1.** Sample size (N) and description of each subset of vegetation plots used in major analyses. In 1999, fifty-five circular, permanent plots were established in the monodominant pine forest from 1695–3050 m a.s.l. elevation. Given the wide range in tree densities, small (0.05 ha) plots were used in higher density stands (e.g. > 400 stems ha<sup>-1</sup>) and large (0.1 ha) plots in lower density stands based on a visual assessment of density; in total, 20 small and 35 large plots were placed in 1999. Forty-nine of the 55 plots burned in the 2005 fire. After the 2005 fire, burned plots were re-measured in 4 censuses: 44 plots in 2007 (9 small, 35 large), 38 in 2010 (12 small, 26 large), 38 in 2015 (6 small, 32 large), and 48 in 2018–2019 (22 small, 26 large). For the analysis of post-fire demography, 33 burned plots had trees that survived the fire. The 6 unburned plots were only re-measured in 2019, and hence have one pre-fire (1999) and post-fire measurement (2019); due to the fires' extent, unburned pine plots were few and thus 2 unburned plots were located below the pine–cloud forest ecotone. We refer to the 2018–2019 census as ‘2018’ as most plots were measured that year; however, all analyses were per the year a plot was measured.

Analysis	No. of plots (N)	Description of plots
<u>Patterns of fire severity</u>		
-Moran's eigenvector mapping <sup>1</sup>	49	All burned plots measured in 1999 and 2007
<u>Post-fire patterns in canopy tree growth and mortality</u>		
-General controls		
<i>Linear and logistic mixed models</i>	33 <sup>2</sup>	All burned plots with trees surviving the fire
-Pre- vs. post-fire		
<i>Generalized estimating equations</i>		All burned plots with trees surviving the fire
Growth & Mortality: 1999 to 2007	33	
Growth & Mortality: 2007 to 2010	26	
Growth & Mortality: 2010 to 2015	26	
Growth & Mortality: 2015 to 2018	33 <sup>2</sup>	
-Unburned vs. burned		
<i>Generalized estimating equations</i>	39 <sup>2</sup>	All burned plots with trees surviving the fire and all unburned plots
<u>Stand structure and understorey community dynamics</u>		
-Change in stand structure over time		
<i>Generalized estimating equations</i> <sup>3</sup>		All burned and unburned plots
1999	54	
2007	43	
2010	37	
2015	37	
2018	47	
-Post-fire controls of regeneration		
<i>Negative binomial regression models</i> <sup>3</sup>	40 <sup>4</sup>	All burned plots with trees surviving the fire
-Community change		
<i>NMDS</i> <sup>3</sup>		All burned and unburned plots
1999	54	

2007	42 <sup>5</sup>	
2018	47	
<i>PERMANOVA</i> <sup>3</sup>		All burned and unburned plots
1999	54	
2007	42 <sup>5</sup>	
2010	37	
2015	37	
2018	47	
<i>Linear regression model</i>	41	All burned plots with understorey stems

---

<sup>1</sup> Five plots with stand replacing fires had 100% of their trees killed by fire but their understories were not measured in 2007.

<sup>2</sup> All live trees in one plot died between 2015–2018, therefore there was one fewer plot for growth analyses that used 2018 DBH data.

<sup>3</sup> Due to an extreme outlier with hyperabundant pine regeneration, one burned plot was removed from these analyses.

<sup>4</sup> One plot was excluded from analysis because its understory was not measured in 2007.

<sup>5</sup> One plot was excluded in 2007 because it had no understory stems, precluding it from multivariate analysis.

**Table S2.** Pre-fire monthly climate deviations and Palmer Drought Severity Indices (PDSI) in the Cordillera Central, Dominican Republic. Monthly percentage deviations were calculated against long-term mean monthly averages from 1961–1990. These data were compiled from a gridded 4-km resolution global climate dataset, TerraClimate (Abatzoglou et al., 2018).

