Received: 27 August 2019 | Revised: 31 January 2020 | Accepted: 17 March 2020

DOI: 10.1111/btp.12801

ORIGINAL ARTICLE

biotropica ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

Climatic sensitivity of species' vegetative and reproductive phenology in a Hawaiian montane wet forest

Stephanie Pau[1] | Susan Cordell[2] | Rebecca Ostertag[3] | Faith Inman[2] | Lawren Sack[4]

[1]Department of Geography, Florida State University, Tallahassee, FL, USA

[2]Institute of Pacific Islands Forestry, Pacific Southwest Research Station, USDA Forest Service, Hilo, HI, USA

[3]Department of Biology, University of Hawai'i at Hilo, Hilo, Hawai'i, USA

[4]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA

Correspondence
Stephanie Pau, Department of Geography, Florida State University, Tallahassee, FL, USA.
Email: spau@fsu.edu

Funding information
NSF, Grant/Award Number: 0546784; NSF EPSCoR, Grant/Award Number: 0554657 and 0903833; National Geographic Society, Grant/Award Number: WW-235R-17; EPSCoR, Grant/Award Number: 0554657 and 0903833; Forest Service; University of Hawai'i; University of California, Grant/Award Number: 0546784

Associate Editor: Ferry Slik
Handling Editor: Norbert Kunert

Abstract

Understanding how tropical tree phenology (i.e., the timing and amount of seed and leaf production) responds to climate is vital for predicting how climate change may alter ecological functioning of tropical forests. We examined the effects of temperature, rainfall, and photosynthetically active radiation (PAR) on seed phenology of four dominant species and community-level leaf phenology in a montane wet forest on the island of Hawai'i using monthly data collected over ~ 6 years. We expected that species phenologies would be better explained by variation in temperature and PAR than rainfall because rainfall at this site is not limiting. The best-fit model for all four species included temperature, rainfall, and PAR. For three species, including two foundational species of Hawaiian forests (*Acacia koa* and *Metrosideros polymorpha*), seed production declined with increasing maximum temperatures and increased with rainfall. Relationships with PAR were the most variable across all four species. Community-level leaf litterfall decreased with minimum temperatures, increased with rainfall, and showed a peak at PAR of ~ 400 $\mu mol/m^2 s^{-1}$. There was considerable variation in monthly seed and leaf production not explained by climatic factors, and there was some evidence for a mediating effect of daylength. Thus, the impact of future climate change on this forest will depend on how climate change interacts with other factors such as daylength, biotic, and/or evolutionary constraints. Our results nonetheless provide insight into how climate change may affect different species in unique ways with potential consequences for shifts in species distributions and community composition.

KEYWORDS

climate change, Hawaiian Islands, Laupāhoehoe Forest Dynamics Plot, leaf production, seed production, tropical forest

© 2020 The Association for Tropical Biology and Conservation

1 | INTRODUCTION

In the tropics, the growing season is potentially year-round and there is remarkable diversity in patterns of tropical flowering (Newstrom, Frankie, Baker, & Newstrom, 1994; Sakai, 2001), seed and leaf production (Frankie, Baker, & Opler, 1974; Leishman, Wright, Moles, & Westoby, 2000; Mendoza et al., 2018; Reich, 1995). Seasonal changes in temperate regions are more pronounced than in the tropics. Thus, temperate phenological sensitivities to climate change are easier to identify (Cook et al., 2012; Newstrom et al., 1994; Pau et al., 2011). Unlike the mounting evidence from temperate regions for "spring advancement," *that is*, the earlier occurrence of first bud burst and flowering due to warming temperatures, there is little information on changes in tropical plant phenology in response to climate change (Abernethy, Bush, Forget, Mendoza, & Morellato, 2018; Cook et al., 2012; Menzel et al., 2006). Instead, tropical plant phenology has been hypothesized to be more closely tied to biotic factors such as pollinator abundance or competition for resources rather than seasonal changes in climate (Pau et al., 2011). Yet underlying selective forces and proximate factors that cue phenological events often interact and can be difficult to separate (Rathcke & Lacey, 1985; van Schaik, Terborgh, & Wright, 1993). Phenological cues are usually consistent changes in the abiotic environment, which then trigger physiological processes controlling flower, fruit, or leaf production (van Schaik et al., 1993).

Research on tropical plant phenology—both leaf and reproductive phenology—has focused on changes in rainfall, particularly in seasonally dry habitats (Borchert, 1994; Frankie et al., 1974; Lieberman, 1982; Reich, 1995; Sakai & Kitajima, 2019; Wright, 1991; Zimmerman, Wright, Calderón, Pagan, & Paton, 2007). A comprehensive review of Neotropical phenology studies showed that 74.3% of studies examined rainfall as a climatic driver of fruiting phenology, whereas only 19.3% and 3.2% of studies examined air temperature or solar radiation/photoperiod, respectively (Mendoza, Peres, & Morellato, 2017). Many tropical and subtropical regions experience a dry season associated with the seasonal movement of the Intertropical Convergence Zone (ITCZ). Although the dry season results in seasonal water deficits, there are also often fewer clouds, allowing greater light interception by the canopy (but see Philippon, Cornu, Monteil, Gond, & Moron, 2019). Both experiments and observational data in tropical forests across multiple continents show that greater light availability is associated with greater community-level flower, fruit, and leaf production (Chapman, Valenta, Bonnell, Brown, & Chapman, 2018; Graham, Mulkey, Kitajima, Phillips, & Wright, 2003; Morellato et al., 2000; Pau et al., 2013; Wright & Calderón, 2006; Zimmerman et al., 2007). In Panama, flowering times for ten species was predicted by increases in solar irradiance, and of the 19 total species examined, none were explained by the timing and intensity of rainfall (Wright & Calderón, 2018).

Although temperature has not received as much attention as an abiotic driver of tropical plant phenology, temperature is a fundamental constraint on numerous biological processes (Kingsolver, 2009). Tropical species may be adapted to a narrower range of temperatures and may be living closer to their upper thermal limits (Janzen, 1988; Tewksbury, Huey, & Deutsch, 2008; Wright, Muller-Landau, & Schipper, 2009). Seasonal flowering patterns were related to temperature at two tropical sites with long-term data (Pau et al., 2013). In a lowland moist seasonal forest in Panama and a montane ever-wet forest in Puerto Rico, greater flowering occurred in warmer months (Wright & Calderón, 2006). Few physiological experiments have examined the temperature sensitivity of tropical reproduction, but reproductive organs are known to be highly sensitive to temperature (Larcher & Winter, 1981; Slot & Winter, 2016). It is unclear if tropical leaf phenology is also sensitive to temperature fluctuations, but both leafing and flowering in the Brazilian Atlantic forest is tied to seasonal changes in temperature and daylength (Morellato et al., 2000).

