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RESEARCH ARTICLE

Warming, drought, and disturbances lead to shifts in functional composition: A millennial-scale analysis for Amazonian and Andean sites

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Abstract

Tropical forests are changing in composition and productivity, probably in response to changes in climate and disturbances. The responses to these multiple environmental drivers, and the mechanisms underlying the changes, remain largely unknown. Here, we use a functional trait approach on timescales of 10,000 years to assess how climate and disturbances influence the community-mean adult height, leaf area, seed mass, and wood density for eight lowland and highland forest landscapes. To do so, we combine data of eight fossil pollen records with functional traits and proxies for climate (temperature, precipitation, and El Niño frequency) and disturbances (fire and general disturbances). We found that temperature and disturbances were the most important drivers of changes in functional composition. Increased water availability (high precipitation and low El Niño frequency) generally led to more acquisitive trait composition (large leaves and soft wood). In lowland forests, warmer climates decreased community-mean height probably because of increased water stress, whereas in highland forests warmer climates increased height probably because of upslope migration of taller species. Disturbance increased the abundance of

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acquisitive, disturbance-adapted taxa with small seeds for quick colonization of disturbed sites, large leaves for light capture, and soft wood to attain fast height growth. Fire had weak effects on lowland forests but led to more stress-adapted taxa that are tall with fast life cycles and small seeds that can quickly colonize burned sites. Site-specific analyses were largely in line with cross-site analyses, except for varying site-level effects of El Niño frequency and fire activity, possibly because regional patterns in El Niño are not a good predictor of local changes, and charcoal abundances do not reflect fire intensity or severity. With future global changes, tropical Amazonian and Andean forests may transition toward shorter, drought- and disturbance-adapted forests in the lowlands but taller forests in the highlands.

KEYWORDS

Amazon, Andes, climate change, El Niño, fire, fossil pollen, functional traits, tropical forest

1 | INTRODUCTION

Old-growth tropical forests were long thought to be in a stable state. However, direct observations are accumulating that over the past decades forests are showing changes in productivity (Brienen et al., 2015), species composition (Feeley, Davies, et al., 2011), and functional trait composition (van der Sande et al., 2016). These changes can be caused by climate change, such as warming, droughts or increased atmospheric CO₂ concentration, or by natural and anthropogenic disturbances such as logging, hurricanes, and fires (Hirota et al., 2021). Understanding forest responses to multiple potential drivers is of critical importance, as it will help to understand forest responses to future changes. It is, however, difficult to understand the responses of tropical forest to multiple drivers, as they can have opposing effects and act at different timescales, and are therefore rarely considered in the same study. Most studies assess changes in tropical forests across a few decades (Brienen et al., 2015; Feeley, Davies, et al., 2011; van der Sande et al., 2016), whereas the recruitment and growth of trees to the canopy can take centuries, and the successional changes to old-growth forest composition even longer (Rozendaal et al., 2019). We therefore need to assess tropical forest responses at temporal scales of centuries to millennia.

Traditionally, long-term (100–1000 of years) palynological studies link changes in pollen taxon associations (González-Carranza et al., 2012; Smith & Mayle, 2018) to their ecological niche space to interpret the underlying environmental drivers of vegetation change. However, this way to infer the factors driving environmental change can be made more mechanistic by using functional plant trait characteristics. Functional traits are plant characteristics that determine plant establishment, growth, and survival, and thus the responses of species (Poorter et al., 2006; Violle et al., 2007) and ecosystems (Becknell & Powers, 2014; van der Sande et al., 2018) to environmental change. Therefore, using pollen data to analyze how the trait composition of plant communities is affected by human disturbance and climate change over centennial to millennial timescales will allow

for a better mechanistic understanding of forest responses to global changes (Sakschewski et al., 2016). Various studies have used such a functional trait approach by determining the community-weighted mean trait values, to assess short-term, decadal forest responses to environmental change (Enquist & Enquist, 2011; Fauset et al., 2012; van der Sande et al., 2016; Zhou et al., 2014).

Recently, we presented a new approach that analyzed millennial-scale shifts in functional trait composition, based on species abundance changes from fossil pollen records (van der Sande et al., 2019, 2020). We found that over a time period of 7000 years, the trait composition of a lowland forest in Peru was affected by past climate change and human disturbance (van der Sande et al., 2019). Using eight different traits, we showed that the community-mean wood density (WD), an indicator of drought and shade tolerance, decreased during times of high precipitation. Also, the community-mean leaf size increased with precipitation, probably because large leaves need more water for transpirational cooling and/or larger leaves are needed to intercept more light in wetter and denser forests. Furthermore, the community-mean tree height and seed mass (SM) increased with fire activity, perhaps because large species can escape crown fire, and seedlings from large seeds grow faster and have a greater chance of surviving a possible next fire. However, to date no studies have been done to assess how these relationships hold up across the diverse forests of the Amazon and Andes, and we do not know to what extent environmental drivers similarly affect trait composition for other forest types and at broader spatial scales.

Here, we assess the functional trait composition of eight South American tropical forest landscapes (ranging from 0 to 3200 m asl) and their millennial-scale responses to past climate change and disturbances. Along elevation, marked decreases occur in water availability, temperature, atmospheric pressure, and insolation, resulting in changes in species and trait composition (Enquist et al., 2017; Llerena-Zambrano et al., 2021; Maharjan et al., 2021). Such differences in environmental conditions and trait composition may lead to different forest responses to climate change and disturbances. For example, while the distributions of lowland tropical tree taxa

are strongly influenced by mean annual rainfall (Toledo et al., 2012), the distributions of montane tree taxa, such as *Weinmannia* and *Polylepis*, are mostly determined by mean annual temperature (Duque et al., 2015; Fadrique et al., 2018; Groot et al., 2013). From ca. 2300m, upslope night frost may occur, making resistance to night frost important for taxa occurring in these sites. This could suggest that Amazonian lowland forests respond most strongly to changes in rainfall, whereas highland Andean forests respond most strongly to changes in temperature and occurrence of night frost (Fadrique et al., 2018). In addition, intense droughts, such as those caused by El Niño events, are generally strongest in eastern and northern Amazonian lowland forests (Marengo et al., 2021). Furthermore, during the Holocene, tropical forests have seen varying degrees of human occupation and associated disturbances (McMichael & Bush, 2019). In many wet tropical forest ecosystems, fires do not naturally occur at high intensity or frequency, and are therefore often considered a human disturbance (Gosling et al., 2022). Forests with a longer history of natural or anthropogenic disturbances, such as fire or clearcut for agriculture (Iriarte et al., 2020), may be more resilient and show weaker responses (due to high resistance and/or fast recovery) to an increase in disturbances (Cole et al., 2014). On the other hand, frequent disturbances such as fires can also reduce an ecosystem's resilience and cause drastic shifts in state, for example to a savanna ecosystem (Staver et al., 2011).

