



# Seed rain composition responds to climate change in a subtropical forest

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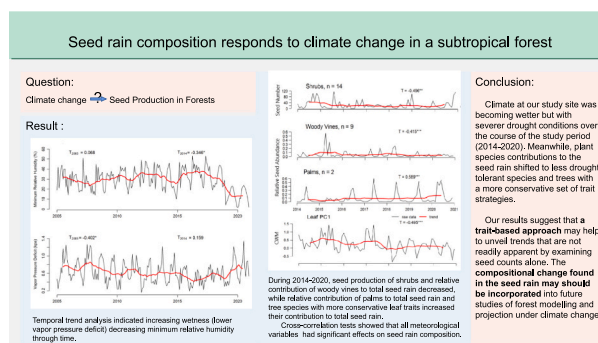
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## HIGHLIGHTS

- Vapor pressure deficit was decreasing during the 2005–2020 period.
- Minimum relative humidity was decreasing during the 2014–2020 period.
- Shrub seed production was decreasing.
- Relative contribution of woody vines and palms was decreasing and increasing, respectively.
- Tree species with conservative traits increased their contribution to seed rain.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Recent climate change has been shown to alter aspects of forest plant demography, such as growth and mortality, but less attention has been focused on how climate change alters the reproduction of plant populations through time. We hypothesized that the plant seed production would respond to climate change, and that the response would differ according to plant life form and functional traits. We tested this hypothesis by examining climate change from 2005 to 2020 and by determining the temporal trends of seed rain and seed production from plants with different life forms (e.g., herbs, vines, trees, palms) and of tree species with different statures as well as leaf, seed and wood traits during 2014–2020. We also tested the correlation between meteorological variables and time series of seed rain using cross correlation analysis. We found increasing wetness (lower vapor pressure deficit) through time but with decreasing minimum relative humidity, which is a pattern consistent with trends seen in many other parts of the world. During the study period, seed production of shrubs and relative contribution of woody vines to total seed rain decreased, while relative contribution of palms to total seed rain and tree species with more conservative leaf traits increased their contribution to total seed rain. Overall, these trends were well explained by the trends of meteorological variables and the responses of these life forms to climate change in previous studies. Additionally, the increasingly conservative leaf traits were also consistent with shifts in traits following recovery from disturbance. Our results suggest that a trait-based approach may help to unveil trends that are not readily apparent by examining seed counts alone. The compositional change found in the seed rain may indicate future shifts in forest species composition and should be incorporated into future studies of forest modelling and projections under climate change.

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## 1. Introduction

In recent decades, climate change, including a global increase in temperature and shifts in precipitation patterns towards more variable extremes, has caused dramatic changes to organisms and populations, communities and ecosystems (Lovejoy and Hannah, 2019; Pörtner et al., 2021). Forest communities and their ecosystem functions are strongly influenced by variation in climatic conditions (Currie and Paquin, 1987; Keil and Chase, 2019; Craven et al., 2020). As a consequence, climate change via changed temperature and precipitation regimes are likely to alter plant demography in forests worldwide, such as altered mortality and growth rates (van Mantgem et al., 2009; Feeley et al., 2011; da Costa et al., 2010, Hartmann et al., 2022). These altered demographic rates can in turn influence forest biodiversity and ecosystem functioning (Trumbore et al., 2015; Albrich et al., 2020; Forzieri et al., 2022). Although there has been moderate attention on altered mortality and growth during climate change, less attention has been paid to the impact of climate change on seed production in natural forests with most of these studies conducted in tropical forests (e.g., Wright and Calderón, 2006; Chang-Yang et al., 2016; Caignard et al., 2017; O'Brien et al., 2018; Zimmerman et al., 2018; Wright et al., 2021). Nevertheless, understanding how seed production is influenced by climate change is critical for the modelling, projection and conservation of forests worldwide.

Seed production is critical to population maintenance and forest regeneration (Martinez-Ramos and Soto-Castro, 1993). Seeds (and the fruits in which they are embedded) provide food for a wide range of seed predators and frugivores, including birds, insects and mammals (Kelly et al., 2008; Canham et al., 2014). Furthermore, seed production can have cascading effects on the population dynamics, diversity, and distributions of interacting species (Norden et al., 2007a, 2007b; Canham et al., 2014; Piotta et al., 2019). Seed production is influenced by multiple factors that vary in space and time, including resources, interacting species (e.g., pollinators, seed predators), and climatic conditions (Kelly and Sork, 2002; Fenner and Thompson, 2005). Changing temperature and precipitation during climate change can alter seed production in different directions via multiple pathways. For example, longitudinal studies of seed production have shown that some species increase flower and seed production with increasing temperature and drought (Wright and Calderón, 2006; Caignard et al., 2017; Wright et al., 2021), while others decrease seed production (Zimmerman et al., 2018; Wright et al., 2021). Likewise, plants in regions with increasing precipitation due to climate change may have increased reproductive output (Chapman et al., 2005).

Plants of different life forms can vary in their response to climate change, and trees might be expected to be the most affected by climate change. This is because the metabolism of large canopy trees may be affected by changing climates due to exposure of their crown to heavy heat and drought stress from direct sunlight (Bin et al., 2022), which could directly influence their ability to produce seeds. Furthermore, larger trees tend to be less drought tolerant than smaller ones when the climate warms and dries (Zhou et al., 2013; Bennett et al., 2015). In contrast, herbs and shrubs in the understory may be less affected by changing climates since they grow under relatively mild environmental conditions created by the crowns of overstory tree species (Bin et al., 2022). Likewise, woody vines may experience a relative advantage under hotter and drier conditions because they are typically more drought tolerant than trees (Schnitzer, 2005; Schnitzer and Bongers, 2011).

As trees are key components of forests, their functional traits may provide insight into the overall temporal trends of seed production. In tropical and subtropical forests, in recent decades, there has been a trend towards increasing abundance of smaller-statured species and of species with increased photosynthetic rates, specific leaf areas and hydraulic conductivity in recent decades (Feeley et al., 2011; Zhou et al., 2014; Li et al., 2015; Tymen et al., 2016). However, it is less known that how

these and other temporal trends are related to trends in seed production during climate change.

We examined temporal trends of climate change at the Dinghushan Nature Reserve, a subtropical forest in the Guangdong province of China, and related them to 6 years of seed rain data from a 20 ha forest plot. Climate change was observed in the Dinghushan region in an analysis of data from 1950 to 2009 (Zhou et al., 2011). Specifically, total soil moisture declined and the rainfall pattern has shifted towards increased seasonality (more heavy rains in the wet season, more dry events in the dry season) since around 1980 (Zhou et al., 2011). This pattern of climate change is consistent with the trends in many parts of the world (Easterling et al., 2000; Ummenhofer and Meehl, 2017), and it is projected to continue into the foreseeable future (IPCC, 2019). We examined climate trends in the Dinghushan region and compared them to temporal trends for total seed rain, as well as the seed production of tree species with different life forms and functional traits. If the climate trends continued towards drier and more variable levels of precipitation, we might expect a trend towards increasing relative abundances of lianas and smaller-sized species but a decreasing trend for trees with shifts in their functional traits. However, it is also possible that the climate change trends in the region shifted more recently towards wetter and/or less variable precipitation patterns, which might be expected to shift the production and composition of seeds in the opposite direction.

## 2. Materials and methods

### 2.1. Study site and meteorological variables

The Dinghushan (DHS) Nature Reserve (112°30'39" - 112°33'41"E, 23°09'21" - 23°11'30"N, Guangdong province, China) is characterized by a south-subtropical monsoon climate, with a mean annual temperature of 20.9 °C and a mean annual precipitation of 1929 mm. The climax vegetation for this nature reserve is subtropical monsoon evergreen broadleaved forest with a forest canopy height of ~30 m.

