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LETTER

Synchrony, compensatory dynamics, and the functional trait basis of phenological diversity in a tropical dry forest tree community: effects of rainfall seasonality

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Abstract

Interspecific variation in phenology is a key axis of functional diversity, potentially mediating how communities respond to climate change. The diverse drivers of phenology act across multiple temporal scales. For example, abiotic constraints favor synchronous reproduction (positive covariance among species), while biotic interactions can favor synchrony or compensatory dynamics (negative covariance). We used wavelet analyses to examine phenology of community flower and seed production for 45 tree species across multiple temporal scales in a tropical dry forest in Puerto Rico with marked rainfall seasonality. We asked three questions: (1) do species exhibit synchronous or compensatory temporal dynamics in reproduction, (2) do interspecific differences in phenology reflect variable responses to rainfall, and (3) is interspecific variation in phenology and response to a major drought associated with functional traits that mediate responses to moisture? Community-level flowering was synchronized at seasonal scales (~5–6 mo) and at short scales (~1 mo, following rainfall). However, seed rain exhibited significant compensatory dynamics at intraseasonal scales (~3 mo), suggesting interspecific variation in temporal niches. Species with large leaves (associated with sensitivity to water deficit) peaked in reproduction synchronously with the peak of seasonal rainfall (~5 mo scale). By contrast, species with high wood specific gravity (associated with drought resistance) tended to flower in drier periods. Flowering of tall species and those with large leaves was most tightly linked to intraseasonal (~2 mo scale) rainfall fluctuations. Although the 2015 drought dramatically reduced community-wide reproduction, functional traits were not associated with the magnitude of species-specific declines. Our results suggest opposing drivers of synchronous versus compensatory dynamics at different temporal scales. Phenology associations with functional traits indicated that distinct strategies for coping with seasonality underlie phenological diversity. Observed drought responses highlight the importance of non-linear community responses to climate. Community phenology exhibits scale-specific patterns highlighting the need for multi-scale approaches to community dynamics.

Introduction

Changes in seasonality are a major aspect of climate change (Rauscher *et al* 2008, Feng *et al* 2013) and phenology is an important aspect of community responses to climate (Ovaskainen *et al* 2013, Wolkovich *et al* 2014b, Butt *et al* 2015). A functional perspective on phenology may shed light on mechanisms by which organisms respond to environmental change (Visser *et al* 2010). Species differences in phenology are a key dimension of biodiversity and potentially promote species coexistence (Gonzalez and

Figure 1. Patterns of species reproductive phenology (green lines) with respect to phenology of other species ((A), (B), solid, dashed and dotted lines correspond to different species), rainfall (blue line), and traits we expect will be associated with phenological variation (C), (D). In (C) we show a species that responds to seasonal rainfall (solid green line) and is constrained to reproducing in the rainy season, and a species that also responds to intraseasonal rainfall variation (dashed green line). Note that multiple mechanisms may act simultaneously and multiple patterns may emerge at distinct temporal scales.

Loreau 2009, Godoy and Levine 2013, Wolkovich *et al* 2014a). However, temporal niche differences and associated trait variation remain understudied, especially in diverse communities of long-lived organisms such as tropical forests (Kelly and Bowler 2005, Zimmerman *et al* 2007, Pau *et al* 2013). Temporal rainfall seasonality influences tropical ecosystems (Frankie *et al* 1974, van Schaik *et al* 1993, Pau *et al* 2010, Hulshof *et al* 2011, Guan *et al* 2014), but its role in mediating community phenology is not well understood due to variability at multiple temporal scales and lag effects.

Organisms in seasonal environments face the problem of weathering harsh periods and exploiting advantageous periods. Stressful conditions may limit offspring recruitment or adult allocation to reproduction (Wheelwright 1985, van Schaik *et al* 1993, Khurana and Singh 2001, Hulshof *et al* 2011), favoring phenological synchrony among species (figure 1) (Borchert *et al* 2004, Vasseur *et al* 2014). Nevertheless, phenological variation is common even in systems with extreme climate seasonality, where strong constraints on phenology are expected (Janzen 1967, Frankie *et al* 1974, Reich and Borchert 1984, Murali

and Sukumar 1994, Lechowicz 1995). Biotic interactions can favor both synchronous (i.e. positive temporal covariation) and compensatory (i.e. negative temporal covariation or anti-synchrony) phenology, depending on whether interactions exhibit positive or negative density dependence (figure 1) (Janzen 1967, Gentry 1974, Stiles 1977, Rathcke and Lacey 1985, Curran and Leighton 2000, Elzinga *et al* 2007, Botes *et al* 2008, Gonzalez and Loreau 2009, Jones and Comita 2010, Albrecht *et al* 2015). By contrast, species that exhibit asynchrony (i.e. a lack of synchrony) may have mechanisms allowing them to cope with unfavorable periods or may be subject to opposing drivers of phenology that weaken response to seasonality. Despite evidence for specific abiotic and biotic drivers of population phenology (Rathcke and Lacey 1985, Elzinga *et al* 2007), studies of whole community reproductive phenology and associated drivers at multiple temporal scales are lacking (Herrera 1998, Olesen *et al* 2008, Yang *et al* 2013).