Year	Month	Deviation of mean PPT	Deviation of mean Tmax	Deviation of mean Tmin	PDSI
2004	Jan	64%	107%	112%	3.09
2004	Feb	25%	106%	127%	2.24
2004	Mar	59%	101%	119%	1.50
2004	Apr	116%	100%	110%	1.45
2004	May	232%	96%	110%	2.54
2004	Jun	2%	99%	118%	1.48
2004	Jul	117%	101%	108%	1.46
2004	Aug	9%	101%	114%	-2.02
2004	Sep	44%	101%	107%	-2.93
2004	Oct	45%	99%	114%	-3.42
2004	Nov	57%	98%	111%	-4.52
2004	Dec	112%	101%	126%	-4.51
2005	Jan	72%	96%	117%	-4.91
2005	Feb	14%	96%	98%	-5.59
2005	Mar	117%	108%	123%	-5.23
<b>Mean</b>		<b>72%</b>	<b>101%</b>	<b>114%</b>	-

**Table S3.** Post-fire monthly climate deviations and Palmer Drought Severity Indices (PDSI) during droughts (i.e. PDSI of < -2.00 for six consecutive months) in the Cordillera Central, Dominican Republic. Monthly percentage deviations were calculated against long-term mean monthly averages from 1961–1990. These data were compiled from a gridded 4-km resolution global climate dataset, TerraClimate (Abatzoglou et al., 2018).

Year	Month	Deviation of mean PPT	Deviation of mean Tmax	Deviation of mean Tmin	PDSI
2011	Sep	4%	99%	102%	-2.02
2011	Oct	63%	100%	112%	-2.57
2011	Nov	59%	99%	107%	-3.25
2011	Dec	91%	96%	115%	-3.27
2012	Jan	42%	94%	120%	-3.70
2012	Feb	53%	98%	138%	-4.06
2012	Mar	46%	97%	119%	-4.38
2013	Oct	40%	106%	112%	-2.50
2013	Nov	32%	99%	111%	-3.13
2013	Dec	28%	102%	120%	-3.78
2014	Jan	48%	108%	131%	-4.35
2014	Feb	80%	106%	144%	-4.56
2014	Mar	138%	105%	109%	-4.05
2014	Apr	45%	105%	131%	-4.45
2014	May	184%	96%	110%	-3.39
2014	Jun	49%	104%	111%	-3.53
2014	Jul	36%	103%	115%	-4.16
2014	Aug	190%	104%	108%	-2.40
2014	Sep	18%	103%	113%	-3.10
2014	Oct	47%	104%	109%	-3.61
2014	Nov	111%	105%	121%	-3.72
2014	Dec	43%	105%	128%	-3.94
2015	Jan	32%	107%	134%	-4.24
2015	Feb	133%	108%	112%	-3.85



**Table S4.** Correlation matrix of predictor variables used to model patterns of fire severity. Vegetation data is from pre-fire stand structure measured in 1999.

Predictor variables	Orography	Elev.	Aspect	Slope	TSI	Basal area	Density	Understorey pines	Shrubs	SD DBH	QMD	Necromass
Orography <sup>1</sup>	1											
Elevation (m)	0.02	1										
Aspect <sup>2</sup> (°)	0.42	0.31	1									
Slope (°)	0.08	-0.22	-0.05	1								
TSI <sup>3</sup>	-0.29	-0.13	-0.27	0.08	1							
Tree basal area <sup>4</sup>	0.01	0.01	-0.17	0.02	-0.04	1						
Tree density <sup>5</sup>	0.12	-0.46	-0.23	0.05	-0.16	0.44	1					
Understorey pines <sup>6</sup>	-0.31	0.28	-0.24	-0.23	-0.06	0	-0.28	1				
Shrubs <sup>7</sup>	-0.19	-0.4	-0.35	0.03	0.12	0.03	0.42	0.11	1			
SD DBH <sup>8</sup>	-0.13	0.47	0.14	-0.16	-0.06	0.05	-0.55	0.41	-0.15	1		
QMD <sup>9</sup>	-0.15	0.55	0.22	0.03	0.1	0.07	-0.74	0.34	-0.44	0.56	1	
Necromass <sup>10</sup>	0.45	0.16	0.52	0.02	-0.11	-0.27	-0.18	-0.16	-0.25	-0.1	0.26	1

<sup>1</sup> Orography is a binary variable (0 for leeward, 1 for windward).