We ask two questions. First, how do temporal changes in past climate (precipitation, temperature anomalies, and the frequency of El Niño events) and past disturbances (fire activity and disturbances in general) determine shifts in community-mean trait values across Neotropical forests over at least the last 2000 years (for some of our sites up to 12,000 years). We hypothesized that increased rainfall and decreasing droughts increase the relative abundance of drought-vulnerable taxa that may have a combination of low WD, large adult stature with large hydraulic path lengths, and large leaves (Aleixo et al., 2019; Guillemot et al., 2022). High disturbance intensity (e.g., from fire, hurricanes, or land-use change) can have contrasting effects: on the one hand, it can create more open spaces and increase the relative abundance of pioneer species with low WD and large leaves. On the other hand, when disturbance events occur frequently, it could increase the relative abundance of taxa that can resist disturbance (e.g., with dense wood), can resprout, or that have a shorter life cycle (e.g., short adult stature). Second, how do these responses of trait composition to climate and disturbances depend on elevation? We hypothesized that precipitation and El Niño effects are stronger at low elevation, because water availability is a more limiting resource, while temperature effects are stronger at high elevation, because of its limiting effect on tree growth (Table 1). To address these questions, we use data from eight fossil pollen records, which we match with data of four key functional leaf, stem, and whole-plant traits that capture the global spectra in plant form and function (Díaz et al., 2015). Subsequently, we calculate community-mean trait values across time and link these to disturbance indices (charcoal to indicate fire, and abundance of the pioneer genus *Cecropia* spp. to indicate disturbances) and independent

climate proxies (for precipitation, temperature, and El Niño events). We test these hypotheses using cross-site analyses and site-specific analyses.

2 | MATERIALS AND METHODS

2.1 | Sites

We focused this study on eight sites in forest-dominated landscapes in the Amazon and Andes (Table 2; Figure 1). We selected four lowland (5–600m), one mid-elevation (1250m), and three highland (2780–3150m) sites. For each site, we had one fossil pollen record derived from lake sediments to assess changes in pollen taxonomic composition for the last two millennia, while some pollen records reflect a longer period up to the last ca. 12 kyr. We linked the pollen taxa names in these records (at genus level) to leaf and stem trait data to quantify “community-mean traits” changes over time. From the selected lake sediment cores, we also obtained data on charcoal for fire activity (Whitlock & Larsen, 2001) and quantified the abundance of *Cecropia* pollen as a proxy of forest openness (Zalamea et al., 2012), which was used as indicator of general disturbances. Furthermore, we used independent, external sources for climatic proxies of precipitation, temperature, and the frequency of El Niño events (see for a complete description below).

2.2 | Fossil pollen records

We used data from eight published fossil pollen records that covered at least the most recent 2000 years of the Holocene (mean = 6830 and max = 10,020 cal years BP; Table 2). Pollen grains and charcoal particles washed or blown in from land are well preserved in lake sediments and are therefore used to assess changes in vegetation and fire through time. We used the calibrated years before present (cal years BP) data as published per site (see references in Table 2), which were obtained from age models based on ^{14}C from the sediment cores.

We selected these eight fossil pollen and charcoal records because they cover the most recent part of the Holocene, have high temporal resolution to track forest dynamics (i.e., one sample every 20–50 years), and high resolution of botanical identification of the fossil pollen (for most taxa up to genus level). The number of pollen samples in the selected records varies from 40 to 451 (on average 150 samples per record). The temporal resolution of the records varies from 0.5 to 5.1 samples per 100 years (on average 2.6). For additional explanation of the lakes, the surrounding ecosystem, and the methods used for pollen analyses, see the original publications listed in Table 2. In total across all records, we had pollen data from 1200 pollen samples (i.e., 1200 points in time).

Samples were prepared following standardized methods (Faegri & Iversen, 1989). Pollen grains in the samples were identified and counted, in most cases up to 300 pollen grains per sample. Details

TABLE 1 Hypotheses for the effects of environmental variables (precipitation, temperature, El Niño frequency, fire activity, and general disturbances) on the temporal changes in four community-mean traits (adult height, leaf area, seed mass, and wood density).

	Adult height (H)	Leaf area (LA)	Seed mass (SM)	Wood density (WD)
Precipitation	<p>High precipitation increases H because less drought allows the establishment of tall taxa that have longer hydraulic pathlengths (Bennett et al., 2015; Olson et al., 2018)</p>	<p>High precipitation increases LA because large-leaved species largely rely on transpiration for their heat cooling, which is easier at high precipitation (Greenwood et al., 2017)</p>	<p>High precipitation increases SM because large-seeded taxa are more shade-tolerant and can better germinate and persist in wet forests that are generally taller and more shaded (Baraloto et al., 2005; Moles et al., 2005; Poorter & Rose, 2005)</p>	<p>High precipitation decreases WD because soft-wooded taxa are less resistant to drought-induced cavitation (Eller et al., 2018; Greenwood et al., 2017; Markesteijn et al., 2011)</p>
Temperature	<p>Temperature decreases H at low elevation because of higher evaporative demand and a relative advantage of taxa with short hydraulic path lengths (Olson et al., 2018). However, temperature increases H at high elevation because of lower risk of freezing-induced cavitation and a relative advantage of tall, cavitation-vulnerable taxa (Mao et al., 2018)</p>	<p>Temperature decreases LA at low elevation because small leaves have more efficient convective heat cooling, but high temperature increases LA at high elevation because of denser vegetation and more light competition</p>	<p>Temperature decreases SM at low elevation because these species germinate better in the more open conditions due to gap formation and shorter trees, but increases SM at high elevation because these species establish better in the denser and taller forest</p>	<p>Temperature increases WD at low elevation because of the higher evaporative demand and a relative advantage of drought-tolerant taxa with high WD (Liang et al., 2021). However, temperature decreases WD at high elevation because of lower risk of freezing-induced cavitation and a relative advantage of cavitation-vulnerable taxa with wide vessels (Yang et al., 2020) and, hence, low WD</p>

TABLE 1 (Continued)

(b)	Adult height (H)	Leaf area (LA)	Seed mass (SM)	Wood density (WD)
El Niño frequency	High frequency of droughts increases the abundance of short taxa with short hydraulic path length and short adult size	High frequency of droughts decreases the abundance of small-leaved species because of more efficient convective cooling and less need for transpirational cooling	High frequency of droughts decreases SM because of more small, short-lived species	High frequency of droughts increases the abundance of drought-tolerant taxa with high WD
Fire	Fire activity increases H because tall taxa are more likely to escape and survive fire because of less crown fire and thicker bark (Barlow & Peres, 2008; Brando et al., 2012), or fire activity decreases H because it mainly favors disturbance-adapted species with short life cycle	Fire activity increases LA because disturbance would favor taxa with large leaves to take advantage of high-light conditions (although some pioneer species have small, compound leaves (Poorter & Rozendaal, 2008)), or fire activity decreases LA because of more efficient convective cooling in more open and warmer conditions	Fire activity decreases SM because small but many seeds enhance colonization of burned sites), or fire activity increases SM because large seeds are associated with high resprouting capacity and fast growth of seedlings, which enhances their chances to escape fire (Lahoreau et al., 2006; Westoby, 1998)	Fire activity increases WD, because dense wood is associated with less fire damage and with high resprouting capacity probably due to more carbohydrate reserves (Brando et al., 2012; Poorter et al., 2010)
Disturbances	Disturbances decrease H because pioneer species are often short, although long-lived pioneer species can be tall	Disturbances increase LA because high light availability favors the establishment of pioneer species with large leaves (although some pioneer species have small leaves, e.g., <i>Vismia</i> spp. and <i>Trema</i> spp.)	Disturbances decrease SM because high light availability favors the establishment of small-seeded species that regenerate well in full light	Disturbances (e.g., due to clearcut, hurricanes) decrease WD because open areas favor the establishment of soft-wooded pioneer species

Note: The cartoon in (a) provides a simplified overview of relative changes in trait composition that we expect with increased precipitation and reduced droughts (upper row), increased temperature (second row), increased fire activity (third row), and increased general disturbances (last rows). Note that these represent relative changes over time in response to different drivers, and do not represent absolute differences between elevations and drivers. The table in (b) provides more detailed hypotheses on each of the environmental effects (rows) on the four community-mean traits (columns).