The Hawaiian flora provides unique insight into the ecology and evolution of plant diversity and is considered a model system due to its isolation, endemism and the relative simplicity of its processes due to low species diversity (Price & Wagner, 2004; Sakai, Wagner, Ferguson, & Herbst, 1995; Wagner & Funk, 1995). Yet there are few published studies on the reproductive phenology of Hawaiian forests (e.g., Berlin, Pratt, Simon, & Kowalsky, 2000; Drake, 1992; van Riper III, 1980). More work has examined monthly leaf litterfall, yet these studies have generally focused on leaf litter's role in nutrient cycling and contributions to aboveground net primary productivity (e.g., Austin, 2002; Raich, 1998; Schuur & Matson, 2001; Vitousek, Gerrish, Turner, Walker, & Mueller-dombois, 1995), not seasonality and responses to climatic variability. This lack of understanding limits our knowledge of how climate change may alter Hawaiian forest phenology and associated ecosystem functions. Hawaiian forests have lower tree diversity, but are structurally similar to other continental tropical forests (Ostertag, Inman-Narahari, Cordell, Giardina, & Sack, 2014) with tropical phenological strategies represented. Their extreme isolation in the Pacific makes them a unique signal for climate change impacts on ecological communities, unlike forests such as the Amazon, which experience large local feedbacks between the canopy and atmosphere (Kooperman et al., 2018), complicating the climate signal. In this study, we examine monthly seed production of the four dominant tree species and community-wide leaf litterfall from a montane wet forest on the Island of Hawai'i. We expect that species phenologies will be better explained and more sensitive (i.e., magnitude of response) to variation in temperature and PAR than rainfall because rainfall at this site is not limiting, and that some species will be more sensitive to climatic variation than others.

2 | METHODS

2.1 | Study site, phenology, and climate data

The Laupāhoehoe Forest Dynamic Plot (FDP; 19°55′N, 155°17′W), part of the Forest Global Earth Observatory (ForestGEO) network (https://forestgeo.si.edu/), is a montane wet forest at 1,120 m in elevation on the Island of Hawai'i. The forest includes 18 woody flowering tree species,

3 tree fern species, and the vegetation is highly representative of montane wet forests in Hawai'i (see Ostertag et al., 2014 for detailed site information). Mean annual precipitation is 3,440 mm, and mean annual temperature is 16°C based on long-term island-wide extrapolation of climate records over a 30-year period (Giambelluca *et al.* 2013).

To monitor reproductive and leaf phenology, sixty-four litter traps within a 4-hectare plot were placed in a regular grid, 10-meters apart, and monitored as part of the Hawai'i Permanent Plot Network (HIPPNET). Reproductive (fruit and seeds) and leaf litterfall were censused each month following standard protocol (Wright, Muller-Landau, Calderón, & Hernandéz, 2005). Fruits and seeds were identified to species and converted to number of seeds for each fruit. Leaf litterfall, for all species combined, was weighed to the nearest 0.1 grams. Sixty-five months of fruit/seed data were available between the months of October 2009 to March 2018 (with occasional missing collections between 2009 and 2014, only part of 2015 and 2017 collected, and none of 2016 collected; a full 12-month record was only available for two years prohibiting year-to-year models; see Figure S1). Thirty-two months of community leaf litterfall data were available. Because some collections could only be attributed to a month and year, leaf litterfall rates (e.g., $g/m^2\ day^{-1}$) could not be determined accurately.

The climate station at Laupāhoehoe FDP was established in 2009 is maintained by HIPPNET and record daily temperature (° C; HMP45C-L, Vaisala), rainfall (mm; tipping bucket rain gauge; TB3 CS700, Hydrological Services), and photosynthetically active radiation (PAR; $\mu mol/sm^{-2}$; Quantum sensor). All climate data were aggregated to monthly averages except for rainfall, which was summed each month.

Of the 21 plant species present at Laupāhoehoe, 12 were present at least once in the litter baskets and 4 dominant species were ultimately examined (in order of abundance): *Metrosideros polymorpha* ('ōhi'a lehua; bird or insect pollinated, wind dispersed, Myrtaceae), *Acacia koa* (koa; insect pollinated, wind dispersed, Fabaceae), *Coprosma rhynchocarpa* (pilo; wind pollinated, bird dispersed, Rubiaceae), and *Cheirodendron trigynum* ('ōlapa; bird or insect pollinated, bird dispersed, Araliaceae). These four dominant species account for 57.5% of the total number of trees and 52.7% of the total basal area of the Laupāhoehoe FDP and were the trees that reached canopy and sub-canopy levels (Ostertag et al., 2014). The other 8 species occurred too infrequently in the litter traps for statistical analysis. For these four species, as well as for leaf litterfall, circular histograms were created showing the average seed production or leaf litterfall each month to visualize monthly seasonality.

2.2 | Statistical analyses

The coefficient of variation (CV) across months was calculated each year, using only years where all twelve months were represented, for seed production and leaf litterfall. To examine relationships between seed production (counts) and leaf litterfall (grams) with climatic factors, we used generalized additive mixed models (GAMMs) to estimate flexible, potentially non-linear smoothing functions to predictors and response variables (for mathematical descriptions see Venables & Ripley 1999; Wood 2006; Zuur, Ieno, Walker, Saveliev, & Smith, 2009; Polansky & Boesch, 2013; Polansky & Robbins, 2013). We used a Poisson log-link likelihood for seed production and a Gaussian log-link likelihood for leaf litterfall. We estimated response curves (i.e., "smooth terms") using cubic regression splines for the climatic predictors—temperature, rainfall, and PAR—as well as for "month" (to account for monthly seasonality independent from climatic seasonality) and "time," which was a variable of sequential months from the first census (to account for any long-term trend, which is not the focus of this study). We included "trap" as a random effect to account for spatial variation among traps and non-independence within traps. Rainfall was log-transformed because a few large values resulted in a skewed distribution. We also included daylength as a predictor, but large (>0.80) concurvity values (i.e., a generalization of collinearity for smooth terms in GAMs) limited accurate interpretation (see Supporting Information; Figure S2 and S3, Table S1). Because time-series data are often non-independent, we accounted for serial autocorrelation in the error term using an AR(1), that is, an autoregressive term of 1 month. Model residuals were examined and showed no significant autocorrelation. Seed production was modeled separately for each species using concurrent monthly climate data because fruit maturation, dispersal, and germination should be timed to climate (van Schaik et al., 1993). Leaf litterfall, however, is not as clearly associated with climate as leaf production might be. Thus, leaf litterfall was examined using collection dates lagged one month prior to collection (when leaves had not yet fallen and are still on the canopy). A one-month lag resulted in higher Pearson correlation coefficients than a two- or three-month lag.

Because phenology may be linked to climatic extremes (Butt et al., 2015), we compared the statistical responses of seed production and leaf litterfall to minimum and maximum temperatures in addition to mean temperatures using the corrected Akaike Information Criterion (AICc) (Burnham & Anderson, 2010). AICc indicates the likelihood of the data given the model, penalizing for the number of additional parameters in the model. After choosing which temperature metric bestfit the data, we compared the full model—including all climatic factors—with all possible reduced models to assess which climatic factor or combination of factors best explained the data using AICc. The "month" and "time" parameters, as well as the random effect of "trap" were included in all model comparisons. Statistical analyses were conducted using the functions "UGamm" and "dredge" in the packages "mgcv" and "MuMIn" in R version 3.6.0.