To capture the trends of extreme climate conditions, we obtained maximum air temperature (°C), minimum relative humidity (%) and maximum wind speed ( $\text{m}\cdot\text{s}^{-1}$ ) for each month during 2005 to 2018 from Science Data Bank (Liu et al., 2020) and from 2019 to 2020 from Dinghushan Forest Ecosystem Research Station (<http://dhf.cern.ac.cn/>). We calculated vapor pressure deficit from the average air temperature (T) and average relative humidity (RH); hence, vapor pressure deficit was calculated to indicate average conditions. The saturated vapor pressure (SVP), in unit of kpa, can be calculated as  $\text{SVP} = 0.6108 \times e^{17.27T/(T + 237.3)}$ , where T is the temperature (°C) and vapor pressure deficit =  $(100 - \text{RH})/100 \times \text{SVP}$  (He et al., 2022). Vapor pressure deficit was the difference between saturated vapor pressure and the actual vapor pressure. That is, increased temperature or the decreased relative humidity result in increased vapor pressure deficit, indicating a drier condition.

### 2.2. The 20 ha forest plot and seed rain collection

In 2005, we set up a 20 ha plot (400 m × 500 m) in the Dinghushan nature reserve. Following Condit (1998), all stems with a diameter at breast height (DBH)  $\geq 1$  cm in the plot were mapped, tagged, measured and identified to species. The first census of the plot found 71,617 individuals of 210 species (119 genera, 56 families). Fagaceae, Theaceae, Juglandaceae and Lauraceae were the dominant families in the plot (Ye et al., 2008; Bin et al., 2019).

In 2008, 149 seed traps were established in the plot. Seed traps were 0.7 m × 0.7 m with a 1 mm mesh bag suspended ~0.7 m from the ground with a polyvinyl chloride (PVC) frame and were arranged along the trails in the plot. Seeds were collected from each trap twice a month from October 2008 to December 2020 (we did not collect data from December 2012 to October 2013 due to logistical constraints) (Bin et al., 2019). We identified and enumerated the collected seeds and fruits to

the species level, and determined whether each seed or fruit was mature (filled, Wright and Calderón, 2006). When seeds were contained within fruits, we estimated the average number of seeds per fruit by dissecting 20 fruits per species and multiplying the number of fruits by the average number of seeds per fruit (Bin et al., 2019). For our analyses, we only considered mature seeds and fruits, since only they can germinate and contribute to the population. Seeds were categorized into six groups including herbs, herbaceous vines, woody vines, shrubs, trees and palms. Palms included an independently standing species and a rattan. Plant species in all groups except palms are dicotyledons.

### 2.3. Tree functional traits and their community-weighted means

We compiled published data measured in this plot on several functional traits for 33/36 of the tree species in this study (Shen et al., 2013; Bin et al., 2019; Bin et al., 2022). These 36 species accounted for 99.5 % of the total seeds of tree species we collected from 2014 to 2020. The remaining species without trait data were excluded from this analysis. Specifically, we used data on leaf traits (leaf area, leaf thickness, leaf density, leaf dry matter content, and specific leaf area), wood density, seed mass and maximum DBH. Leaf traits and wood density were measured using the standard methods of Cornelissen et al. (2003) (Shen et al., 2013; Bin et al., 2022). Seed mass data were obtained by weighing seed samples after drying them at 80 °C for 72 h, or they were taken from the literature (Bin et al., 2019). Maximum diameters of tree species were derived from the plot censuses.

The traits we used represent different aspects of the plant's life-history. Specifically, leaf-traits are related to vegetative growth, seed mass is related to reproduction, wood density is related to the tree's structural support and maximum diameter is related to species' size and drought tolerance (Zhou et al., 2013; Bennett et al., 2015). For leaf traits, we first log-transformed leaf area and specific leaf area to reduce the skewness and then standardized (subtracted by mean and divided by standard deviation) all leaf traits to extract the principal components (PC). We took the score of the leaf PC1 to denote leaf characteristics of the species in the seed rain. It explained 63.7 % of the total variance in leaf traits and was positively loaded by leaf area (0.446) and specific leaf area (0.537) and negatively by leaf density (−0.545) and leaf dry matter content (−0.464). Thus, small values of leaf PC1 denote more conservative strategies. In addition, lower seed mass indicates strong colonization ability by both long-distance dispersal and a high fecundity (Bin et al., 2019) and lower wood density indicates high hydrological conductance (Larjavaara and Muller-Landau, 2010). In general, large leaf PC1, lower seed mass, and lower wood density are associated with pioneer species whereas the opposite traits are associated with late successional species (Poorter, 2009; Poorter et al., 2010). Additionally, maximum diameter may influence drought tolerance in a way that smaller-statured trees are generally more drought-tolerant (Zhou et al., 2013; Bennett et al., 2015).

To evaluate temporal trends in the functional composition of species in the seed rain, we calculated a community weighted mean (CWM) for each of the functional traits (leaf PC1, wood density and seed mass) individually for the monthly records of the seed rain (Garnier et al., 2004). CWM was calculated as

$$CWM = \sum_{i=1}^n p_i T_i \quad (1)$$

where  $p_i$  and  $T_i$  are the relative abundance and the mean trait value of species  $i$  collected in the plot within a month, respectively.

### 2.4. Temporal trends of meteorological variables and seed rain

We examined temporal trends across the time series for the following: (1) each of the meteorological variables; (2) different aspects of seed production, including the total number of seeds of all species,

total and relative abundances of seeds from species of different life forms (tree, shrub, woody vine, herbaceous vine, herb, palm), and community weighted means of leaf PC1, wood density, seed mass and maximum diameter for tree species in the seed rain.

For each time series, we decomposed data into trend, seasonal, and random components (Kendall and Stuart, 1983; Mutanga et al., 2013). This process first determines the trend component using a moving average, computes the seasonal component by averaging each month's data across all periods, and then determines the error component by removing the trend and seasonal components from the original time series. We performed this decomposition using the *decompose* function in R 4.1.2 (R core team, 2021).

After decomposing the time series, we extracted the trend component and tested whether there was a significantly monotonic (decreasing or increasing) trend using Mann-Kendall tests (Mann, 1945; Kamal and Pachauri, 2018) with 1000 bootstrap simulations. We computed Mann-Kendall tests using the *notrend\_test* function in the *funtimes* package on the R platform (Lyubchich et al., 2022).

For the seed data, we include only data from January 2014 to December 2020. For the meteorological data, we used these tests for the whole time series as well as only from 2014 to 2020, which corresponded to the time period for which continuous seed data were available.

### 2.5. Seed production in relation to meteorological variables

We tested how seed production was related to meteorological variables using cross-correlation analysis (Brockwell and Davis, 1991; Wright and Calderón, 2006; Zimmerman et al., 2018). We correlated the trend components of seed rain time series (including total seed production, seed production for each life form in both absolute number and relative abundance, and community weighted means for leaf traits, seed mass, wood density, and maximum DBH for tree species in the seed rain) with the meteorological variables after removing seasonality with lags of 0 to 12 months.