TABLE 2 List of metadata information for the eight sites used ordered from high to low elevation.

	Llaviucu	Condores	Cocha	Pindo	Sauce	Pata	Kumpak ^a	Caraná	
Letter in Figure 1	a	b	c	d	e	f	g	h	
Elevation (m asl)	3150	2860	2780	1250	600	360	330	5	
Country	Ecuador	Peru	Colombia	Ecuador	Peru	Brazil	Ecuador	Brazil	
Latitude	-2.84	-6.89	1.08	-1.45	-6.7	0.28	-2.84	-2.84	
Longitude	-79.15	-77.69	-77.15	-78.08	-76.22	-66.68	-77.96	-55.04	
Avg present-day annual temp (°C)	11-12	12-17	11.6	20.8	25	25	24	27.2	
Avg present-day annual prec (mm/year)	>2000	3600	1400	4800	1475	3300	2500	3109	
Timespan (cal years BP)	-59-11,358	-57-2067	130-11,945	-63-8096	84-6856	-59-7593	-61-2415	-59-4318	
Paleo-precipitation record	El Tigre Perdido cave (van Breukelen et al., 2008)	Palestina cave (Apaéstegui et al., 2014)	El Tigre Perdido cave	El Tigre Perdido cave	El Tigre Perdido cave	El Tigre Perdido	El Tigre Perdido cave	Paraiso cave (Wang et al., 2017)	
Human disturbance	Yes, relatively constant	Yes, mainly until 1150 cal years BP, and low-intensity until 750 cal years BP	Yes, starting 1500 cal years BP with deforestation	Yes, sporadically	Yes, throughout	No	Yes, sporadically until ~750 cal years BP, and in recent 50 years	Yes, since ~4500 years BP	
Samples per 100 years	2.3	4.3	4.2	0.5	1.4	1.6	5.1	1.2	
Sample size	258	92	493	40	94	119	126	52	
Current vegetation type	Montane forest on steep slopes, rich in <i>Weinmannia</i> , <i>Alnus</i> , <i>Podocarpus</i> , <i>Rubiaceae</i> , <i>Hedyosmum</i> , <i>Urticaceae</i> , and <i>Myrsine</i> . Up to 3800 m there is forest dominated by <i>Polylepis</i> and <i>Gynoxys</i> , and paramo vegetation at higher elevation	Montane forest, rich in <i>Araliaceae</i> , <i>Ericaceae</i> , <i>Hedyosmum</i> , <i>Lauraceae</i> , <i>Melastomataceae</i> , <i>Rubiaceae</i> , <i>Urticaceae</i> and <i>Weinmannia</i>	Andean forest up to ~3550 m. <i>Paramo</i> vegetation with patches of <i>Polylepis</i> and <i>Gynoxys</i> dwarf forest at higher elevation	Mid-elevation, lower montane rain forest, at transition between lowland rainforest and paramo vegetation	Lowland tropical moist forest	Lowland tropical rainforest, Rich in <i>Alchornea</i> , <i>Anacardiaceae</i> , <i>Burseraceae</i> , <i>Melastomataceae</i> , <i>Meliaceae</i> , and <i>Myrtaceae</i> . In swampy areas on the Hill, <i>Mauritia</i> and <i>Mauritiella</i> were abundant	Lowland tropical rainforest	Lowland tropical rainforest	Lowland tropical rainforest
References	Nascimento et al. (2020)	Åkesson et al. (2020); Matthews-Bird et al. (2017)	Flantua et al. (2014); González-Carranza et al. (2012)	Montoya et al. (2018), Bush et al. (2016), Montoya et al. (2021)	Nascimento et al. (2019)	Åkesson et al. (2021)	Maezumi et al. (2018)		

Note: For each site, metadata are provided on elevation, country, coordinates (in decimal degrees), current-day average annual temperature and precipitation, the source of the paleo-precipitation record used, information on the human disturbance history of the site, the timespan of the pollen and environmental records used per site, the average temporal resolution of the pollen record (and, hence, of the environmental records), the sample size of the site, a description of the current vegetation, and the publications with the original data.

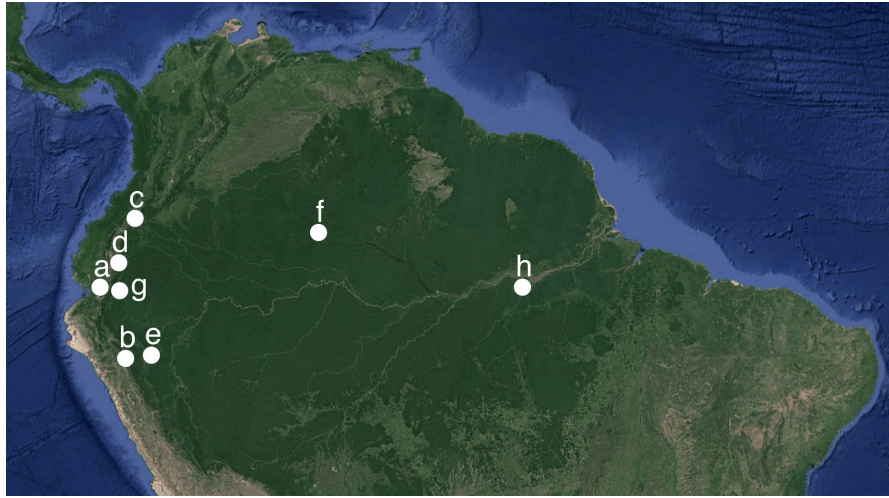


FIGURE 1 Map showing the locations of the eight sites, referred to by the name of the lake, and ordered from high to low elevation; (a) Llaviucu (3150 m asl), (b) Condores (2860 m asl), (c) Cocha (2780 m asl), (d) Pindo (1250 m asl), (e) Sauce (600 m asl), (f) Pata (360 m asl), (g) Kumpak^a (330 m asl), and (h) Caranã (5 m asl). Sites are ordered the same as in Table 1 and Figure 4.

of methods for pollen extraction and identification used for each of the sites can be found in earlier publications, see Table 2. Here, we only focus on taxa identified to genus level and occurring in the GlobalTreeSearch of the Botanic Gardens Conservation International (BGCI) and/or occurring as trees in The Plant List (<http://www.theplantlist.org>), because all sites are tree dominated (see pictures in Figure 4), and we want to assess how the tree community is changing. We included pollen abundances from all identified genera, including those identified with some uncertainty (e.g., the taxa identified as “c.f.”), as this was the best available identification. The sites varied in their proportion sampling coverage (between 0.37 and 0.97; Appendix S1) but sampling coverage was similar across years within sites, indicating that the coverage differences between sites would have little effect on the analyses (in which sites are included as random factors, see Section 2.8).

2.3 | Functional traits

To evaluate past shifts in functional composition in forests, we use four tree traits that likely respond differently to underlying environmental changes: (1) WD, which is part of the wood economics spectrum (Chave et al., 2009) and associated with drought and shade tolerance and with species successional stage; (2) leaf area (LA), which is part of the plant size spectrum (Díaz et al., 2015) and associated with light capture and convective cooling; (3) adult height (H) as a strategy to avoid crown fire, enhanced light exposure, and is linked with drought vulnerability (Rowland et al., 2015) and vulnerability to strong wind (Onoda & Anten, 2011); and (4) SM, which enhances establishment success in the dark forest understory (Grimme & Jeffrey, 1965) but reduces the number of seeds produced (Paul-Victor & Turnbull, 2009).