3 | RESULTS

3.1 | Seed production

The most strongly seasonal species was *C. rhynchocarpa*, with protracted annual seed production from June to February and peak seed production in December (Figure 1). The other three species generally

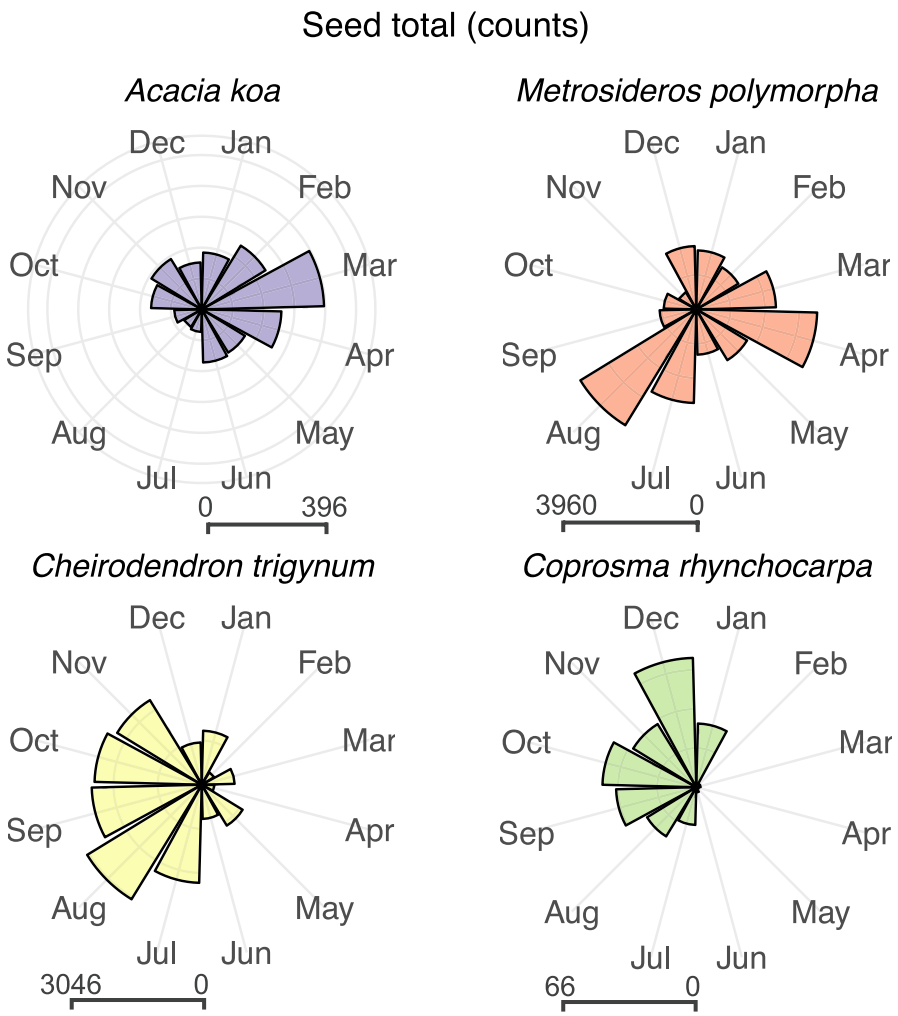

FIGURE 1 Circular histograms of average monthly seed production of four dominant species in a Hawaiian montane wet forest. Maximum seed totals are labeled underneath each histogram so relative differences each month can be compared.

produced seeds year-round; however, some still exhibited seasonality in seed production. *C. trigynum* had a clear peak season of seed production from July to November, whereas seed production by *A. koa* and *M. polymorpha* were highly variable throughout the year. *A. koa* had the most variable monthly seed production with a coefficient of variation (CV) ranging each year from 0.85 to 3.00. The CV of monthly seed production ranged from 0.65 to 1.35 for *C. trigynum*, from 0.77 to 1.18 for *M. polymorpha*, and from 0.22 to 1.05 for *C. rhynchocarpa*. Across years, *A. koa* seed production had the largest interannual variation indicated by the highest CV (1.24), followed by *C. rhynchocarpa* (0.74), *C. trigynum* (0.64), and *M. polymorpha* (0.38).

Seed production was not better explained by temperature and PAR than by rainfall based on AICc model comparisons. The best-fit models for all species' seed production included all three climatic factors with close to 100% AICc weight (Table S2a-d), and all GAM smooth terms (i.e., response curves to climatic factors) were significant ($p < .001$; Figure 2a–d). For three species, *A. koa*, *C. rhynchocarpa*, and *M. polymorpha*, using maximum temperatures resulted in the lowest AICc, whereas *C. trigynum* seed production was best explained by mean temperatures (Table S3 a-d). Response curves to other climatic factors did not change substantially when using maximum versus. mean temperatures. Seed production by *A. koa*, *C. rhynchocarpa*, and *M. polymorpha* markedly declined at high maximum temperatures, whereas *C. trigynum* showed less dramatic declines at high mean temperatures. Seed production by all species was positively associated with greater rainfall with the exception of *C. rhynchocarpa*, which showed an initial rapid increase with rainfall up to ~ 200 mm per month followed by a gradual decline at higher values of monthly rainfall. Responses to PAR were the most variable across species, with *A. koa* increasing with PAR, *C. rhynchocarpa* declining with PAR, *M. polymorpha* saturating between ~ 400 and 500 μmol/sm^{-2}, and *C. trigynum* showing a protracted peak in seed production between ~ 300 and 400 μmol/sm^{-2}.

Comparing species, *A. koa* and *C. rhynocparpa* were more sensitive to climatic variation than *M. polymorpha* and *C. trigynum* (Figure S4). Comparing climatic factors, the seed production of *A. koa* and *C. rhynchocarpa* was most sensitive (i.e., magnitude of response) to variation in PAR relative to other climatic factors (Figure 2). The seed production of *C. trigynum* was most sensitive to changes in rainfall and that of *M. polymorpha* was sensitive to all three climatic factors similarly.

3.2 | Leaf litterfall

Leaf litterfall did not show strong seasonality (Figure 3). All GAM smooth terms were significant ($p < .001$) and model comparisons