<sup>2</sup> Aspect was transformed as  $\cos(45^\circ - \text{aspect}) + 1$ , such that its maximum is a northeast-facing aspect.

<sup>3</sup> Terrain shape index, from McNab (1989).

<sup>4</sup> Basal area of living trees ( $\text{m}^2 \text{ha}^{-1}$ ).

<sup>5</sup> Density of living pine trees ( $\text{stems ha}^{-1}$ ).

<sup>6</sup> Density of living pine saplings and seedlings ( $\text{stems ha}^{-1}$ ).

<sup>7</sup> Density of living woody understorey species ( $\text{stems ha}^{-1}$ ).

<sup>8</sup> Standard deviation of tree DBH (cm). DBH measured at 1.3 m height.

<sup>9</sup> Quadratic mean diameter (QMD) of tree DBH (cm), which gives greater weight to large trees than the arithmetic mean. In stands with large tree diameters and a wide range of diameters present or strongly skewed diameter distributions, the difference between arithmetic mean and QMD can be large.

<sup>10</sup> Density ( $\text{stems ha}^{-1}$ ) of recently dead (e.g. standing dead, tipped, and snapped) trees before the fire.

**Table S5.** Measurements of the central tendency and dispersion of plot-scale environmental and vegetation variables used to model patterns of fire severity. All vegetation variables were calculated in each plot from pre-fire stand structure measured in 1999.

Predictor variables	Min	Max	Median	Mean	SE
Orography <sup>1</sup>	0.00	1.00	0.00	0.27	0.06
Elevation (m)	1695	3094	2450	2436.8	46.06
Aspect <sup>2</sup> (°)	0.00	2.00	1.26	1.05	0.10
Slope (°)	0.33	35.13	20.54	20.74	1.06
TSI <sup>3</sup>	-3.56	0.59	-0.18	-0.29	0.10
Tree basal area <sup>4</sup>	1.83	35.10	16.46	16.19	0.97
Tree density <sup>5</sup>	10.1	1202.9	360.9	419.0	41.4
Understorey pines <sup>6</sup>	0.00	28235	4167	6732	947
Shrubs <sup>7</sup>	0.00	36176	7941	10478	1329
SD DBH <sup>8</sup>	0.00	24.08	9.89	10.42	0.69
QMD <sup>9</sup>	14.31	48.47	23.10	26.47	1.38
Necromass <sup>10</sup>	0.00	180.84	20.09	29.3	5.26

<sup>1</sup> Orography is a binary variable (0 for leeward, 1 for windward).

<sup>2</sup> Aspect was transformed with  $\cos(45^\circ - \text{aspect}) + 1$ , such that its maximum is a northeast-facing aspect.

<sup>3</sup> Terrain shape index, from McNab (1989).

<sup>4</sup> Basal area of living trees ( $\text{m}^2 \text{ha}^{-1}$ ).

<sup>5</sup> Density of living pine trees ( $\text{stems ha}^{-1}$ ).

<sup>6</sup> Density of living pine saplings and seedlings ( $\text{stems ha}^{-1}$ ).

<sup>7</sup> Density of living woody understorey species ( $\text{stems ha}^{-1}$ ).

<sup>8</sup> Standard deviation of tree DBH (cm). DBH measured at 1.3 m height.