Wood density was obtained from the global WD database (Zanne et al., 2009) and previously collected data (van der Sande et al., 2016,

2017). LA (including all leaflets for species with compound leaves) and adult height were obtained from previously collected data and the Botanical Information and Ecology Network (BIEN) database (<http://bien.nceas.ucsb.edu/bien/>) using the BIEN package in R (Maitner et al., 2018). SM was obtained from the Seed Mass Database of Kew Royal Botanical Gardens (<http://data.kew.org/sid/>). For all traits, we only filtered data collected from the Neotropics.

Per tree genus present in the fossil pollen records, we calculated average trait values based on data from multiple species. These four traits generally show a strong significant phylogenetic signal (Coelho de Souza et al., 2016; van der Sande et al., 2019), indicating that species traits are generally similar to their genus-average or even family-average traits. For our dataset, the phylogenetic signal and the variation of species traits explained by genus was especially high for WD, H, and SM, and weaker but still significant for LA (Appendix S2). This uniformity suggests that within-genus variation in these traits is relatively small, and quantifying a genus-average trait value is meaningful. We only included genera in the calculation of community-mean trait values if we had data for at least three species of that genus or, for genera with less than nine species, data for at least one species in that genus. Despite the generally high phylogenetic signal, some genera contained species with widely different elevational distribution ranges, which can potentially result in strong differences in trait values among congeneric species. We therefore checked the within-genus variation by calculating the coefficient of variation (CV) per genus and per trait. We categorized our sites into elevation ranges: up to 1000 m asl for the lowland sites (Pata, Caranã, Kumpak, and Sauce), from 500 to 2000 m asl for the mid-elevation site (Pindo), and above 2000 m asl for the high-elevation sites (La Cocha, Llaviucu, and Condores). Where genera had a CV higher than 1 (i.e., the standard deviation was greater than the mean), we used elevational data from GBIF to eliminate species that occurred exclusively outside the elevation range of the given site from the calculation of genus-average trait values.

2.4 | Community-mean traits

We calculated the community-mean traits for each pollen sample, weighted by ln-transformed tree taxon abundance. We ln-transformed abundance of the taxa to reduce the weight of taxa with high pollen production, and we ln-transform the traits to reduce extreme values. Our previous study showed that the relationship between community-mean traits of forests and elevation was accurately captured by tropical pollen assemblages, both at the species level and genus level (van der Sande et al., 2020). This coherence creates opportunities for assessing the effect of environmental gradients (either spatial or temporal) on community-mean traits from pollen assemblages. It is possible that the absolute estimated community-mean trait value did not well represent the actual community-mean traits of the surrounding forest, as the abundance of pollen taxa did not reflect the abundance of plant species in the real vegetation. As demonstrated before (van der Sande et al., 2020), we foresee that this did not influence the outcomes of the current study as we focused on the direction of change (i.e., the standardized slope of the regression models). Hence, we here primarily focus on the direction of the slope of environmental effects on community-mean traits, and do not interpret the absolute values of community-mean traits. Similar approaches to assess changes in trait composition using fossil pollen records have been previously used for tropical forest (van der Sande et al., 2019) and temperate forest (Brussel et al., 2018).

On average per site, from the total tree pollen counts we had data on WD for 73%, on H for 80% on LA for 84% and on SM for 68%. We refer to community-weighted mean traits as “community” traits throughout the manuscript.

2.5 | Climate

To understand temporal changes in community traits, we included three climatic proxies, all derived from independent data sources. First, we included reconstructed mean annual precipitation values, based on published speleothem records (i.e., formations of mineral groundwater deposits in caves) of $\delta^{18}\text{O}$. The $\delta^{18}\text{O}$ records used are the nearest records to each of the sites that overlapped with the time window of each pollen records and had similar or higher temporal resolution. $\delta^{18}\text{O}$ values were multiplied by -1 so that high values indicate high precipitation, which facilitated interpretation of results. Second, we included reconstructed mean annual temperature variability based on the dataset published by Kaufman et al. (Kaufman, McKay, Routson, Erb, Dätwyler, et al., 2020). Kaufman et al. reconstructed global mean surface temperature anomalies of the last 12,000 years as the deviation from the mean temperature between 1800 and 1900. The reconstructions were based on the “Temperature 12k” database (Kaufman, McKay, Routson, Erb, Davis, et al., 2020) using five statistical approaches. Here, we used the published average estimation across the five approaches of temperature anomalies for time bins of 100 years. We used the data provided for

the southern tropics (0°S – 30°S). Third, as an indicator of extreme climatic disturbances, we used the frequency of El Niño events derived from lake Pallcacocha in western Ecuador (Moy et al., 2002). We used this dataset for all sites because El Niño events affect large parts of the Amazon and Andes with intense drought periods. Nevertheless, El Niño events are usually most severe in central Amazon and less severe in western Amazon and the Andes (Jiménez-Muñoz et al., 2016), and can even have slightly inversed effects (i.e., wetter conditions) in regions in Ecuador (Flantua et al., 2016). Indeed, for our Ecuadorian sites (Llaviucu, Pindo and Kumpak), the modern El Niño 3.4 index correlates weakly positively with precipitation, whereas it correlates negatively with precipitation for the other sites (Appendix S3). To take these inverse effects into account, we multiplied the El Niño frequency of the Ecuadorian sites (Pindo and Llaviucu) by -1 , so that high values would also indicate more drought stress. This transformation (data not shown) showed to be similar to the original results, and we therefore further only present the original results. The precipitation, temperature, and El Niño data were interpolated to the same years as the calibrated years BP from the pollen records, using the `na.approx` function of the `zoo` package in R (Grimme & Jeffrey, 1965). For information on the original resolution of the data, see Appendix S4.

2.6 | Fire activity

We used charcoal concentration as measure of fire activity, as high charcoal concentration could indicate the occurrence of spatially larger fires, multiple fires within the timespan of the sample, and/or severe fires with high amounts of biomass consumed (Gosling et al., 2019; Whitlock & Larsen, 2001). Hence, we use the term “fire activity” instead of fire intensity, severity or frequency, as we do not know which of these is the cause of high charcoal abundance. In many wet tropical forest ecosystems, fires do not naturally occur at high severity or frequency, and are therefore often considered a human disturbance (Gosling et al., 2022). However, discussion remains on the origin of fires in the tropics, and we therefore refer to them as “fire-related disturbance” in general.

Charcoal concentrations were quantified from the same records used for pollen analyses, although often at a higher temporal resolution. In case charcoal data were available at different sample depths than the pollen analyses, we used the charcoal sample that was used at the time equal or directly preceding the pollen sample, to assess short-term forest responses to fire. Methods of charcoal counting (e.g., charcoal particle-size range) differed between records and values cannot be compared directly. We therefore standardized the charcoal data in two ways. First, we used the approach proposed by McMichael et al. (2021), using their “proportional relative scaling” within each site, that is, as $(c_i - c_{\min}) / (c_{\max} - c_{\min})$, where c_i is the charcoal in the sample, c_{\min} is the minimum charcoal count in the record, and c_{\max} is the maximum charcoal count in the record. This value was then multiplied by the proportion of samples in the record with charcoal.

Second, we applied z-transformations within records by using the *scale* function in R, as also done for the other predictor variables. Results of these two approaches are very similar, and we therefore present the latter approach to apply a consistent scaling method for all our predictor variables. At the sites of Lake Pata and Lake Kumpak³, although charcoal was counted, almost none was found. For Lake Pata, this is consistent with an absence of human occupation (Nascimento et al., 2019).