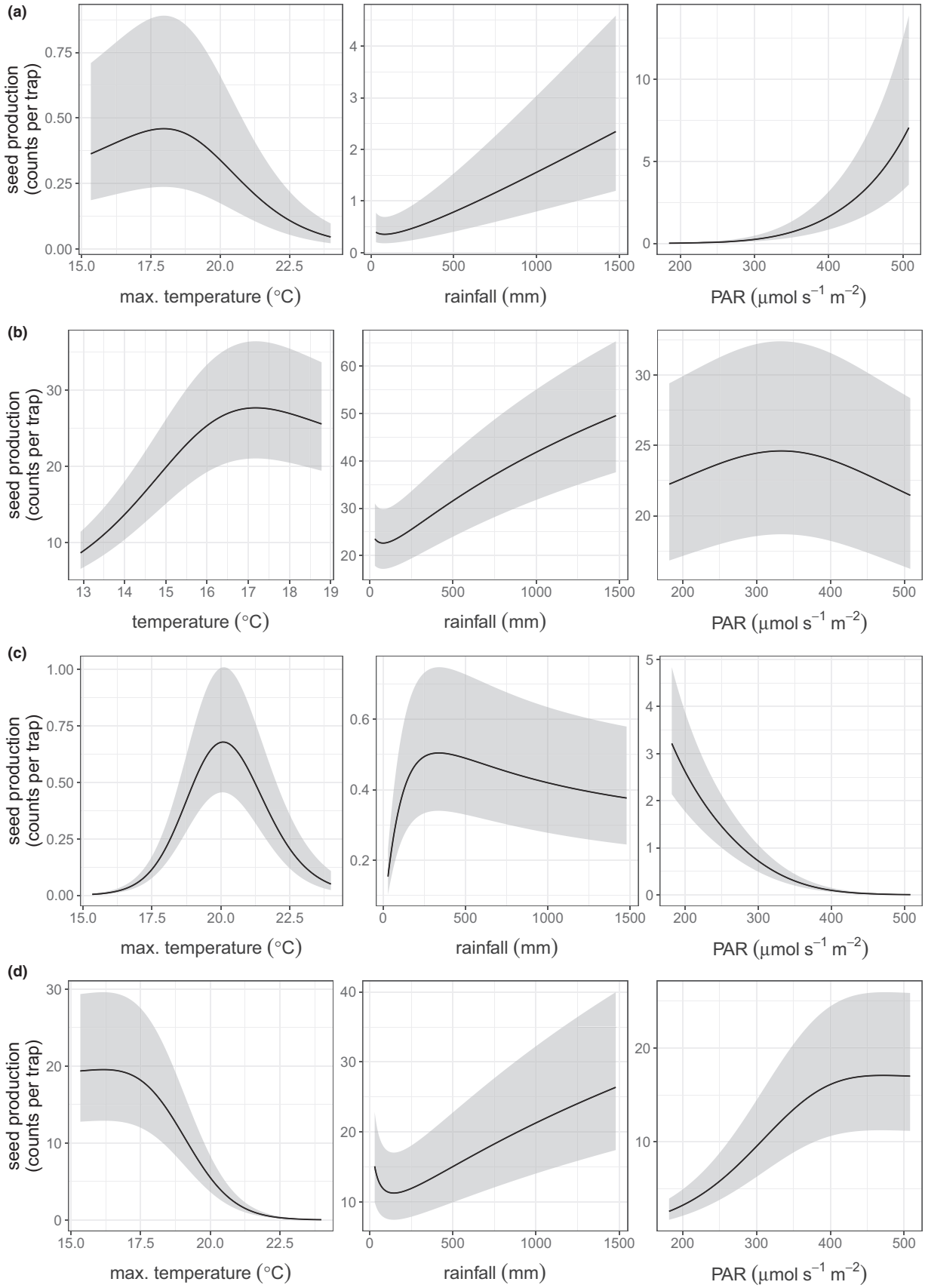

FIGURE 2 Monthly seed production relationships to climatic factors holding other climatic factors at their mean. The best-fit model (ΔAIC > 10) included all climatic factors for all species. All GAM smooth terms were significant for all species ($p < 0.001$; gray shading shows 95% confidence intervals). (a) *A. koa*, (b) *C. trigynum*, (c) *C. rhynchocarpa*, and (d) *M. polymorpha*. Note: different y-axis scale.

based on AICc showed that the best-fit model included all three climatic factors with close to 100% AICc weight (Table S1e). Leaf litterfall was best-fit using minimum temperatures compared with mean or maximum temperatures (Table S3e). Leaf litterfall decreased with rising minimum temperatures, increased with more rainfall, and increased with PAR up to ~ 400 μmol/sm^{-2}, after which leaf litterfall declined (Figure 4). Of the three climatic factors, leaf litterfall was most sensitive to changes in rainfall.

4 | DISCUSSION

Seed and leaf production are highly responsive to climatic variation in unique ways at our tropical montane forest site. Because the low latitudes are thought to be climatically stable and many species are active year-round, variation in tropical species' phenologies have been understudied (Chambers et al., 2013; Cook et al., 2012; Mendoza et al., 2017). However, many tropical plant species exhibit distinct phenological patterns that are linked to seasonal changes in the abiotic environment (Newstrom et al., 1994; Sakai, 2001; van Schaik et al., 1993). The degree of sensitivity among tropical species to climatic variation is unknown in many regions, impeding our ability to understand their differing vulnerabilities to climate change.

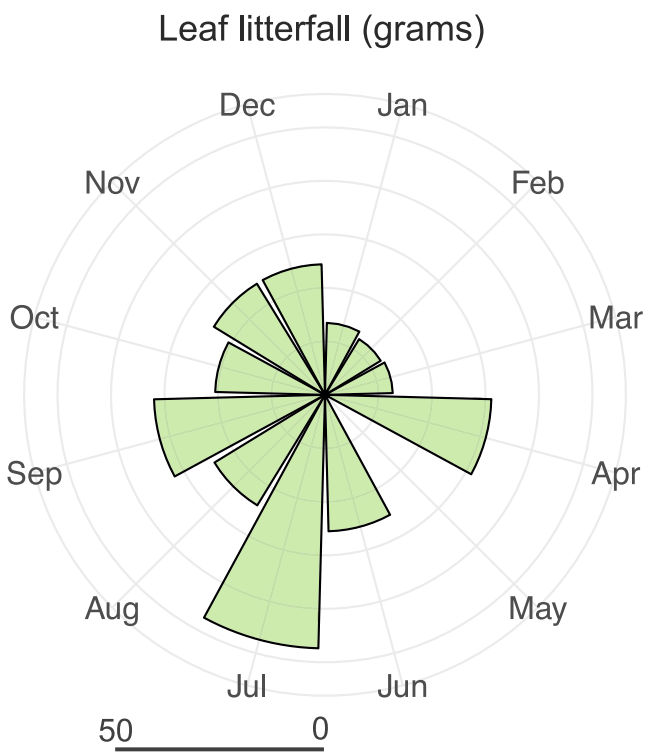

FIGURE 3 Circular histogram of average monthly community-wide leaf litterfall in a Hawaiian montane wet forest. Gray lines represent increments of 10 grams of leaf litterfall. The month of May averaged 0.7 grams.

4.1 | Seed production

Seed production of three species, including two foundational species in Hawaiian forests (*A. koa* and *M. polymorpha*), declined as maximum temperatures increased. The declines in seed production may have dramatic repercussions for future forest functioning given rising global temperatures. However, the magnitude of declines with temperature was generally smaller than positive responses to other climatic factors. For example, *A. koa* seed production declined with temperature, but increases with more rainfall and PAR were larger in magnitude. It is unclear how interactions between all three climatic factors will affect seed production and continued monitoring or controlled experiments will be critical to disentangling these interactions.

Factors other than climate are important for understanding drivers of phenology. The eight species that reproduced too irregularly (and at low numbers) for statistical analyses appear to not be highly sensitive to climate variability at this site. For the four dominant species examined, much of the variability in seed production per trap each month was unexplained by our models (Figure S5). There was some support for the effect of daylength for all four species examined (see Supplementary Information). In addition, unexplained variability in seed production may be due to the spatial distribution and behavior of individual trees in the plot. For example, disturbances such as canopy gaps allow for more light, which could promote greater seed production in only localized regions. We additionally did not examine biotic factors such the presence of pollinators or seed predators, and competition for resources. While biotic factors may exert underlying selective pressures on the timing of fruit and leaf phenology, plants may still rely on a climatic cue, and furthermore, the productivity (versus. timing) of fruits and leaves should be influenced by climatic conditions and resource availability.

Another unexamined factor that may explain climatic cues is conservatism within lineages (Davies et al., 2013; Wright & Calderón, 1995). A unique feature of Hawaiian plants is that founder populations come from both temperate and tropical regions. Thus, phenological patterns may not necessarily indicate local adaptations or be timed to local conditions. Instead, they may reflect phylogenetic conservatism from distant ancestors. The four species considered here are all of Australasian descent, with colonists of *A. koa* from Australia and colonists of *M. polymorpha*, *C. trigynum*, and *C. rhynopc*arpa from New Zealand (Price & Wagner, 2018). However, the drivers of their founder populations' phenologies are difficult to determine in part because these lineages occur in diverse habitats (temperate, arid, tropical dry, tropical wet, etc.) with potentially distinct phenologies.