## 3. Results

### 3.1. Temporal trends of meteorological variables

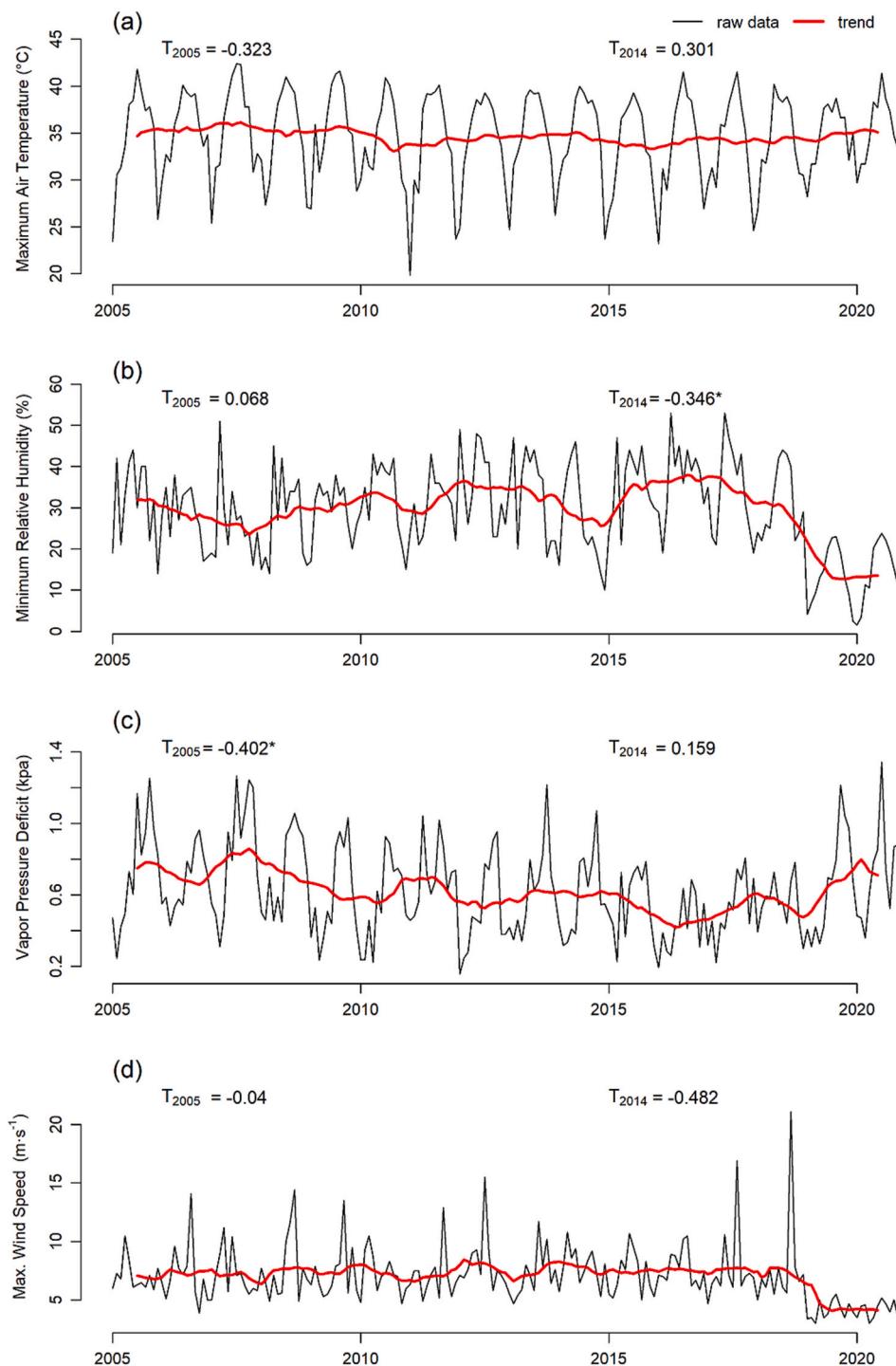
We found no trends in air temperature and maximum wind speed during either the 2005–2020 or the 2014–2020 periods (Fig. 1a, d). There were decreasing trends for minimum relative humidity from 2014 to 2020 and for vapor pressure deficit from 2005 to 2020 (Fig. 1b, c).

### 3.2. Temporal trends of seed rain

Over the six complete years of our study (2014–2020), we collected 56,992 seeds, resulting in a seed rain density of 130.1 m<sup>-1</sup>y<sup>-1</sup>. These seeds belong to 68 species, including two herbs, 14 vines, 14 shrubs, 36 trees and 2 palms. Among the 14 vines, five are herbaceous and nine are woody (lianas).

We found no significant temporal trend for total seed number during the study periods (Fig. 2a), but we did detect some trends in both the absolute number (Fig. 2b-g) and relative abundance (Fig. 3) of seeds from species with different life forms. Specifically, for herbs, herbaceous vines and trees, there were no changes in the absolute number and relative abundances of seeds over the time period (Figs. 2, 3). Shrubs decreased in absolute seed number but showed no trends in relative seed abundance in the study period (Figs. 2d, 3c). On the contrary, woody vines showed no trends in absolute seed number (Fig. 2e) but decreased in relative abundance over the study period (Fig. 3d). Finally, palms had no trends in absolute abundance (Fig. 2g), but increased in relative abundance over the study period (Fig. 3f).

For the analysis of trends of tree species seed production with different traits, we found that the community weighted mean of the leaf



**Fig. 1.** Temporal trends for meteorological variables during 2005–2020: maximum air temperature (a); minimum relative humidity (b); vapor pressure deficit (c); maximum wind speed (d). Temporal trends for the whole period (2005–2020) and since the year of the start of seed collection (2014–2020) were tested using Mann-Kendall test with 1000 bootstrap simulations. The T statistics was given on top of each panel, labeled with the starting years. Codes for significance: \*:  $p < 0.05$ ; \*\*:  $0.05 \leq p < 0.01$ ; \*\*\*:  $0.01 \leq p < 0.001$ .

PC1 decreased through time during the study period (Fig. 4a). We found no significant trends for the community weighted means of wood density (Fig. 4b), seed mass (Fig. 4c) or maximum DBH (Fig. 4d) during either time period.

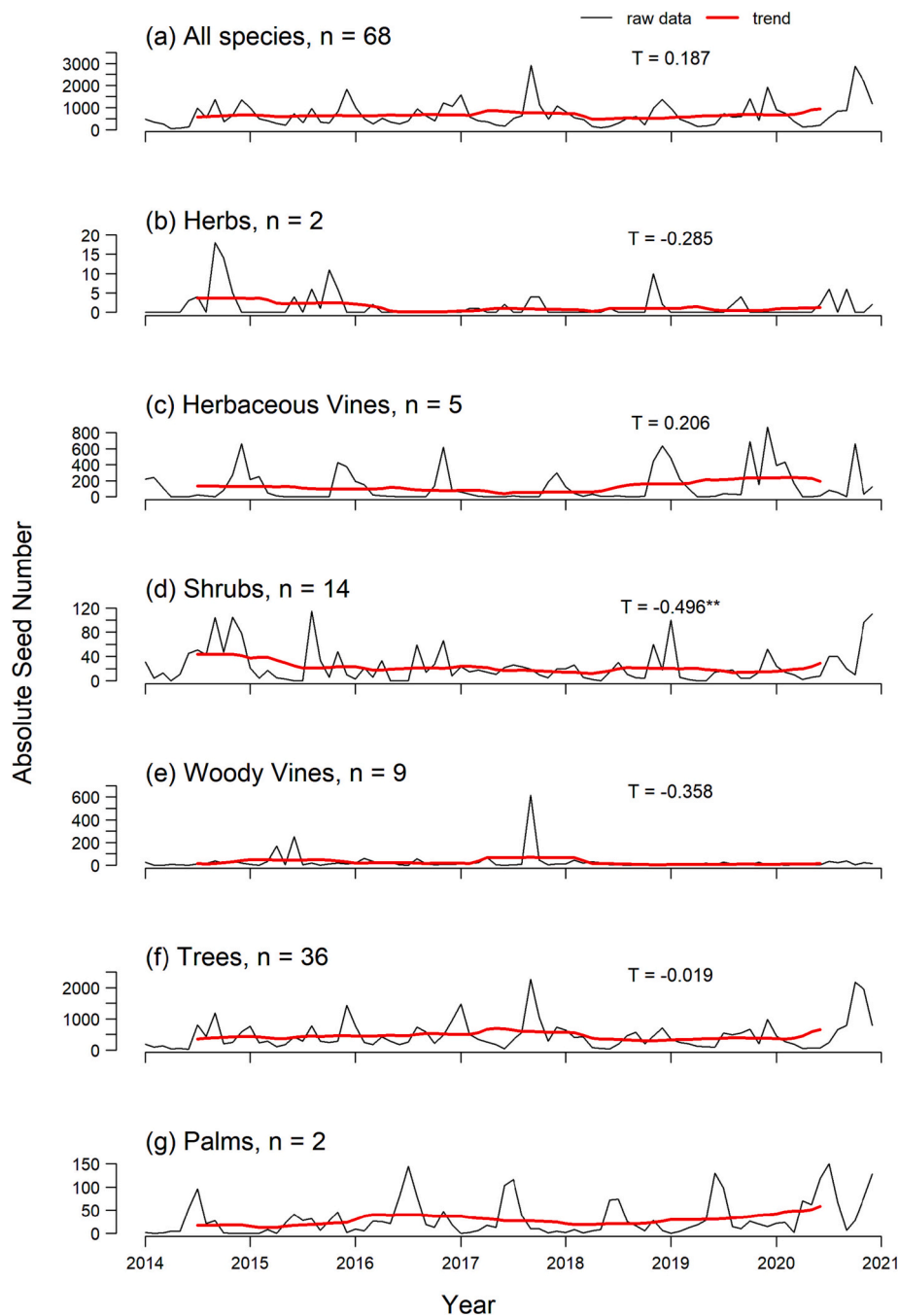
### 3.3. Seed production in relation to meteorological variables