2.7 | General disturbance

As a proxy of general disturbances, for example caused by land-use conversion by humans, landslides, or hurricanes, we used the proportion of *Cecropia* pollen relative to the pollen sum (including pollen that were not identified, identified to family level, and different life forms such as grasses). Although the average *Cecropia* abundance differs between sites, the genus is present in all sites and likely increases with disturbances in low- and high-elevation sites. Therefore, the within-site increases in the proportion of *Cecropia* pollen indicates increasing frequency, intensity, and/or extent of disturbances.

Cecropia is also included as one of the genera in the calculation of community-mean traits. Therefore, the effect of *Cecropia* abundance on community-mean traits may not be fully independent. To assess whether this influenced our results, we also ran the analyses described below using community-mean traits without *Cecropia*. The results are similar (Appendix S9) and we therefore present the community-mean traits based on all tree genera including *Cecropia*.

2.8 | Analyses

To assess the effect of reconstructed climate (precipitation, temperature, and El Niño frequency) and disturbance (fire activity and general vegetation disturbance) on temporal changes in tree trait composition, we used one linear mixed model per trait. Some of the predictor variables were derived using different laboratory techniques (e.g., the charcoal abundance was based on different charcoal size particles) or data sources (e.g., precipitation) among sites and could therefore not be compared in an absolute way. To remove such differences, we first scaled all variables per site, by subtracting the mean and dividing by the standard deviation, and then merged the data of the eight sites. In each model, we included reconstructed proxies for mean annual precipitation (i.e., $\delta^{18}\text{O}$ from stalagmites, multiplied by -1), mean annual temperature anomalies (Kaufman, McKay, Routson, Erb, Dätwyler, et al., 2020), El Niño frequencies (from Moy et al., 2002), fire activity (from charcoal data), and general vegetation disturbance (from *Cecropia* abundance) as standardized fixed predictor variables, site as random intercept, and year as random slope per site to account for repeated measures (i.e., temporal autocorrelation). To test how the effects of climate and disturbance on changes in trait composition depend on the

elevation of the site, we also included elevation and the interactions between elevation and all the other predictor variables. Note that the main effect of elevation cannot be significant as site differences have been removed by scaling the community-mean trait data within site. Nevertheless, there may be interactions between elevation and the other predictor variables, which is of our interest. Nonsignificant interaction effects were removed from the model. Hence, the final models included the main effects of the six fixed predictor variables (precipitation, temperature, El Niño, fire activity, general vegetation disturbance, and elevation) and a maximum of five interaction terms. We ran linear mixed models using the nlme package in R (Pinheiro & Bates, 2016).

To assess whether this overall model provides similar results to site-specific models, we also ran one generalized least square regression model per site per trait, including precipitation, temperature, El Niño frequency, fire activity, and general vegetation disturbance as fixed predictors. Furthermore, to account for potential temporal autocorrelation in the data, we included a temporal autocorrelation structure using the corCAR1 function, which is designed to deal with a continuous time covariate (Pinheiro & Bates, 2016). We standardized all response and predictor variables (by subtracting the mean and dividing by the standard deviation) prior to analyses so that we could compare effect sizes between models and sites. We ran generalized linear models using the gls function and the corCAR1 function from the nlme package in R (Pinheiro & Bates, 2016). For all analyses, R version 3.6.1 was used (R Core Team, 2019). Models based on a similar time window between sites of 2100 y gave similar results to using the maximum available time window per site (Appendix S5).

3 | RESULTS

We assessed how the community-mean tree traits (weighted by pollen abundance) changed with past climate (precipitation, temperature, and El Niño frequency) and disturbances (fire activity and general vegetation disturbances), and how these relationships varied with elevation. The most common tree genera in the pollen records were *Acalypha*, *Cecropia*, *Hedyosmum*, *Hypericum*, *Miconia*, *Podocarpus*, and *Weinmannia* in the high-elevation sites, *Cecropia* and *Miconia* in the mid-elevation site, and *Alchornea*, *Caesalpinia*, *Cecropia*, *Iriartea*, *Mauritia*, and *Trema* in the low-elevation sites (Appendix S6).

3.1 | Adult tree height

Precipitation increased community tree height, whereas temperature decreased height and El Niño frequency tended to decrease height (Figure 2a). The temperature effect, however, was positive at high elevations and negative at low elevations (Figure 3b). The effect of fire activity was negative at high elevations and tended to be positive at low elevations (Figure 3d), and the effect of disturbance was positive only at high elevations (Figure 3e).

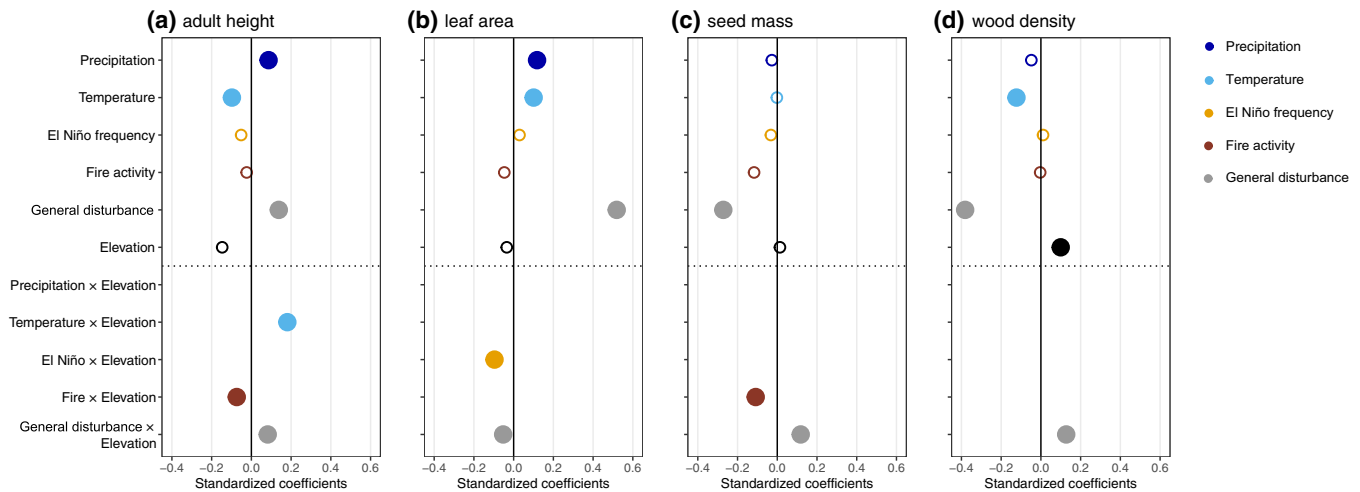


FIGURE 2 Standardized regression coefficients of the effect of environmental and disturbance variables on four community-mean functional traits: (a) adult height, (b) leaf area, (c) seed mass, and (d) wood density. Environmental variables are: mean annual precipitation (dark blue), mean annual temperature (light blue), El Niño frequency (yellow), fire activity (dark red), general disturbance (gray), elevation (black), and the interaction of elevation with the other five variables (below the dashed line). Large, filled dots represent significant ($p < .05$) effects and small, open dots represent nonsignificant effects. Nonsignificant interaction effects were excluded from the model and thus not shown here. See [Figure 3](#) for visualizations of the interaction effects.