Although seed production should follow flower production, there can be different climatic cues or resource requirements for seed rather than flower production (Augspurger, 1983; Slot & Winter, 2016; Wright & Calderón, 2006). *A. koa* flowers often but seed development does not always follow. While the presence of flowers was not recorded in censuses, PhenoCam (i.e., a tower-based digital camera; Richardson et al., 2009, 2018) observations overlapped with censuses from 2017 to 2018, and seed production

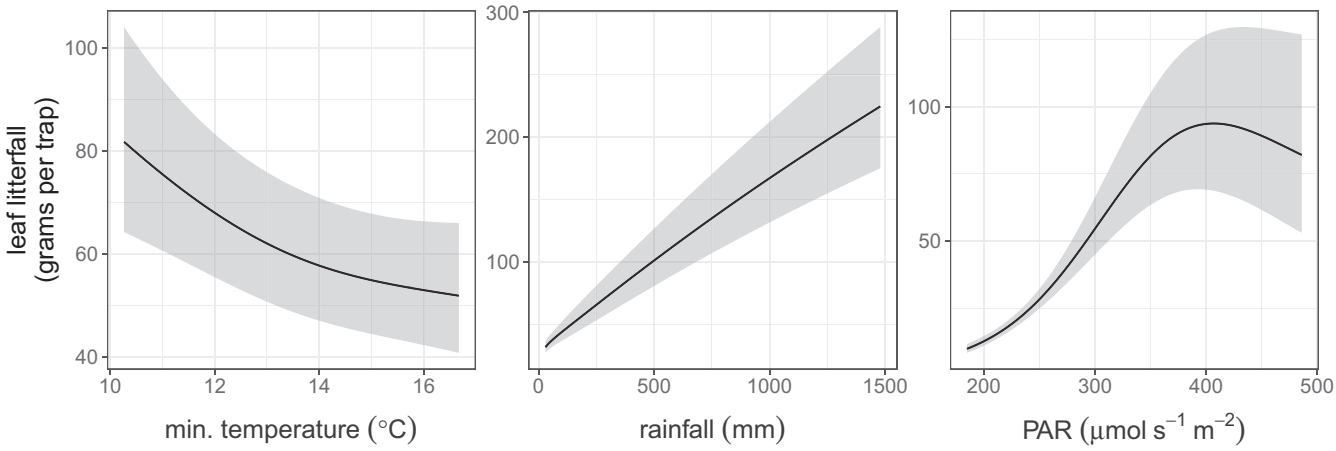

FIGURE 4 Monthly leaf litterfall relationships to climatic factors holding other climatic factors at their mean. All GAM smooth terms were significant ($p < 0.001$; gray shading shows 95% confidence intervals).

followed flowering both years (Figure S6). Flowering of *A. koa* in PhenoCam images generally occurred December—March (although it began in February in 2018) while seed production peaked, on average, between February and April (Figure 1).

Even when viable seeds are produced, conditions for establishment may limit recruitment (Inman-Narahari et al., 2013). For example, *M. polymorpha* and *C. trigynum* do not appear to be seed or dispersal limited, but instead limited by favorable sites for establishment (Drake, 1992; Inman-Narahari et al., 2013). In other cases, seed limitation and dispersal failure may contribute to the decline of native species on Hawaii (Chimera & Drake, 2010; Inman-Narahari et al., 2013).

4.2 | Community-level leaf litterfall

Monthly leaf litterfall was better explained by climatic variation than seed production (Fig. S5). Leaf litterfall was more responsive in magnitude to increasing rainfall compared with temperature or PAR. A synthesis of leaf litterfall from tropical South America showed that across sites, litterfall seasonality was associated with rainfall seasonality, wherein sites that had more seasonal litterfall also had more seasonal rainfall (Chave et al., 2010) However, there was no relationship between leaf litterfall accumulation and total annual rainfall (Chave et al., 2010).

Responses of leaf litterfall to rainfall and PAR were in the same direction. This could be explained by a large diffuse component of PAR, which can scatter more light through the canopy, as opposed to casting strong shadows, increasing light availability (Butt, New, Lizcano, & Malhi, 2009; Butt et al., 2010; Pau et al., 2013; Roderick, Farquhar, Berry, & Noble, 2001). Satellite and eddy-covariance measurements have shown positive greening or productivity responses to increases in light availability in tropical wet forests (Huete et al., 2006; Saleska, Didan, Huete, & da Rocha, 2007). In contrast, water-limited sites have shown reduced photosynthesis during the dry season, thus different tropical forest types can exhibit distinct responses to climatic variability (Pau, Okin, & Gillespie, 2010; Wu et al., 2016; Zhang, Wang, Hamilton, & Lauer, 2016). The dry season greening of tropical forests, even in wet sites, has been intensely debated (Morton et al., 2014; Samanta et al., 2010), and there are rarely ground measurements of tropical leaf phenology to corroborate satellite measures (Asner & Alencar, 2010). One of the few studies that compared satellite observations and ground-based measures of leaf litterfall in Amazonian forests showed that litterfall was associated with the production of new leaves and greater canopy LAI, which drove increases in satellite measures of greenness (Wu et al., 2016). On the contrary, leaf litterfall records from a Panamanian forest appear to coincide with reduced standing leaf area (Detto, Wright, Calderón, & Muller-Landau, 2018). Given the divergent interpretations of the relationship between leaf litterfall and standing leaf area in tropical forests, identifying site- and species-specific relationships using ground-based observations are necessary for understanding mechanisms underlying satellite patterns of greenness and drivers of leaf phenology and productivity.

4.3 | Phenological shifts to long-term climate change

Plant phenology has important cascading effects throughout the community by structuring the timing of food availability for many organisms. Species responding differently in magnitude or direction to climate change may result in phenological mismatches and novel ecological communities (Thackeray et al., 2016; Visser & Both, 2005). Species-poor island flora may be accompanied by low functional redundancy, that is, species perform unique roles in their communities (McConkey & Drake, 2015). Thus, communities with strong species' dependencies are more vulnerable to shifts in the timing of seed or leaf production.

Shifts in phenology may therefore be viewed as having negative impacts on a community (i.e., phenological mismatch) or

viewed positively as an ability to adapt to climate change (Visser & Both, 2005). Species that track climate change by adjusting their phenologies may be more likely to persist under future conditions (Cleland et al., 2012). Indeed, research has shown that phenological sensitivity to climate is associated with increased population sizes; however, most of this evidence is from temperate regions where phenological sensitivity is defined as the number of days a species' shifts a phenological event per degree temperature change (Cleland et al., 2012). These species can maintain optimal performance (e.g., flowering or fruiting at a different time), whereas species that do not track climate change may face unfavorable conditions (e.g., climate that is too warm for optimal seed production).

Given the length of our record (~ 6 years), we do not examine phenological tracking. But we show that four dominant species at our site are highly sensitive to monthly climatic variability, and the direction of responses represents favorable or unfavorable conditions for growth and reproduction. End of the century climate projections show an average temperature increase of 2 – 4°C over the Hawaiian Islands with more warming at higher elevations. Increased rainfall and more cloud cover are projected for the windward side of the islands, where this study site is located, whereas the leeward side is projected to become drier with fewer clouds (Lauer, Zhang, & Eliosn-Timm, 2013; Zhang, Xiao, et al., 2016). Although tropical regions are not warming as much or as fast as high latitude regions (IPCC, 2014), the tropics may experience novel climates outside of their historical range much sooner (Mahlstein, Knutti, Solomon, & Portmann, 2011; Mora et al., 2013, 2015; Williams, Jackson, & Kutzbach, 2007). Consequently, the physiological tolerance of tropical species combined with the pace of environmental change will determine their vulnerability to future climate change (Kingsolver, 2009; Tewksbury et al., 2008).