We found that total seed production increased with maximum wind speed and minimum relative humidity but decreased with vapor pressure deficit during the study period (Figs. 5–8).

When we analyzed data for the different life forms, we found that the relationship of absolute seed number of a life form with a meteorological

variable seldom contradicted the corresponding relationship of relative abundance, i.e. both absolute number and relative abundance of seeds of trees were positively associated with maximum wind speed (though at different lags; Figs. 5–8). Eleven of 68 (16.2 %) relationships between time series of seed rain and meteorological variables were positive at some lags and negative at other lags (Figs. 5–8). Seven of these relationships were with minimum relative humidity (Figs. 5–8).

Seed production of palms and herbaceous vines showed similar relationships with meteorological variables. They both were associated negatively with maximum wind speed and positively with vapor pressure deficit, while other life forms (herbs, shrubs, trees and woody vines), in general, exhibited the opposite relationships with these two



**Fig. 2.** Temporal trends for absolute number of seeds of all species (a) and different life forms (b-h). The number of species (n) included in each life form was given on top of each panel. Temporal trends during 2014–2020 were tested using Mann-Kendall test with 1000 bootstrap simulations. The T statistics was given on top of each panel. Codes for significance: \*:  $p < 0.05$ ; \*\*:  $0.05 \leq p < 0.01$ ; \*\*\*:  $0.01 \leq p < 0.001$ .

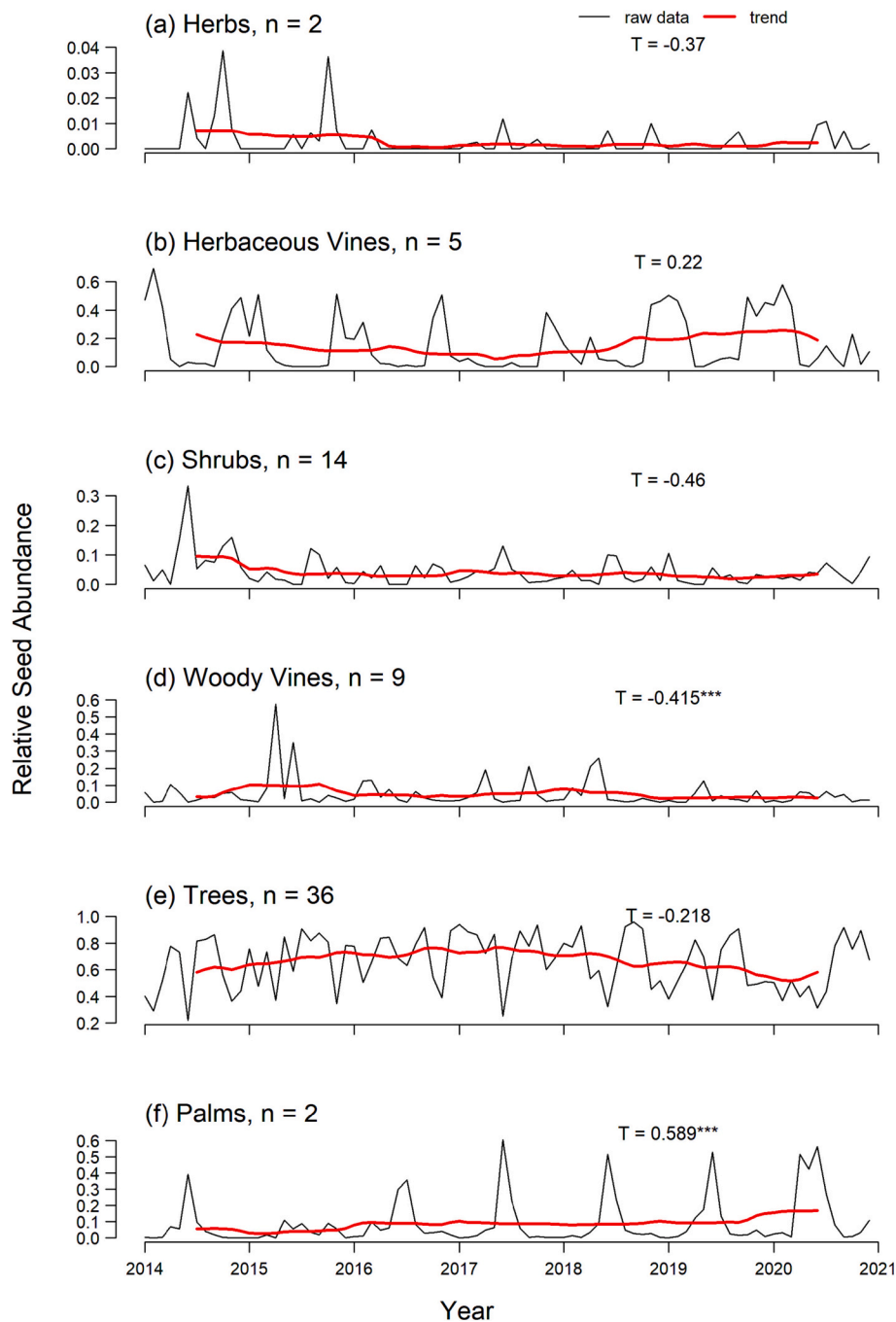
meteorological variables (Figs. 6, 8).

Maximum air temperature was negatively associated with seed production of shrubs, herbs and woody vines in terms of either absolute number (shrub) or relative abundance (woody vines) or both (herbs) (Fig. 5 b, d, h, k). On the contrary, the relationship was positive between maximum air temperature and the relative abundance of seeds of palms (Fig. 5 m). Seed production of trees and traits of tree species in the seed rain were not significantly associated with maximum air temperature (Fig. 5 f, i, n-q).