3.2 | Leaf area

Precipitation, temperature, and general disturbance increased community LA ([Figure 2b](#)). The El Niño frequency decreased LA at high elevations and increased LA at low elevations ([Figure 3h](#)), and the disturbance effect is especially strong at low elevations ([Figure 3j](#)).

3.3 | Seed mass

General disturbance decreased community SM ([Figure 2c](#)). The negative effect of general disturbance ([Figure 3o](#)) on SM was strongest at low elevation. Fire activity decreased SM at high elevation but increased SM at low elevation ([Figure 3n](#)).

3.4 | Wood density

Temperature and general disturbance decreased WD ([Figure 2d](#)). This negative effect of general disturbance on WD was especially strong at low elevation ([Figure 3t](#)).

4 | DISCUSSION

We assessed how community tree trait composition across eight lowland and highland Neotropical forest sites relates to past climate change and disturbances. All four traits responded to these environmental variables, but the direction of effects often varied depending on elevation. Overall, the most important predictor was our measure for general vegetation disturbances, which increased

tree height and LA and reduced SM and WD across the lowland and highland sites. Temperature was the most important climatic predictor, leading to increased LA and tree height at high elevations, and to decreased WD and tree height at low elevations. Tree height and LA respond strongly to these drivers, whereas SM and WD respond more weakly. Here, we will first discuss the overall responses of tropical lowland and highland forests and then highlight some of the main site-specific differences.

4.1 | More favorable climatic growing conditions lead to more acquisitive trait values

We expected that, under benign conditions, there would be an increase in the abundance of taxa with acquisitive trait values that are associated with fast growth. Such benign conditions would occur with increased water availability (i.e., increased precipitation and decreased El Niño frequency), increased temperatures at high elevation because they prolong the growing season and reduce freezing-induced cavitation risk, and decreased temperatures at low elevation because they reduce evaporation and, hence, reduce atmospheric drought stress ([Table 1](#)). We indeed found that community-mean adult height and LA ([Figure 2a,b](#)) increased with precipitation, indicating that increased water availability allows for higher dominance of taller taxa with longer hydraulic path lengths (Bennett et al., 2015) and larger leaves with higher transpirational demand (Wright et al., 2017). Interestingly, WD was not affected by changes in precipitation, as we had earlier found for one of the sites (van der Sande et al., 2019). Perhaps increasing precipitation leads on the one hand to higher water availability and an advantage of drought-vulnerable, fast-growing species with soft wood, and on

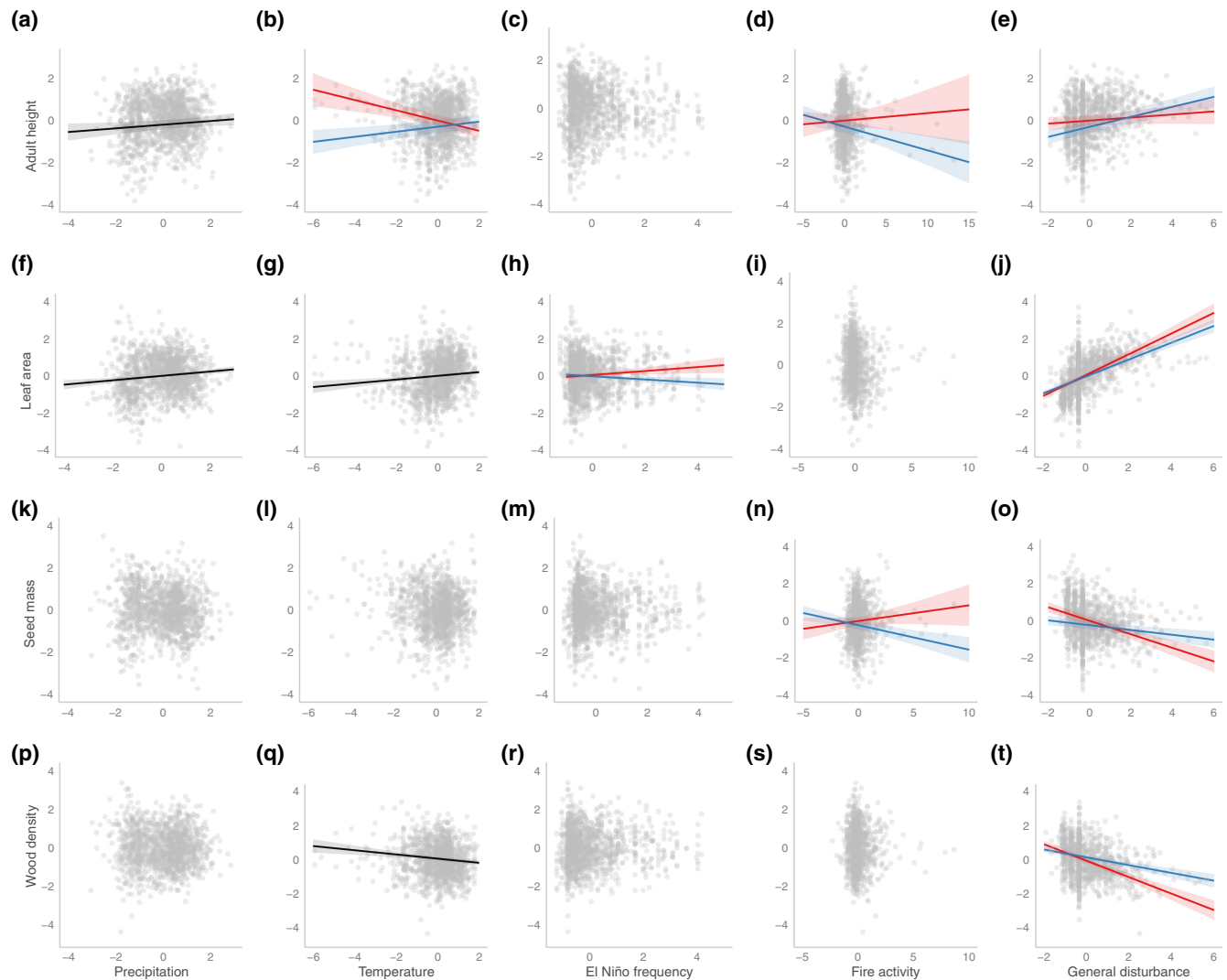


FIGURE 3 Visualizations of all relationships between the five environmental variables in columns (precipitation, temperature, El Niño frequency, fire activity, and general disturbance) and the four community-mean functional traits in rows [(a–e) adult height, (f–j) leaf area, (k–o) seed mass, and (p–t) wood density]. The relationships that showed a significant interaction with elevation (see Figure 2) are here visualized as two lines: low elevation (red, predicted for an elevation of 100m asl) and high elevation (blue, predicted for an elevation of 3000m asl). Significant relationships that did not show an interaction with elevation are visualized as one gray line. Nonsignificant relationships are shown without line. The axes represent the scaled axes (scaling was done per site, by subtracting the site's mean and dividing by the site's standard deviation).

the other hand to denser forests and an advantage of shade-tolerant species with dense wood (Markesteijn et al., 2011). These opposing effects could have canceled each other out. Therefore, nexus traits that relate to multiple aspects of plant functioning (e.g., WD relating to drought and shade tolerance) may provide less clear relationships when opposing forces are at play.