Understanding climate change impacts on species and communities has focused on predicting species' range shifts using bioclimatic envelopes (i.e., correlative models of species presence and mean climate; Elith & Leathwick, 2009; Guisan & Thuiller, 2005). Shifts in some species' range and distribution but not others may result in the formation of novel communities (Williams et al., 2007). The range of a species can expand in unfavorable conditions if there is continual dispersal. However, stable populations at equilibrium require conditions that allow a species to complete their life cycle. Thus, each species' distinct reproductive niche is critical for understanding species range shifts (Bykova, Chuine, Morin, & Higgins, 2012; Chuine, 2010). Divergent responses to climate change could alter community composition if reproduction or growth declines for some species but not others. How the reproduction and growth of different species will respond to climate change has potential consequences for future shifts in species distributions and the persistence of biodiversity.

ACKNOWLEDGMENTS

We thank the National Geographic Committee on Exploration (Grant number #WW-235R-17). Support for HIPPNET has included NSF EPSCoR (Grants No. 0554657 and 0903833) and the USDA Forest Service, the University of Hawai'i, and the University of California, Los Angeles (NSF Grant No. 0546784). We thank Kaikea Blakemore, Christa Nicholas, Leila Ayad, and Evan Blanchard for their help with data collection and processing, and Daniel K. Okamoto for help with statistical analyses.

DATA AVAILABILITY STATEMENT

Data available in the Knowledge Network for Biocomplexity: https://doi.org/10.5063/F15M6421 (Pau, Cordell, Ostertag, Inman, & Sack, 2020).

ORCID

Stephanie Pau https://orcid.org/0000-0001-8135-9266
Susan Cordell https://orcid.org/0000-0003-4840-8921

REFERENCES

Abernethy, K., Bush, E., Forget, P., Mendoza, I., & Morellato, L. (2018). Current issues in tropical phenology. *Biotropica*, *50*(3), 477–482. https://doi.org/10.1111/btp.12558

Asner, G. P., & Alencar, A. (2010). Drought impacts on the Amazon forest: The remote sensing perspective. *New Phytologist*, *187*, 569–578. https://doi.org/10.1111/j.1469-8137.2010.03310.x

Augspurger, C. (1983). Phenology, flowering synchrony, and fruit set of six Neotropical shrubs. *Biotropica*, *15*(4), 257–267. https://doi.org/10.2307/2387650

Austin, A. T. (2002). Differential dffects of precipitation on production and decomposition along a rainfall gradient in Hawaii. *Ecology*, *83*(2), 328–338.

Berlin, K. E., Pratt, T. K., Simon, J. C., & Kowalsky, J. R. (2000). Plant phenology in a cloud forest on the Island of Maui. *Hawaii. Biotropica*, *32*(1), 90–99.

Borchert, R. (1994). Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, *75*(5), 1437–1449. https://doi.org/10.2307/1937467

Burnham, K. P., & Anderson, D. R. (2010). *Model selection and multimodel inference: A practical information-theoretic approach*, 2nd ed.. New York: Springer.

Butt, N., New, M., Lizcano, G., & Malhi, Y. (2009). Spatial patterns and recent trends in cloud fraction and cloud-related diffuse radiation in Amazonia. *Journal of Geophysical Research*, *114*(D21), 1–9. https://doi.org/10.1029/2009JD012217

Butt, N., New, M., Malhi, Y., Lola de Costa, A. C., Oliveira, P., & Silva-Sspejo, J. E. (2010). Diffuse radiation and cloud fraction relationships in two contrasting Amazonian rainforest sites. *Agricultural and Forest Meteorology*, *150*, 361–368. https://doi.org/10.1016/j.agrformet.2009.12.004

Butt, N., Seabrook, L., Maron, M., Law, B. S., Dawson, T. P., Syktus, J., & Mcalpine, C. A. (2015). Cascading effects of climate extremes on vertebrate fauna through changes to low-latitude tree flowering and fruiting phenology. *Global Change Biology*, *21*(9), 3267–3277. https://doi.org/10.1111/gcb.12869

Bykova, O., Chuine, I., Morin, X., & Higgins, S. I. (2012). Temperature dependence of the reproduction niche and its relevance for plant species distributions. *Journal of Biogeography*, *39*(12), 2191–2200. https://doi.org/10.1111/j.1365-2699.2012.02764.x

Chambers, L. E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L. J., Crawford, R. J. M., … Wolfaardt, A. C. (2013). Phenological changes in the Southern Hemisphere. *PLoS ONE*, *8*(10), https://doi.org/10.1371/journal.pone.0075514

Chapman, C. A., Valenta, K., Bonnell, T. R., Brown, K. A., & Chapman, L. J. (2018). Solar radiation and ENSO predict fruiting phenology patterns

in a 15-year record from Kibale National Park. *Uganda. Biotropica*, *50*(3), 384–395. https://doi.org/10.1111/btp.12559

Chave, J., Navarrete, D., Almeida, S., Álvarez, E., Aragão, L. E. O. C., Bonal, D., … Malhi, Y. (2010). Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences*, *7*(1), 43–55. https://doi.org/10.5194/bg-7-43-2010

Chimera, C. G., & Drake, D. R. (2010). Patterns of seed dispersal and dispersal failure in a Hawaiian dry forest having only introduced birds. *Biotropica*, *42*(4), 493–502. https://doi.org/10.1111/j.1744-7429.2009.00610.x

Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3149–3160. https://doi.org/10.1098/rstb.2010.0142

Cleland, E. E., Allen, J. M., Crimmins, T. M., Dunne, J. A., Pau, S., Travers, S. E., … Wolkovich, E. M. (2012). Phenological tracking enables positive species responses to climate change. *Ecology*, *93*(8), 1765–1771. https://doi.org/10.1890/11-1912.1

Cook, B. I., Wolkovich, E. M., Davies, T. J., Ault, T. R., Betancourt, J. L., Allen, J. M., … Travers, S. E. (2012). Sensitivity of spring phenology to warming across temporal and spatial climate gradients in two independent databases. *Ecosystems*, *15*(8), 1283–1294. https://doi.org/10.1007/s10021-012-9584-5

Davies, T. J., Wolkovich, E. M., Kraft, N. J. B., Salamin, N., Allen, J. M., Ault, T. R., … Travers, S. E. (2013). Phylogenetic conservatism in plant phenology. *Journal of Ecology*, *101*(6), 1520–1530. https://doi.org/10.1111/1365-2745.12154

Detto, M., Wright, S. J., Calderón, O., & Muller-Landau, H. C. (2018). Resource acquisition and reproductive strategies of tropical forest in response to the El Niño-Southern Oscillation. *Nature Communications*, *9*(1), 1–8. https://doi.org/10.1038/s41467-018-03306-9

Drake, D. R. (1992). Seed dispersal of *Metrosideros polymorpha* (Myrtaceae): A pioneer tree of Hawaiian lava flows. *American Journal of Botany*, *79*(11), 1224–1228. https://doi.org/10.1002/j.1537-2197.1992.tb13724.x

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Frankie, G., Baker, H., & Opler, P. (1974). Comparative phenological studies of trees in tropical wet and dry forests in the lowlands. *The Journal of Ecology*, *62*(3), 881–919.