Maximum wind speed was positively associated with relative seed abundance of woody vines, absolute seed number of shrubs, absolute number and relative abundance of seeds of herbs and trees and negatively associated with absolute number and relative abundance of seeds

of palms and herbaceous vines (Fig. 6 b-d, f-i, k-m). Regarding traits of tree species in the seed rain, maximum wind speed had a positive relationship with community-weighted means of leaf PC1 and wood density, and it was negatively associated with maximum DBH (Fig. 6 n, o, q). The relationship of maximum wind speed with absolute seed number of woody vines was positive at lags of 0–4 and 5–13 months but negative at lags of 21–24 months (Fig. 6 e).

As mentioned above, seven of the relationships with minimum relative humidity were positive at some lags and negative at other lags (Fig. 7 c, e, f, i, l o, q). These relationships of minimum relative humidity were with absolute seed number of woody vines, absolute number and relative abundance of herbs and trees, and community-weighted means of maximum DBH and wood density (Fig. 7 c, e, f, i, l o, q). Besides these,



**Fig. 3.** Temporal trends for relative abundance of seeds of different life forms (a-g). The number of species (n) included in each life forms were given on top of each panel. Temporal trends during 2014–2020 were tested using Mann-Kendall test with 1000 bootstrap simulations. The T statistics was given on top of each panel. Codes for significance: \*:  $p < 0.05$ ; \*\*:  $0.05 \leq p < 0.01$ ; \*\*\*:  $0.01 \leq p < 0.001$ .

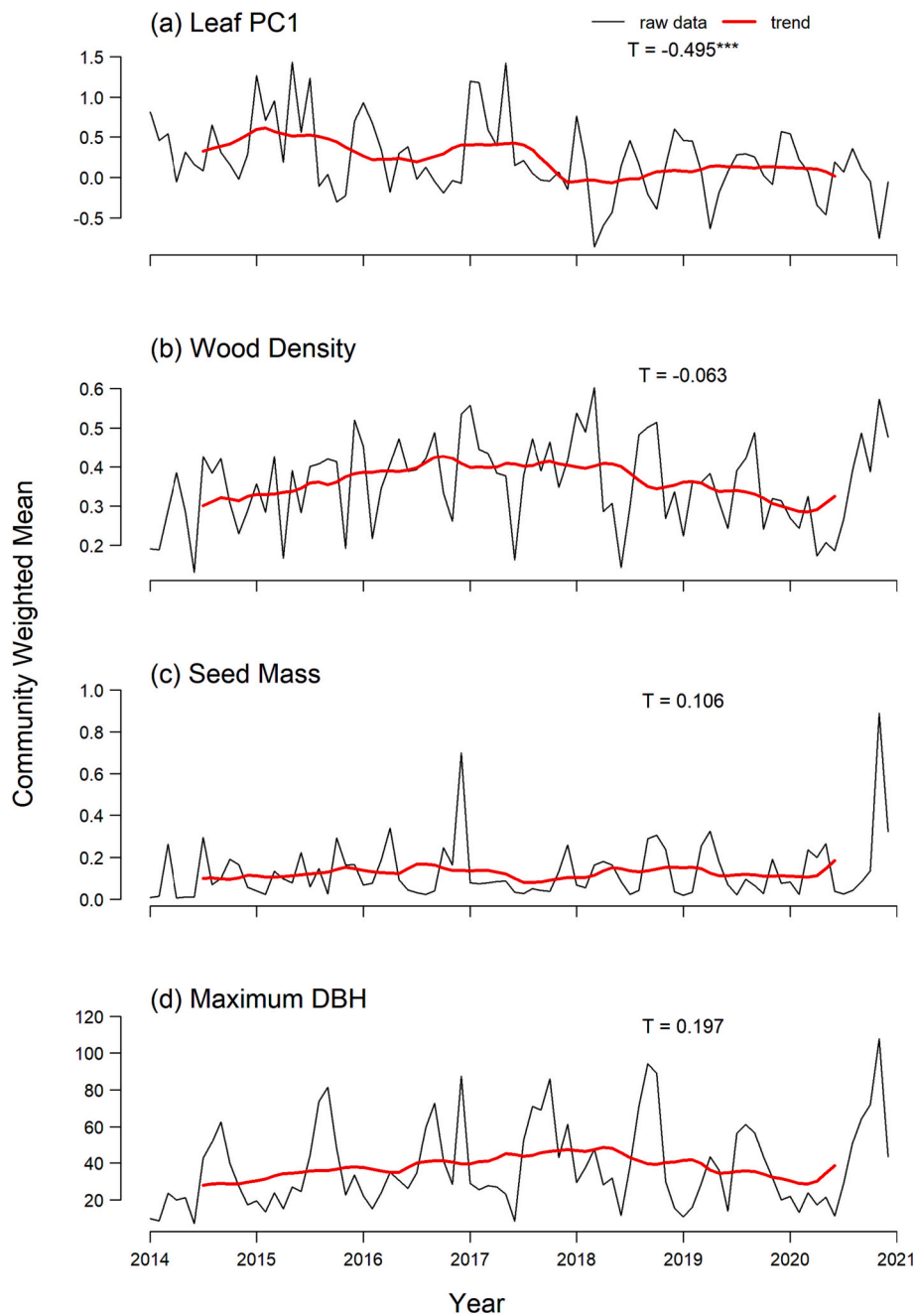
minimum relative humidity was positively associated with relative abundance of seeds of woody vines and absolute number and relative abundance of herbs and shrubs and negatively associated with absolute number and relative abundance of palms (Fig. 7 k, b, d, g, h, j, m). Community-weighted means of leaf PC1 were also positively associated with minimum relative humidity (Fig. 7 n).

Vapor pressure deficit was positively associated with the relative abundance of seeds of palms and absolute number and relative abundance of herbaceous vines (Fig. 8 c, m, i). In contrast, herbs, shrubs, trees and woody vines were negatively associated with vapor pressure deficit in terms of both absolute number and relative abundance (Fig. 8 b, d-f, h, j-l). Community weighted means of leaf PC1 had a negative relationship

with vapor pressure deficit, but those of seed mass, maximum DBH and wood density were associated with vapor pressure deficit positively at some lags but negatively at other lags (Fig. 8 n-q).

#### 4. Discussion

It is now well documented that climate change is leading to altered demographic rates such as mortality and growth in forests worldwide (van Mantgem et al., 2009; da Costa et al., 2010). However, how plants of different life forms and with different traits respond to climate change in terms of their reproductive output is less well known (Chang-Yang et al., 2016; O'Brien et al., 2018; Zimmerman et al., 2018). Here, we