<sup>9</sup> Quadratic mean diameter (QMD) of tree DBH (cm), which gives greater weight to large trees than the arithmetic mean. In stands with large tree diameters and a wide range of diameters present or strongly skewed diameter distributions, the difference between arithmetic mean and QMD can be large.

<sup>10</sup> Density ( $\text{stems ha}^{-1}$ ) of recently dead (e.g. standing dead, tipped, and snapped) trees before the fire.

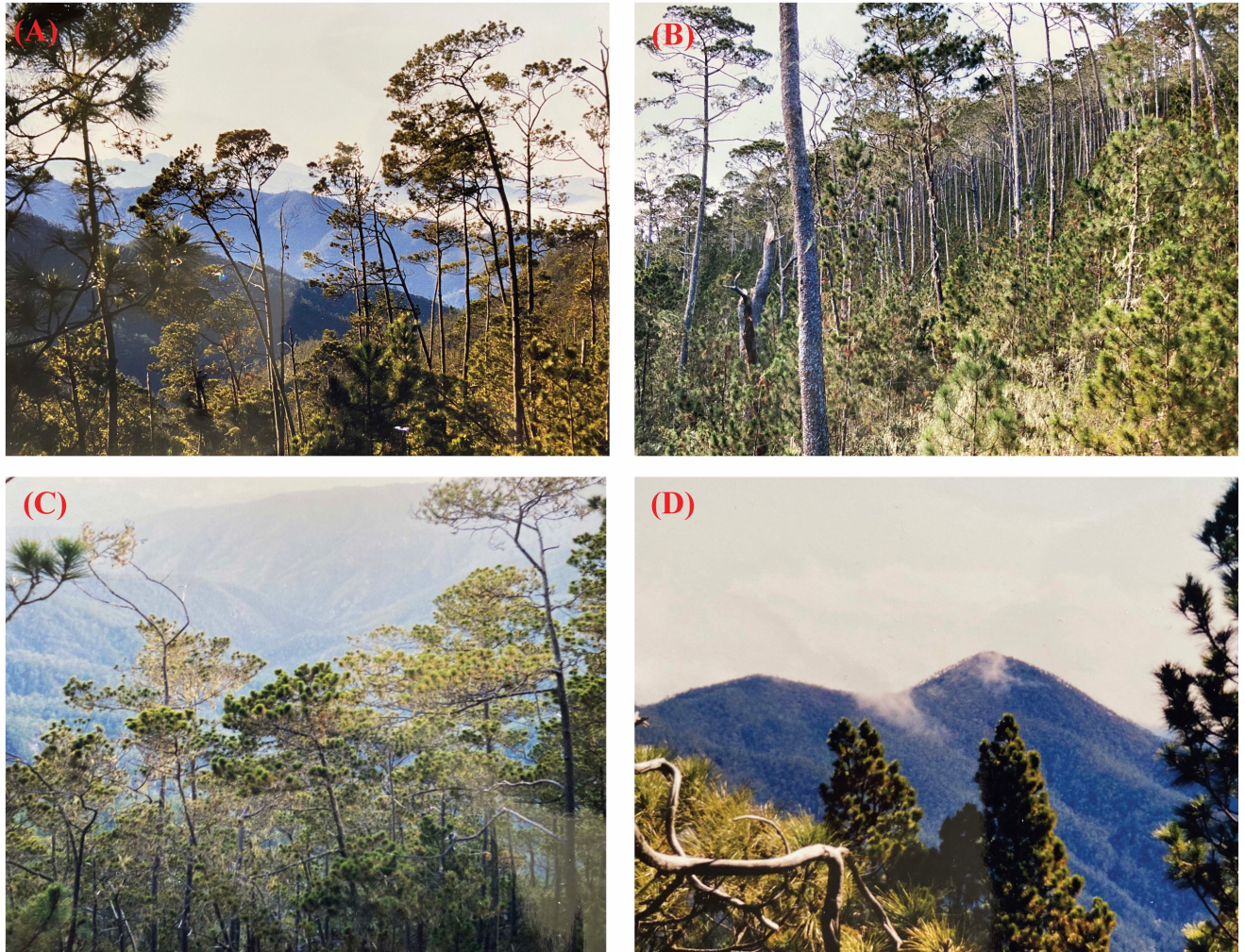
**Table S6.** Woody plant species and growth habits of tallied stems in 55 permanent vegetation plots, including 6 unburned plots which contained tree species additional to *P. occidentalis*. Trees were defined as species with a single main stem and that attain sizes  $\geq 10$  cm DBH, and shrubs as multi-stemmed species that do not attain sizes  $< 10$  cm DBH. Species denoted with “sp.” could not be further identified; genera denoted with “spp.” had 2 or more morphospecies that could not be further identified: *Cyathea* spp. had 2 morphospecies, *Rubus* spp. had 3 morphospecies, and *Cestrum* spp. had 4 morphospecies.