Giambelluca, T. W., Chen, Q., Frazier, A. G., Price, J. P., Chen, Y.-L., Chu, P.-S., … Delparte, D. M. (2013). Online Rainfall Atlas of Hawai'i. *Bull. Am. Meteorol. Soc.*, *94*, 313–316.

Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G., & Wright, S. J. (2003). Cloud cover limits net CO2 uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(2), 572–576. https://doi.org/10.1073/pnas.0133045100

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, *8*, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Huete, A. R., Didan, K., Shimabukuro, Y. E., Ratana, P., Saleska, S. R., Hutyra, L. R., … Myneni, R. (2006). Amazon rainforests green-up with sunlight in dry season. *Geophysical Research Letters*, *33*(6), 2–5. https://doi.org/10.1029/2005GL025583

Inman-Narahari, F., Ostertag, R., Cordell, S., Giardina, C. P., Nelson-Kaula, K., & Sack, L. (2013). Seedling recruitment factors in low-diversity Hawaiian wet forest: Towards global comparisons among tropical forests. *Ecosphere*, *4*, 24.

IPCC. (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. R. K. P. and L. A. M. (eds. Core Writing Team, Ed.). Geneva, Switzerland: IPCC.

Janzen, D. H. (1988). Why mountain passes are higher in the tropics. *The American Naturalist*, *101*, 233–249. https://doi.org/10.1086/282487

Kingsolver, J. G. (2009). The well-temperatured biologist. *The American Naturalist*, *174*(6), 755–768. https://doi.org/10.1086/648310

Kooperman, G. J., Chen, Y., Hoffman, F. M., Koven, C. D., Lindsay, K., Pritchard, M. S., … Randerson, J. T. (2018). Forest response to rising CO_2 drives zonally asymmetric rainfall change over tropical land. *Nature Climate Change*, *8*(5), 434–440. https://doi.org/10.1038/s41558-018-0144-7

Larcher, W., & Winter, A. (1981). Frost susceptibility of palms: Experimental data and their interpretation. *Principes*, *25*, 143–153.

Lauer, A., Zhang, C., & Eliosn-Timm, O. (2013). Downscaling of climate change in the Hawaii region using CMIP5 results: On the choice of the forcing fields. *Journal of Climate*, *26*, 10006–10030. https://doi.org/10.1175/JCLI-D-13-00126.1

Leishman, M., Wright, I. J., Moles, A. T., & Westoby, M. (2000). The evolutionary ecology of seed size. In F. M, (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities* (pp. 31–57). Wallingford, U.K.: CABI: https://doi.org/10.1016/0169-5347(93)90107-Z

Lieberman, D. (1982). Seasonality and phenology in a dry tropical forest in Ghana. *Journal of Ecology*, *70*(3), 791–806. https://doi.org/10.2307/2260105

Mahlstein, I., Knutti, R., Solomon, S., & Portmann, R. W. (2011). Early onset of significant local warming in low latitude countries. *Environmental Research Letters*, *6*(3), https://doi.org/10.1088/1748-9326/6/3/034009

McConkey, K. R., & Drake, D. R. (2015). Low redundancy in seed dispersal within an island frugivore community. *AOB Plants*, *7*, plv088. https://doi.org/10.1093/aobpla/plv088

Mendoza, I., Condit, R., Wright, S. J., Caubere, A., Chatelet, P., Hardy, I., & Forget, P.-M. (2018). Inter-annual variability of fruit timing and quantity at Nouragues (French Guiana): Insights from hierarchical Bayesian analyses. *Biotropica*, *50*(3), 431–441. https://doi.org/10.1111/btp.12560

Mendoza, I., Peres, C. A., & Morellato, LPC. (2017). Continental-scale patterns and climatic drivers of fruiting phenology: A quantitative Neotropical review. *Global and Planetary Change*, *148*, 227–241. https://doi.org/10.1016/j.gloplacha.2016.12.001

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., … Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, *12*(10), 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Mora, C., Caldwell, I. R., Caldwell, J. M., Fisher, M. R., Genco, B. M., & Running, S. W. (2015). Suitable days for plant growth disappear under projected climate change: Potential human and biotic vulnerability. *PLOS Biology*, *13*(6), e1002167. https://doi.org/10.1371/journal.pbio.1002167

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., … Giambelluca, T. W. (2013). The projected timing of climate departure from recent variability. *Nature*, *502*(7470), 183–187. https://doi.org/10.1038/nature12540

Morellato, L. P. C., Talora, D. C., Takahasi, A., Bencke, C. C., Romera, E. C., & Zipparro, V. B. (2000). Phenology of Atlantic Rain Forest trees: A comparative study. *Biotropica*, *32*(4b), 811–823. https://doi.org/10.1111/j.1744-7429.2000.tb00620.x

Morton, D. C., Nagol, J., Carabajal, C. C., Rosette, J., Palace, M., Cook, B. D., … North, P. R. J. (2014). Amazon forests maintain consistent canopy structure and greenness during the dry season. *Nature*, *506*(7487), 221–224. https://doi.org/10.1038/nature13006

Newstrom, L. E., Frankie, G. W., Baker, H. G., & Newstrom, L. E. (1994). A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva. *Costa Rica*, *26*(2), 141–159. https://doi.org/10.2307/2388804

Ostertag, R., Inman-Narahari, F., Cordell, S., Giardina, C. P., & Sack, L. (2014). Forest structure in low-diversity tropical forests: A study of

Hawaiian wet and dry forests. *PLoS ONE*, *9*(8), e103268. https://doi.org/10.1371/journal.pone.0103268

Pau, S., Cordell, S., Ostertag, R., Inman, F., & Sack, L. (2020). Data from: Climatic sensitivity of species' vegetative and reproductive phenology in a Hawaiian montane wet forest. Dryad Digital Repository,https://doi.org/10.5061/dryad.00000

Pau, S., Okin, G. S., & Gillespie, T. W. (2010). Asynchronous response of tropical forest leaf phenology to seasonal and El Niño-driven drought. *PLoS ONE*, *5*(6), e11325. https://doi.org/10.1371/journal.pone.0011325

Pau, S., Wolkovich, E. M., Cook, B. I., Davies, T. J., Kraft, N. J. B., Bolmgren, K., … Cleland, E. E. (2011). Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, *17*(12), 3633–3643. https://doi.org/10.1111/j.1365-2486.2011.02515.x

Pau, S., Wolkovich, E. M., Cook, B. I., Nytch, C. J., Regetz, J., Zimmerman, J. K., & Joseph Wright, S. (2013). Clouds and temperature drive dynamic changes in tropical flower production. *Nature. Climatic Change*, *3*, 838–842. https://doi.org/10.1038/nclimate1934

Philippon, N., Cornu, G., Monteil, L., Gond, V., & Moron, V. (2019). The light-deficient climates of western Central African evergreen forests. *Environmental Research Letters*, *14*, 034007. https://doi.org/10.1088/1748-9326/aaf5d8

Polansky, L., & Boesch, C. (2013). Long-term changes in fruit phenology in a West African lowland tropical rain forest are not explained by rainfall. *Biotropica*, *45*(4), 434–440. https://doi.org/10.1111/btp.12033

Polansky, L., & Robbins, M. M. (2013). Generalized additive mixed models for disentangling long-term trends, local anomalies, and seasonality in fruit tree phenology. *Ecology and Evolution*, *3*(9), 3141–3151. https://doi.org/10.1002/ece3.707

Price, J. P., & Wagner, W. L. (2004). Speciation in Hawaiian angiosperm lineages: Causes, consequence, and mode. *Evolution*, *58*(10), 2185–2200.