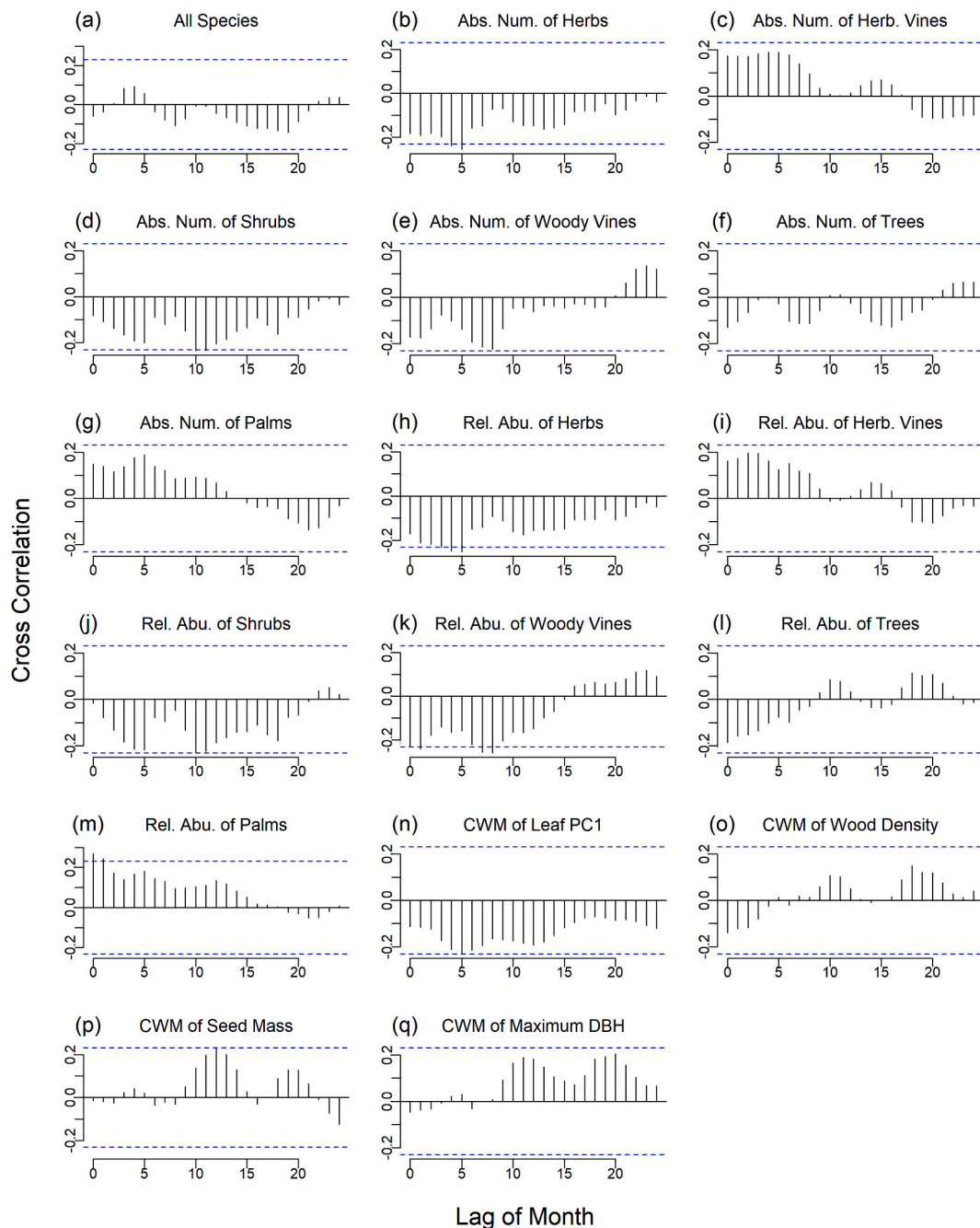


**Fig. 4.** The temporal trend for the community weighted mean (CWM) of traits for the tree species in the seed rain. Temporal trends during 2014–2020 periods were tested using Mann-Kendall test with 1000 bootstrap simulations. The T statistics is given on top of each panel. Codes for significance: \*:  $p < 0.05$ ; \*\*:  $0.05 \leq p < 0.01$ ; \*\*\*:  $0.01 \leq p < 0.001$ .

used a data set spanning 6 years of monitoring changes in climate and seed rain of plant species in the Dinghushan subtropical forest in China to show a general trend towards increased wetness (decreasing vapor pressure deficit calculated using average humidity and air temperature) but more extreme climate conditions (decreasing minimum relative humidity). In response, there were shifts in the absolute and relative abundances of seeds of species with different life forms and of tree species with different leaf, seed, wood and stature traits. In all, our results help to identify which species are influenced by climate change in terms of their seed production, and they can help to predict future structural change in the forest because these seeds provide the basis for forest regeneration.

We found shifts in the absolute number or relative abundance of seeds through time for many groups of species, including declining

trends of shrubs and woody vines and an increasing trend of palms, suggesting potential changes in composition of the forest in the future. Seeds of herbs, shrubs, trees and woody vines were negatively correlated with vapor pressure deficit calculated based on average air temperature and relative humidity, meaning that they produce more seeds in wetter climates. On the other hand, herbaceous vines and palms produce fewer seeds in wetter climate. As a result, the wetting of the climate (declining vapor pressure deficit) over the course of our study led to a reduction of the contribution of shrubs and woody vines and an increase of palms to the overall seed rain. Although a previous study found that smaller statured species including shrubs increased through time in tropical and subtropical China (Zhou et al., 2014), appearing to give a qualitatively different result than ours, the mechanism leading to this change is likely the same. Specifically, due to increased drought tolerance for shrubs and



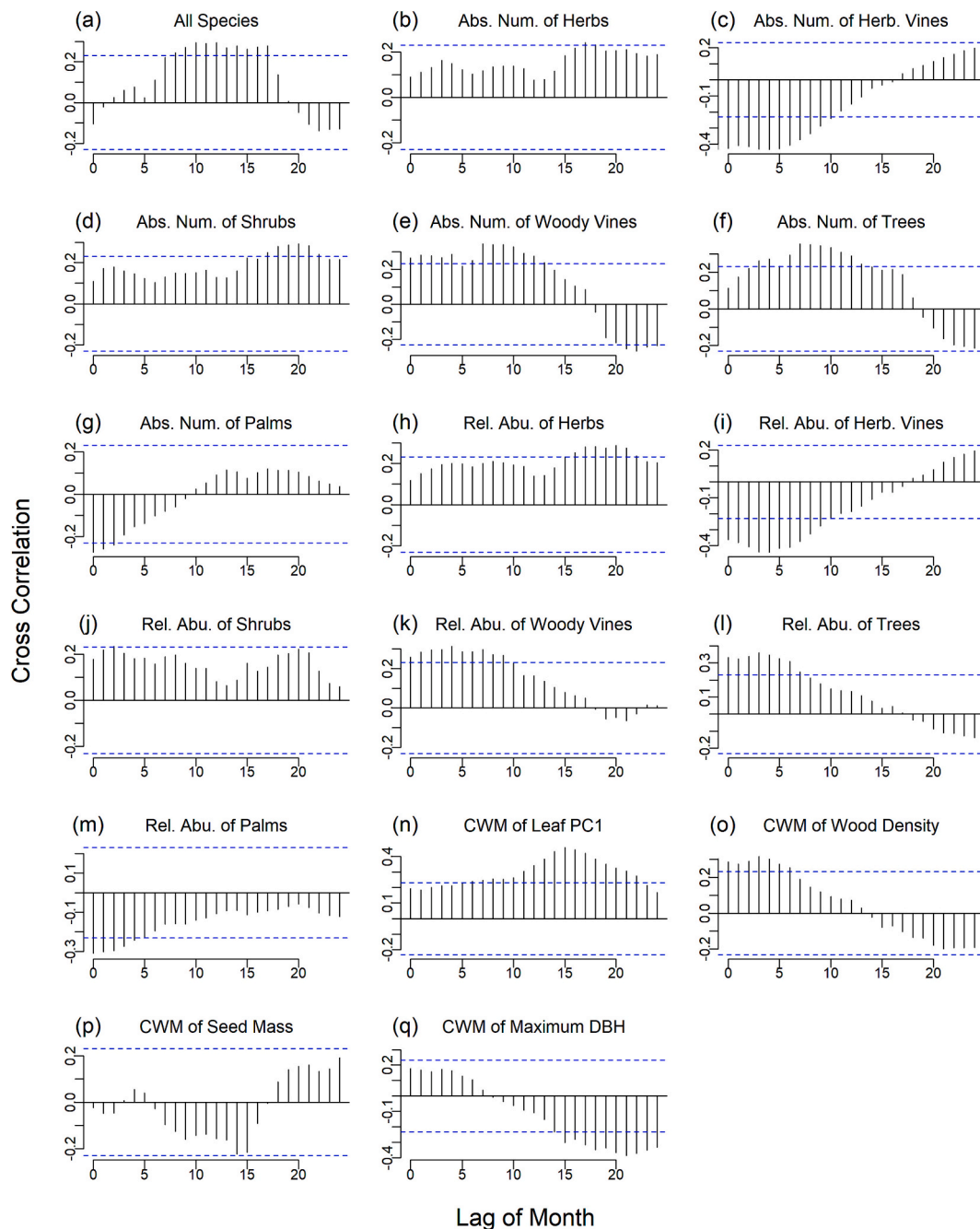
**Fig. 5.** Cross correlation tests for the relationships between maximum air temperature and time series of seed rain. Vertical segments showed the values of the cross correlation index. Two horizontal dash lines showed the 95 % confidence interval for zero correlation so any vertical segments exceeding the horizontal lines along either the positive or negative direction indicate significant relationships. Abs: Absolute; Num: Number; Rel: Relative; Abu: Abundance.