Species List	
Aquifoliaceae	Lauraceae
<i>Ilex impressus</i> Loes. & Ekm. – shrub	<i>Ocotea cicatricosa</i> C.K. Allen. – tree
<i>Ilex repanda</i> Griseb. – tree	<i>Ocotea wrightii</i> (Meissn.) Mez. – tree
Araliaceae	<i>Persea krugii</i> (Urb.) – tree
<i>Oreopanax capitatus</i> (Jacq.) Decne. & Planch. – tree	Melastomataceae
Asteraceae	<i>Clidemia</i> sp. – shrub
<i>Baccharis myrsinites</i> (Lam.) Pers. – shrub	<i>Miconia selleana</i> Urb. & Ekm. – shrub
<i>Eupatorium illitium</i> (Urb.) – shrub	Myricaceae
Brunelliaceae	<i>Myrica picardae</i> Krug. & Urb. – shrub
<i>Brunellia comocladifolia</i> H. & B. – tree	Myrsinaceae
Celastraceae	<i>Myrsine coriacea</i> (Sw.) R. Br. – tree
<i>Torrabasia cuneifolia</i> (C. Wr.) Kr. & Urb. – tree	<i>Wallenia apiculata</i> Urb. – tree
Clusiaceae	Onagraceae
<i>Clusia clusiodes</i> (Griseb.) D'Arcy – tree	<i>Fuchsia pringsheimii</i> (Urb.) – shrub
Cunoniaceae	Papaveraceae
<i>Weinmannia pinnata</i> L. – shrub or tree	<i>Bocconia frutescens</i> L. – shrub
Cyatheaceae	Phytolaccaceae
<i>Cyathea</i> spp. – tree fern	<i>Phytolacca icosandra</i> L. – shrub
<i>Alsophila</i> sp. – tree fern	Pinaceae
Ericaceae	<i>Pinus occidentalis</i> Sw. – tree
<i>Lyonia alainii</i> Judd. – shrub	Podocarpaceae
<i>Lyonia buchii</i> Urb. – tree or shrub	<i>Podocarpus buchii</i> Urb. – tree
<i>Lyonia heptamera</i> Urb. – shrub	Rosaceae
Euphorbiaceae	<i>Rubus</i> spp. – shrub
<i>Ditita maestrensis</i> Borhidi. – tree or shrub	Rubiaceae
Fabaceae	<i>Antirhea oligantha</i> Urb. – tree or shrub
<i>Chamaecrista glandulosa</i> (L.) – shrub	<i>Palicourea eriantha</i> DC. – shrub
Garryaceae	<i>Psychotria berteriana</i> DC. – shrub
<i>Garrya fadyenii</i> (Hooker) – shrub	Solanaceae
Gesneriaceae	<i>Cestrum</i> spp. – shrub
<i>Rhytidophyllum berterioanum</i> Mart. – shrub	Ulmaceae
Hypericaceae	<i>Trema micrantha</i> (L.) Blume. – tree
<i>Hypericum pycnophyllum</i> Urb. – shrub	