Community responses to temperature were stronger than responses to precipitation and El Niño frequency, as three of the four traits were significantly affected by temperature, and temperature had the largest effect sizes (Figure 2). We found that, at high and cold elevation, adult height increased during warmer times (i.e., with high temperature; Figure 3b, blue line). Tree height generally decreases from low to high elevation (Mao et al., 2018; Simard et al., 2011; van der Sande et al., 2020), and tree size is one of the

most important traits predicting species' position along elevation gradients (Maharjan et al., 2021). Hence, increased temperature probably results in less growth limitation and a longer growing season (Mao et al., 2018), which allows for an upslope range expansion of taller species. Such an upward movement of lowland forest species has been observed in Holocene pollen records (Flantua et al., 2014; González-Carranza et al., 2012) and also during current global warming (Fadrique et al., 2018; Feeley, Silman, et al., 2011; Woodall et al., 2013). However, at low and warm elevations, adult height decreased with further warming, probably because stronger vapor pressure deficits and associated atmospheric drought lead to increased mortality of large trees (Figure 3b, red line) (Aleixo et al., 2019; Bauman, Fortunel, Delhaye, et al., 2022), which have longer hydraulic pathlengths and are more drought sensitive.

In both lowland and highland forests, LA increased with temperature (Figures 2b and 3g), which may be determined by different mechanisms. In the lowlands, increased temperatures may increase tree mortality, resulting in more canopy gaps and more establishment opportunities of large-leaved pioneer species that can capture more light (Aleixo et al., 2019). In the highlands, however, higher temperatures reduce the risk of freezing, which may lead to a shift from species with small, dense, and coriaceous frost-tolerant leaves (Olson et al., 2018; Yang et al., 2020) to fast-growing species with large leaves.

High WD is associated with narrow vessels that increase tolerance to drought-induced and freezing-induced cavitation (Olson et al., 2018; Pittermann & Sperry, 2006; Yang et al., 2020), and with high resistance to wind (Putz et al., 1983). Dense-wooded species are therefore often found in dry areas and at higher elevations (Bruehlheide et al., 2018; Olson et al., 2018). At low elevations, we expected that increasing temperature would lead to higher transpirational demand and atmospheric drought stress, and therefore to a higher abundance of drought-tolerant, dense-wooded species. We found, however, a negative effect of temperature on WD, both in lowlands and highlands (Figures 2d and 3q). This does not agree with findings from Bauman, Fortunel, Cernusak, et al. (2022), who show that acquisitive species were more sensitive to negative climate effects on tree growth. This is possibly explained by higher mortality rates and gap formation, which would favor the establishment of fast-growing, soft-wooded, light-demanding species (Aleixo et al., 2019), or by an increased abundance of taxa with high metabolic rates and fast life cycles.

Hence, across these eight forest sites, wetter climates (i.e., higher precipitation, lower El Niño frequency) increased the abundance of more drought-sensitive taxa with long hydraulic path lengths (Koch et al., 2004; Stovall et al., 2019) and large leaves that can capture more light but rely on transpirational cooling (Wright et al., 2017). However, climatic warming has opposite effects along the elevation gradient, providing at high elevation more favorable conditions for taller taxa and at low elevations more favorable conditions for shorter taxa.

4.2 | Fires lead to more stress-adapted species, while general disturbances lead to more acquisitive species

Disturbances can either lead to more open conditions, favoring the establishment of fast-growing, light-demanding species that are tall and have soft wood and large leaves, or lead to more stressful conditions (due to fire damage, topsoil removal by erosion, and supra-optimal temperatures in open conditions), favoring slow-growing, short species with dense wood and small leaves. We found that adult height and SM decreased with fire activity at high elevation (suggesting more stressful conditions), but not at low elevation (Figure 3d,k). Small trees with a fast life cycle and small-seeded species that can quickly colonize burned areas have a relative advantage at high fire

activity. Although fires have been frequent and widespread in lowland tropical forests (Gosling et al., 2022) we found, surprisingly, no clear effect of fire on lowland trait composition. We can think of five possible explanations. First, the long-term fire history resulted in adapted ecosystems that no longer strongly respond to fire in terms of their species and trait composition. This would be especially the case in the drier, eastern part of the Amazon where fires have been more severe and frequent (Gosling et al., 2022). However, it is not very likely for the wet (western) tropical forests where fires have been less frequent and severe despite human intervention (Gosling et al., 2022) and fire-resistance traits such as thick bark are rare (Paine et al., 2010; Poorter et al., 2014; Rosell, 2016). Second, ecosystem responses to fire are quick and at very short temporal scales that cannot be accurately tracked using fossil pollen records. Third, fire frequency and severity show strong differences within a landscape (Jones & Tingley, 2022) due to variation in topography, humidity, and fuel load, and therefore show no clear ecosystem-scale effect. Fourth, fire was used as a tool mainly to manage agricultural land (Maezumi et al., 2018) and may have had little direct effect on the remaining, surrounding forest. And fifth, forests may respond more strongly to fire intensity (e.g., burn temperature) than to fire severity and frequency. New tools may allow to also assess the millennial-scale effects of fire intensity on tropical forests (Gosling et al., 2019; Maezumi et al., 2021).

We used *Cecropia* abundance as an indicator of a wide range of disturbances such as human-induced land conversion, landslides, or hurricanes that create temporal vegetation openness. Increased disturbances were related to increased LA (Figure 2), increased adult height at high elevations (Figure 3e), and decreased SM (Figure 3o), and WD (Figure 3f). These results indicate that such open conditions favor disturbance-adapted taxa that produce many small seeds to colonize disturbed sites, have large leaves to capture more light, and soft wood to attain fast height growth. We expected that the results would be weaker for highland forests, where part of the *Cecropia* pollen may have been blown in from downslope. However, we see similarly strong effects of disturbance on lowlands and highlands, indicating that general disturbances and the effects on functional trait composition can be well captured by *Cecropia* abundance. Our *Cecropia* proxy for general disturbances has stronger effects than fire activity on community traits, possibly because it better reflects and integrates different kinds of disturbance, and/or it indicates disturbances to which the forests respond clearly.

4.3 | Adult height and LA are most responsive to climate and disturbances

Adult height and LA are generally more responsive than WD and SM. Various reasons may explain these differences. The height of trees is strongly limited by water availability (Koch et al., 2004), and tree height is one of the best predictors of drought-induced tree mortality (McDowell & Allen, 2015; Stovall et al., 2019), explaining its strong response to climate and to the indirect climatic changes caused by