a drier climate during 1978–2012, Zhou et al. (2013, 2014) found increasing trends for shrubs. Our study was consistent in that we found a reversal towards a wetter climate at our study site and a consequent decrease of shrubs and woody vines either in terms of absolute number or relative abundance in the seed rain. The relationships were positive between minimum relative humidity and total seed production, seed production of shrubs and herbs as well as their contribution to the total seed rain, suggesting that milder climate conditions are also beneficial to their reproduction. In addition to changing climates, it is also possible that shifts in the contributions of different life forms to the seed rain could be influenced by recovery from previous disturbances. For example, following disturbance understory cover decreases considerably as the tree canopy recovers (Long and Turner, 1975; Lindh, 1994).

In our study site, the reduction in number and relative abundance of seeds of shrubs could have partly resulted from canopy closure during succession.

A decreasing trend was detected for the contribution of seeds from woody vines to the overall seed rain during our study period, which was characterized by a wetter climate as indicated by decreasing vapor pressure deficit. This result is consistent with some studies that found decreasing woody vine abundance through time (Bongers et al., 2020). However, increasing biomass and abundance of woody vines have been observed in many tropical and subtropical regions (Schnitzer, 2005, 2018; Swaine and Grace, 2007; Schnitzer and Bongers, 2011; Pandian and Parthasarathy, 2016), which is often attributed to the drier environments and the increased drought-tolerance of woody vines (O'Brien





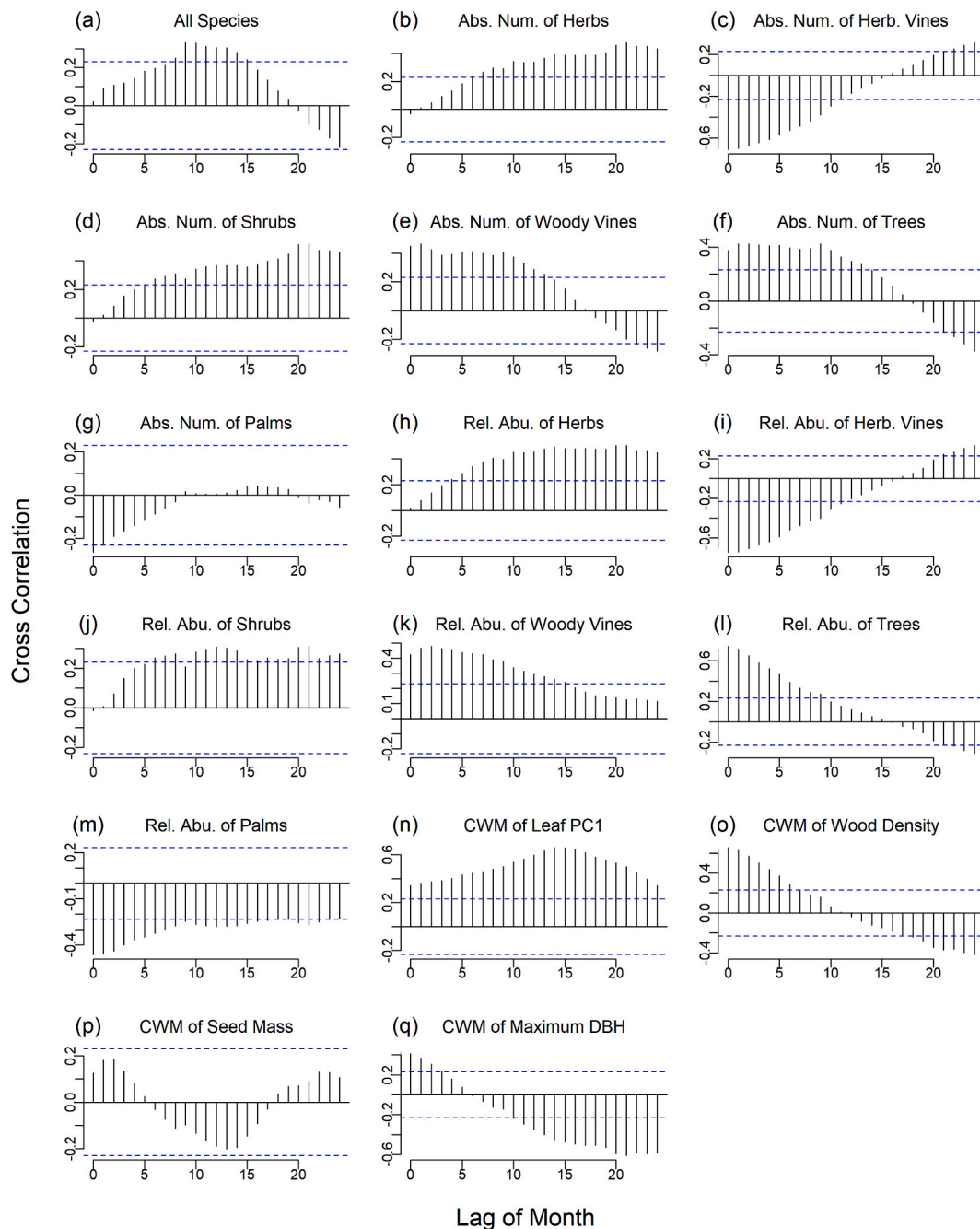
**Fig. 6.** Cross correlation tests for the relationships between maximum wind speed and time series of seed rain. Vertical segments showed the values of the cross correlation index. Two horizontal dash lines showed the 95 % confidence interval for zero correlation so any vertical segments exceeding the horizontal lines along either the positive or negative direction indicate significant relationships. Abs: Absolute; Num: Number; Rel: Relative; Abu: Abundance.

et al., 2018). For the same reason, a wetter climate can drive the reverse trend, as observed in our study. However, we also found negative correlations between woody vine seed production and vapor pressure deficit, indicating that wetter environments promote seed production of woody vines, which contradicted our observation of trends of woody vines in a wetter climate but are consistent with studies that found woody vines being favored in wetter sites (Kusumoto et al., 2008; Bin et al., 2022). The relationship of the relative contribution of woody vines to total seed production with minimum relative humidity was positive, indicating that milder environments are beneficial to the reproduction of woody vines. However, the relationship of seed production of woody vines with minimum relative humidity was positive and negative at different lags. Thus the relationships between climate conditions and

woody vine seed production are complex. Seed rain monitoring combined with aboveground vegetation census of woody vines should contribute to a better understanding of the dynamics of woody vines in our study forest.

The increasing trends we found for relative abundance of palm seeds in the seed rain during the study period are consistent with their positive correlation with wetter environments (lower vapor pressure deficit). This relationship is expected given that most palms are distributed in humid areas across the tropics and subtropics (Fernandes, 1994).