In tropical dry forests, seasonal water limitation can be severe, promoting synchronous reproduction during rainy periods (Borchert *et al* 2004, Singh and Kushwaha 2006). Peaks in reproduction near the onset

of rains (McLaren and McDonald 2005) might reduce water stress on reproductive adults and seedlings (van Schaik *et al* 1993). However, phenology in semiarid regions can defy simple explanations (Reich and Borchert 1984, Murphy and Lugo 1986a, Murali and Sukumar 1994, Guan *et al* 2014), with many forests exhibiting bursts of reproduction during dry periods (Janzen 1967, Frankie *et al* 1974, Selwyn and Parthasarathy 2006). Part of this diversity may be linked to species differences in seed dormancy (Khurana and Singh 2001) and responses to multiple temporal scales of rainfall (Frankie *et al* 1974). Processes acting at one temporal scale might obscure those acting at different scales, necessitating a multi-scale approach (Keitt 2008).
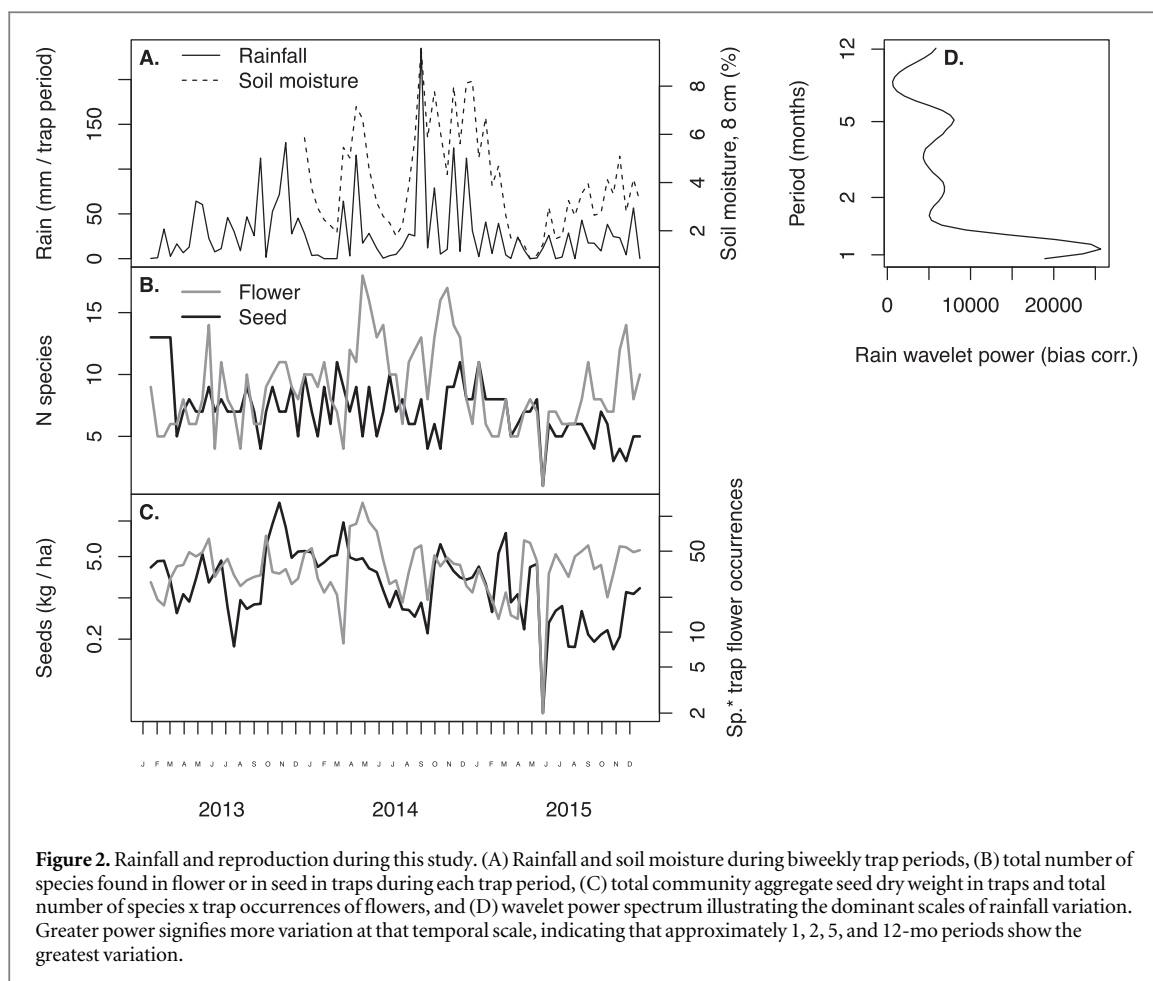
If abiotic conditions constrain phenology, inter-specific variation in phenology may be associated with species' resource allocation strategies and their tolerance to drought/water stress (figure 1) (Reich and Borchert 1984, Borchert *et al* 2004, Wolkovich *et al* 2014a). Species constrained to reproduce under favorable conditions or species that show high sensitivity to intraseasonal abiotic fluctuations (different species may fit these two distinct criteria, Vicente-Serrano *et al* 2013) may have traits allowing rapid exploitation of resources, i.e. an acquisitive strategy. In dry forests, acquisitive species may rapidly exploit soil moisture while conservative species are more tolerant of dry periods (Markesteijn *et al* 2011, Sterck *et al* 2011), allowing them to reproduce during the dry season. Acquisitive species may operate closer to margins of safe resource levels and have traits allowing rapid exploitation of resource pulses (Markesteijn *et al* 2011, Ouédraogo *et al* 2013, Muscarella and Uriarte 2016). Thus acquisitive species may respond strongly to short-term fluctuations in rainfall, rapidly exploiting moisture but being sensitive to short dry periods. Rapid initiation of reproduction following rainfall may come at the expense of allocation to reproductive or somatic tissue across the entire growing season (Cohen 1976, Rathcke and Lacey 1985) or at the risk of an early end to favorable conditions.