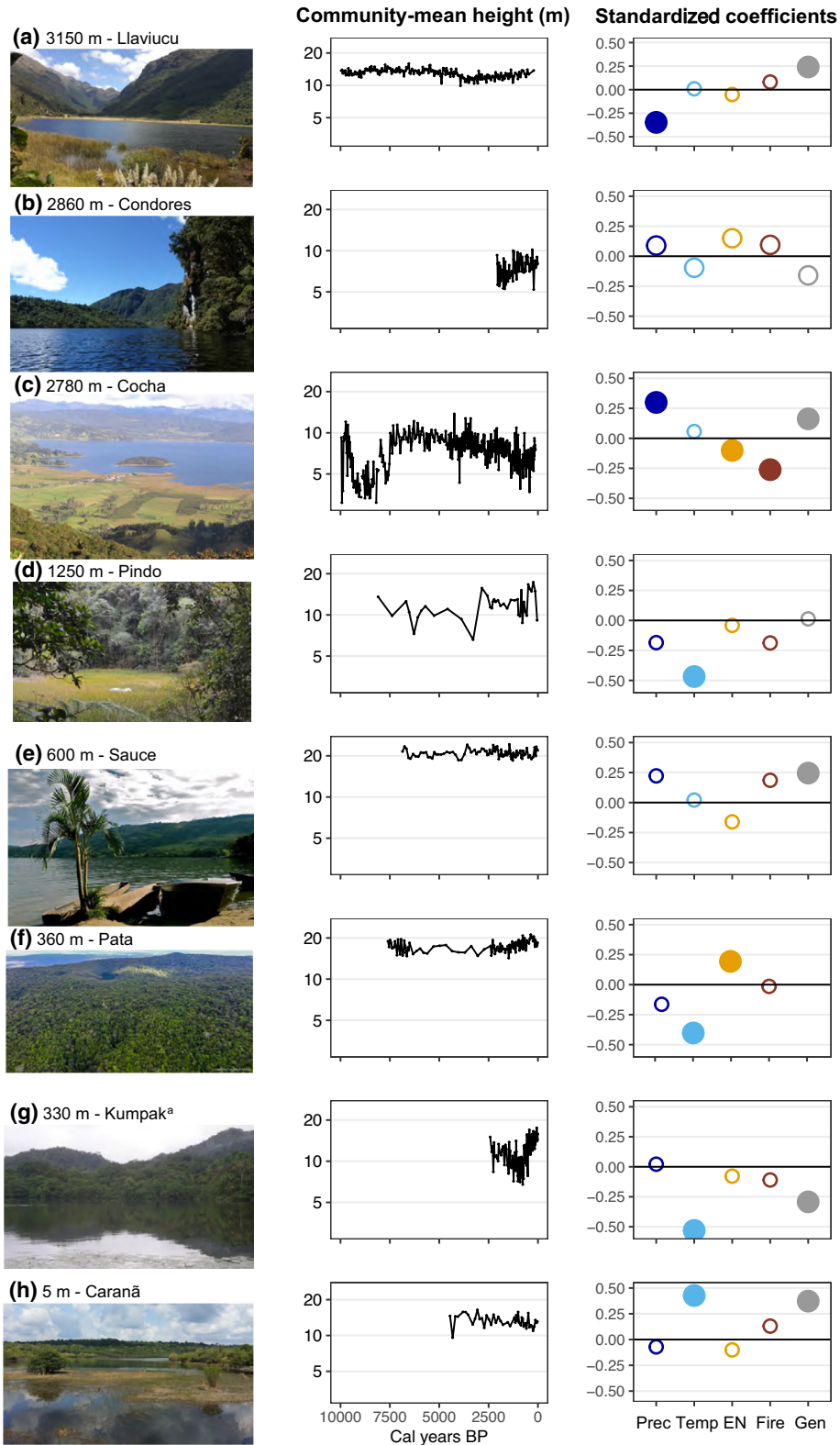


FIGURE 4 The eight sites [(a–h) same order as Figure 1 and Table 2] ordered from highest to lowest elevation, with a picture of the lake and the current vegetation (first column), the temporal changes in community-mean adult height (in meters) (second column), and the standardized regression coefficients of precipitation (Prec; dark blue), temperature (Temp; light blue), El Niño frequency (EN; yellow), fire activity (Fire; dark red) and general disturbance (Gen; gray) on community-mean adult height (third column). We here only show results for height for illustrative purposes. Filled circles represent significant effects and open circles represent nonsignificant effects. Note that the relationships tested (third column) do not test the effect of time. Photos are from R. Marcom (a), M. Bush (b), H. Hooghiemstra (c), E. Montoya (d), A. Sánchez Sierra (e), M. Nascimento (f), C. Akesson (g), and Y. Maezumi (h).

disturbances. The strong responses of LA are striking, given that LA is less strongly conserved within genera (Appendix S2) and, hence, more uncertainty arises when calculating community-mean traits based on genus-average data. WD, on the other hand, is associated with resistance to multiple environmental stressors, such as shade (Markesteijn et al., 2011), drought (Poorter & Markesteijn, 2008), and pathogens (Augsburger & Kelly, 2010). These multiple drivers of WD may have opposite effects and result in less clear temporal changes. SM is one of the main dimensions of global variation in plant traits (Díaz et al., 2015) as it influences reproduction, germination, and seedling survival, but it has no direct impact on adult trees, which most strongly determine the community trait composition. Our study shows that the long-term effects of climate change and disturbances are best captured by changes in traits related to plant and leaf size, rather than by WD and SM.

4.4 | Local disturbance histories determine local responses to climate and disturbances

Overall, 34% of the 156 relationships tested at the site level were significant (Appendix S7), which is similar to the cross-site analyses (35% significant). The strongest site-level drivers were temperature (significant for 47% of the relationships) and general disturbance (significant for 53%), and the directions of these site-level effects were generally similar to the cross-site effects; temperature and disturbance increased community-mean LA and decreased community-mean SM and WD, and temperature also decreased height (Figure 4; Appendices S7 and S8). This is in line with recent increases in abundances of lowland tree taxa across highland forests due to global warming (Fadrique et al., 2018). We found, however, that effects of El Niño frequency and fire activity varied strongly between sites, indicating that site-specific responses to some drivers are context dependent. Nearly all sites had some effects of El Niño and fire, but on different traits and in different directions (Appendix S8). This indicates that El Niño and fire events do impact the forest, but that effects can be opposite and local differences in, for example, soil conditions and seasonality may determine local-scale responses to these drivers. Specifically, the sites that show stronger El Niño effects (e.g., Cocha, Pata) are the sites in which El Niño probably causes strongest reduction in precipitation (Appendix S3). Our index for El Niño frequency is derived from one record for all sites, but the climatic effects of El Niño events can vary strongly across regions (Marengo et al., 2021). Furthermore, locally the degree of human influence during the last 10,000 years can vary strongly (Flantua et al., 2016; Piperno et al., 2015), and sites may respond at different rates, hence with different lag times, to fire. The lack of effects of El Niño and fire does not seem to be determined by weaker variation in these indicators (the CV of El Niño and fire was mostly not lower than the CV of other drivers). Hence, although temperature is a commonly strong driver of change across forests, certain forest ecosystems simply seem less responsive and more resilient to other types of changes (e.g., climate and disturbance events). Future studies are needed to assess how different disturbance regimes in the past influence forest resilience to future disturbances.

5 | CONCLUSIONS

During recent decades, forests have shifted in species and trait composition both in lowland (Enquist & Enquist, 2011; Fauset et al., 2012; van der Sande et al., 2016) and highland (Feeley, Silman, et al., 2011) tropical forests. The direction, speed, and causes of these changes, however, remain uncertain. Here we show on a time-scale of 10,000 years that tropical forests show strong responses to mean temperature and general disturbances; Warmer climates provide more favorable conditions for taller taxa with soft wood at high elevations and for smaller taxa with soft wood at low elevations, and disturbances favor disturbance-adapted taxa that are short with a fast life cycle and have small leaves to cope with increased heat and insolation in open areas. Especially traits related to the plant size spectrum (adult height and LA) showed strong responses to past climate and disturbances.

This study is the first to assess millennial-scale effects of environmental change on functional trait composition across Amazonian and Andean forests. Although we cannot predict absolute changes in functional composition based on pollen composition, future increases in temperature may lead to relative increases in soft-wooded species with large leaves, and relative increase in forest height in the highlands and relative decreases in forest height in the lowlands. These shifts in functional composition also imply shifts in biodiversity and ecosystem functioning, with potentially less carbon storage and sequestration in the lowlands but potentially more carbon sequestration in the highlands.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data underlying the analyses are publicly available via <https://doi.org/10.17026/dans-znr-nydh>.

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