In our study, community-weighted mean of leaf PC1 decreased through time in the seed rain. This suggests that species with more conservative strategies increased over the time period, which is consistent with succession or recovery from disturbance in forests (Poorter

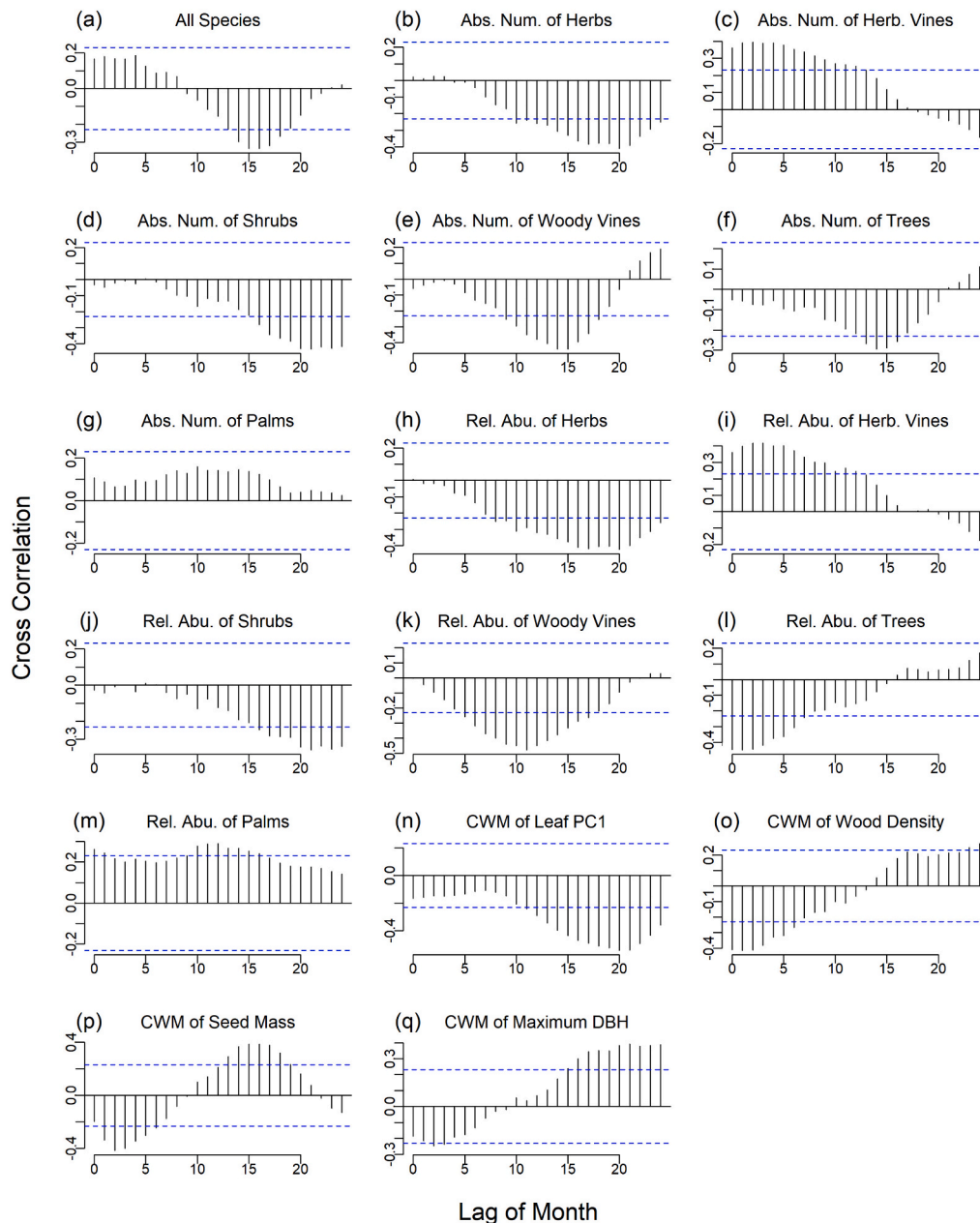


**Fig. 7.** Cross correlation tests for the relationships between minimum relative humidity and time series of seed rain. Vertical segments showed the values of the cross correlation index. Two horizontal dash lines showed the 95 % confidence interval for zero correlation so any vertical segments exceeding the horizontal lines along either the positive or negative direction indicate significant relationships. Abs: Absolute; Num: Number; Rel: Relative; Abu: Abundance.

et al., 2004; Buzzard et al., 2016) where large-seeded, shade tolerant, slow-growing species tend to increase in abundance (Poorter, 2009; Poorter et al., 2010; Bin et al., 2019). Indeed, between 2005 and 2010, censuses of the Dinghushan forest dynamic plot found mortality rates were more than double those in some old growth forests (Shen et al., 2013). It is possible that the death of trees created gaps that caused some of these shifts in species composition through succession or recovery. The decreased leaf PC1 might not be explained by the wetter climate trend, as cross correlation analysis suggested increasing leaf PC1 for wetter climate. Previous studies showed that within species, leaf size, increased with precipitation and wetness (Castro-Díez et al., 1997; Stropp et al., 2017). In our study, leaf PC1 is positively related to leaf size, therefore, increasing leaf PC1 for wetter climate is consistent with

these previous studies (Castro-Díez et al., 1997; Stropp et al., 2017). These studies, together with the positive relationship of leaf PC1 with vapor pressure deficit found in our study, implied that a drier climate might lead to communities with more conservative strategies. This result is in contrast to a study that found increasing specific leaf area in the Dinghushan nature reserve during 1978–2010 when soil moisture strongly declined (Zhou et al., 2011; Li et al., 2015), but it is consistent with leaf morphological change due to heat and drought stress, for example, leaf size, specific leaf area tend to be reduced and leaf density, leaf thickness and leaf dry matter content tend to be increased with height from the ground (Bin et al., 2022; Kenzo et al., 2015).

Although maximum air temperature and maximum wind speed did not show significant trend during the study period, cross correlation



**Fig. 8.** Cross correlation tests for the relationships between vapor pressure deficit and time series of seed rain. Vertical segments showed the values of the cross correlation index. Two horizontal dash lines showed the 95 % confidence interval for zero correlation so any vertical segments exceeding the horizontal lines along either the positive or negative direction indicate significant relationships. Abs: Absolute; Num: Number; Rel: Relative; Abu: Abundance.

tests indicate that increasing maximum air temperature and maximum wind speed, which are expected to occur due to warming in the long run (IPCC, 2019), are likely to alter total seed rain as well as seed production of all life forms and their relative contribution to the total seed rain.

In conclusion, our study showed that the climate at our study site is becoming wetter but with periods of severe drought over the course of the study period (2014–2020). Meanwhile, plant species contribution to the seed rain shifted to less drought tolerant species and trees with a more conservative set of trait strategies. Some of these patterns are consistent with succession and recovery from disturbance, while others were well explained by the temporal trends of meteorological variables. Our study contributes to a better understanding of forests' response to climate change in terms of reproduction and the conservation of species diversity in subtropical forests.

#### CRediT authorship contribution statement

YB, and ZH designed the study. ZH identified the species in the seed rain. HC identified the species in the 20 ha plot. YB, ZH, HC and JL conducted fieldwork. JL organized the field census data and the seed rain data. YB analyzed the data. YB wrote the first draft. YB and JL revised the manuscript. All authors contributed substantially to the interpretation of the results.

#### Declaration of competing interest

The authors declare that they have no conflict of interest.

#### Data availability

Data will be made available on request.

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