Price, J. P., & Wagner, W. L. (2018). Origins of the Hawaiian flora: Phylogenies and biogeography reveal patterns of long-distance dispersal. *Journal of Systematics and Evolution*, *56*(6), 600–620. https://doi.org/10.1111/jse.12465

Raich, J. W. (1998). Aboveground productivity and soil respiration in three Hawaiian rain forests. *Forest Ecology and Management*, *107*, 309–318. https://doi.org/10.1016/S0378-1127(97)00347-2

Rathcke, B., & Lacey, E. P. (1985). Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, *16*, 179–214. https://doi.org/10.1146/annurev.es.16.110185.001143

Reich, P. B. (1995). Phenology of tropical forests: Patterns, causes, and consequences. *Canadian Journal of Forestry*, *73*, 164–174. https://doi.org/10.1139/b95-020

Richardson, A. D., Hollinger, D. Y., Dail, D. B., Lee, J. T., Munger, J. W., & O'keefe, J., (2009). Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. *Tree Physiology*, *29*(3), 321–331. https://doi.org/10.1093/treephys/tpn040

Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Chen, M., Gray, J. M., … Frolking, S. (2018). Tracking vegetation phenology across diverse North American biomes using PhenoCam imagery. *Scientific Data*, *5*, 1–24. https://doi.org/10.1038/sdata.2018.28

Roderick, M., Farquhar, G., Berry, S., & Noble, I. (2001). On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia*, *129*(1), 21–30. https://doi.org/10.1007/s004420100760

Sakai, A. K., Wagner, W. L., Ferguson, D. M., & Herbst, D. R. (1995). Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology*, *76*(8), 2530–2543. https://doi.org/10.2307/2265826

Sakai, S. (2001). Phenological diversity in tropical forests. *Population Ecology*, *43*, 77–86. https://doi.org/10.1007/PL00012018

Sakai, S., & Kitajima, K. (2019). Tropical phenology: Recent advances and perspectives. *Ecological Research*, *(October, 2018)*, 50–54. https://doi.org/10.1111/1440-1703.1131

Saleska, S. R., Didan, K., Huete, A. R., & da Rocha, H. R. (2007). Amazon forests green-up during 2005 drought. *Science*, *318*(5850), 612. https://doi.org/10.1126/science.1146663

Samanta, A., Ganguly, S., Hashimoto, H., Devadiga, S., Vermote, E., Knyazikhin, Y., … Myneni, R. B. (2010). Amazon forests did not green-up during the 2005 drought. *Geophysical Research Letters*, *37*(5), 1–5. https://doi.org/10.1029/2009GL042154

Schuur, E. A., & Matson, P. A. (2001). Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia*, *128*(3), 431–442. https://doi.org/10.1007/s004420100671

Slot, M., & Winter, K. (2016). The effects of rising temperature on the ecophysiology of tropical forest trees. In G. Goldstein, & L. S. Santiago (Eds.), *Tropical Tree Physiology*. Springer International: Switzerland.

Tewksbury, J. J., Huey, R. B., & Deutsch, C. A. (2008). Putting the heat on tropical animals. *Science*, *320*, 1296–1297.

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., … Sparks, T. H. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, *535*(7611), 241–245. https://doi.org/10.1038/nature18608

van Riper III, C. (1980). The phenology of the dryland forest of Mauna Kea, Hawaii, and the impact of recent environmental perturbations. *Biotropica*, *12*(4), 282–291. https://doi.org/10.2307/2387700

van Schaik, C. P., Terborgh, J. W., Wright, S. J., & Van Schaik, C. P. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, *24*(1993), 353–377.

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2561–2569. https://doi.org/10.1098/rspb.2005.3356

Venables, W. N., & Ripley, B. D. (1999). *Modern applied statistics with S*, 4th ed. New York, NY: Springer. https://doi.org/10.1007/978-1-4757-3121-7

Vitousek, P. M., Gerrish, G., Turner, D. R., Walker, L. R., & Mueller-dombois, D. (1995). Litterfall and nutrient cycling in four Hawaiian montane rainforests. *Journal of Tropical Ecology*, *11*, 189–203. https://doi.org/10.1017/S0266467400008634

Wagner, W. L., & Funk, V. A. (1995). In W. L. Wagner, & V. A. Funk (Eds.), *Hawaiian biogeography: Evolution on a hot spot archipelago*. Washington, DC: Smithsonian Institution Press.

Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007)., Vol. *104* (pp. 5738–5742). https://doi.org/10.1073/pnas.0606292104AD. Proceedings of the National Academy of Sciences

Wood, S. N. (2006). *Generalized Additive Models: an Introduction with R*. Boca Raton: Chapman and Hall–CRC.

Wright, S. J. (1991). Seasonal drought and the phenology of understory shrubs in a tropical moist forest. *Ecology*, *72*(5), 1643–1657. https://doi.org/10.2307/1940964

Wright, S. J., & Calderón, O. (1995). Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology*, *83*, 937–948. https://doi.org/10.2307/2261176

Wright, S. J., & Calderón, O. (2006). Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters*, *9*(1), 35–44. https://doi.org/10.1111/j.1461-0248.2005.00851.x

Wright, S. J., & Calderón, O. (2018). Solar irradiance as the proximate cue for flowering in a tropical moist forest. *Biotropica*, *50*(3), 374–383. https://doi.org/10.1111/btp.12522

Wright, S. J., Muller-Landau, H. C., Calderón, O., & Hernandéz, A. (2005). Annual and spatial variation in seedfall and seedling

recruitment in a Neotropical forest. *Ecology*, *86*(4), 848–860. https://doi.org/10.1890/03-0750

Wright, S. J., Muller-Landau, H. C., & Schipper, J. A. N. (2009). The Future of Tropical Species on a Warmer Planet. *Conservation Biology*, *23*(6), 1418–1426. https://doi.org/10.1111/j.1523-1739.2009.01337.x

Wu, J., Albert, L. P., Lopes, A. P., Restrepo-Coupe, N., Hayek, M., Wiedemann, K. T., … Saleska, S. R. (2016). Leaf development and demography explain photosynthetic seasonality in Amazon evergreen forests. *Science*, *351*, 972–976. https://doi.org/10.1126/science.aad5068

Zhang, C., Wang, Y., Hamilton, K., & Lauer, A. (2016). Dynamical downscaling of the climate for the Hawaiian Islands. Part II: Projection for the late twenty-first century. *Journal of Climate*, *29*, 8333–8354. https://doi.org/10.1175/JCLI-D-16-0038.1

Zhang, Y., Xiao, X., Guanter, L., Zhou, S., Ciais, P., Joiner, J., … Stocker, B. D. (2016). Precipitation and carbon-water coupling jointly control the interannual variability of global land gross primary production. *Scientific Reports*, *6*, 1–9. https://doi.org/10.1038/srep39748

Zimmerman, J. K., Wright, S. J., Calderón, O., Pagan, M. A., & Paton, S. (2007). Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: The role of annual changes in irradiance. *Journal of Tropical Ecology*, *23*(02), 231. https://doi.org/10.1017/S0266467406003890

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Pau S, Cordell S, Ostertag R, Inman F, Sack L. Climatic sensitivity of species' vegetative and reproductive phenology in a Hawaiian montane wet forest. *Biotropica*. 2020;52:825–835. https://doi.org/10.1111/btp.12801