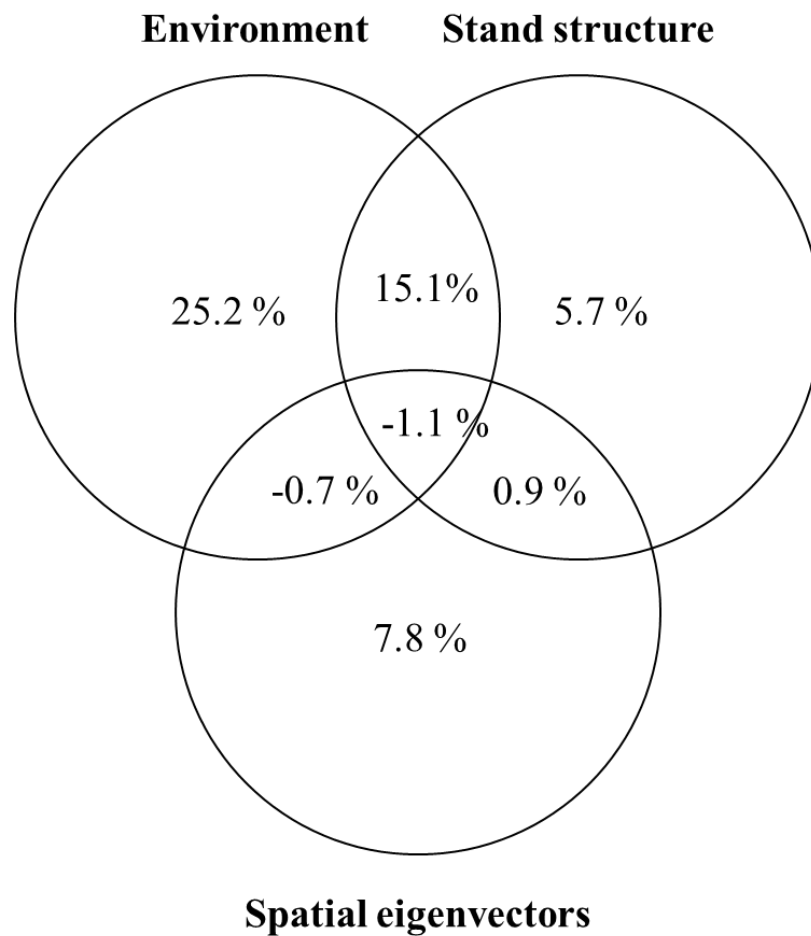
**Table S7.** Linear regression coefficients of mean Bray-Curtis dissimilarity in species composition in 2018 vs. 1999. The model used all burned plots from all fire severity classes ( $n = 41$ ). Total model  $R^2_{\text{adj}} = 46.7\%$  ( $F_{3,37} = 12.66$ ,  $p < 0.001$ ).

Response	Predictors	Coefficient	SE	T value	$p$
Mean dissimilarity 1999 vs. 2018	Intercept	0.9235	0.1308	7.09	< 0.001
	Elevation	-0.0001	0.0001	-2.71	0.010
	Orography <sup>1</sup> (1)	0.9529	0.3310	2.88	0.007
	Elevation * Orography <sup>1</sup> (1)	-0.0004	0.0001	-2.69	0.011

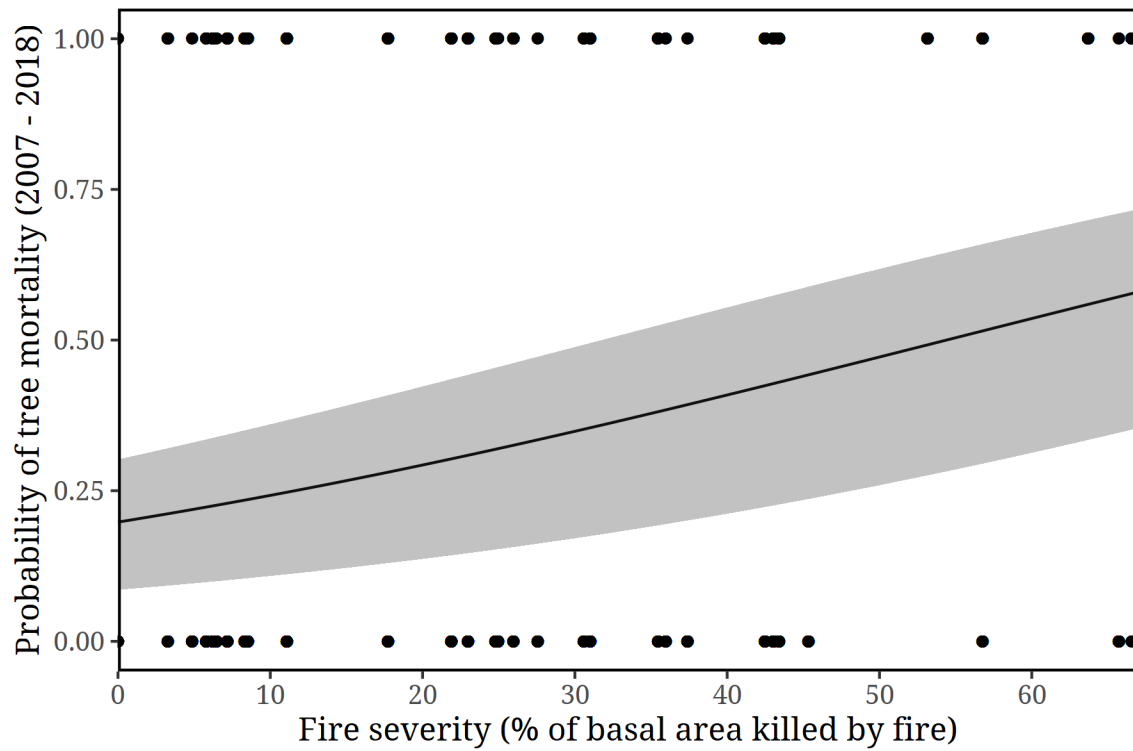
<sup>1</sup> Orography is a binary variable (0 for leeward, 1 for windward).



**Figure S1.** Patterns of pre-fire forest structure in monodominant *Pinus occidentalis* forest stands in the Cordillera Central, Dominican Republic. All photographs were taken in February or March 1999. (A) multi-cohort forests on leeward slopes toward Valle de Tetero (~2200 m a.s.l.); (B) closed-canopy, multi-cohort forests on windward slopes (~2600 m a.s.l.); note the pine stem snapped during Hurricane Georges in left foreground; (C) closed-canopy forests on windward slopes (~2400 m a.s.l.); (D) closed-canopy pine forest in background on the slopes leeward of the main ridge (~2600 m a.s.l.). (Photographs by P.H. Martin).



**Figure S2.** Variation partitioning using partial regression of fire severity patterns. Percentages in each section show the  $R^2_{\text{adj}}$  of each significant predictor alone or in combination with other predictors. Total model  $R^2_{\text{adj}}$  (summing all sections) = 52.8% ( $F_{5,43} = 11.74, p < 0.001$ ). Sections with small or negative  $R^2_{\text{adj}}$  values explained less variation than by random chance and are therefore interpreted as zeros, but were still used to calculate  $R^2_{\text{adj}}$ .



**Figure S3.** Predicted probabilities of post-fire pine tree mortality along a gradient of low and moderate fire severities for the entire post-fire time interval. Predictions were averaged over the random effect term that accounted for trees nested within plots (i.e. average marginal predictions). Shaded area represents 95% confidence interval, and points represent observed survivorship status (where 0 is alive and 1 is dead) along the observed gradient of fire-severities.