Acquisitive strategies in dry forest trees are characterized by low wood density, which is linked to rapid transport and storage of water and fast growth at the risk of cavitation and mortality during drought. Conservative strategies are characterized by low specific leaf area (SLA), which may limit heat and water loss at the cost of reduced photosynthetic capacity, evergreen leaves, low leaf area, low leaf N and P, and presence of a taproot, which facilitates water access and storage (Poorter and Markesteijn 2008, Markesteijn *et al* 2011, McCulloh *et al* 2011, Sterck *et al* 2011, Méndez-Alonzo *et al* 2012). Drought stress on seedlings may also influence phenology, such that species fruiting during rainy seasons may show high germination while those fruiting in dry seasons remain dormant to await wet periods (van Schaik *et al* 1993, Lechowicz 1995, Soriano *et al* 2011). However, we note that

tree functional traits often do not neatly collapse into a single axis of resource acquisitive versus conservative strategies (e.g. Powers and Tiffin 2010). Despite research on drought impacts on tropical moist/wet forests (e.g. Wright *et al* 1999, Condit *et al* 2004, Wright and Calderón 2006), impacts of drought (widespread in the neotropics) on dry forests are less well-understood (but see Enquist and Leffler 2001, Borchert *et al* 2002, Soriano *et al* 2011, Maza-Villalobos *et al* 2013). Studies have rarely quantitatively measured whole community dry forest reproductive phenology at high frequency and for multi-year periods (but see McLaren and McDonald 2005 for two years of monthly observations in Jamaica).

Here, we study community reproductive phenology in a tropical dry forest in Puerto Rico, at a site that exhibits marked precipitation variation at inter- and intra-annual scales, and that is expected to become drier due to anthropogenic climate change (Khalyani *et al* 2016). In 2015 our study site experienced severe drought, allowing us to address the following questions about functional traits and drought response.

(1) Do species reproduce synchronously, suggesting abiotic seasonality constrains community reproduction? Alternatively, do species exhibit asynchronous dynamics, suggesting a large subset of species tolerate reproduction during drought, or compensatory dynamics in phenology, suggesting temporal niche differences? We expected to find synchrony at the scale of rainy/dry seasons, while compensatory dynamics are more likely at intraseasonal scales.

(2) Is interspecific phenological variation associated with response to rainfall? We expected resource-acquisitive species to be strongly constrained to rainy season reproduction, or have reproduction be most strongly correlated with intraseasonal rainfall variability relative to conservative species.

(3) Are species differences in phenological responses to rainfall across scales related to functional traits and life histories? We expected that species able to reproduce during dry seasons and species insensitive to intraseasonal rainfall variation will be characterized by dense wood, small leaves, low SLA, low leaf N and P, taproots, low growth, and high survival (conservative strategies) while species reproducing during rainy seasons will exhibit acquisitive strategies (light wood, large deciduous leaves with high SLA, N, and P, high growth, and low survival). We also expect that species releasing seed during rainy seasons will exhibit relatively higher seed germination in data from published experiments, suggesting phenology minimizes drought stress on seedlings.

Figure 2. Rainfall and reproduction during this study. (A) Rainfall and soil moisture during biweekly trap periods, (B) total number of species found in flower or in seed in traps during each trap period, (C) total community aggregate seed dry weight in traps and total number of species x trap occurrences of flowers, and (D) wavelet power spectrum illustrating the dominant scales of rainfall variation. Greater power signifies more variation at that temporal scale, indicating that approximately 1, 2, 5, and 12-mo periods show the greatest variation.
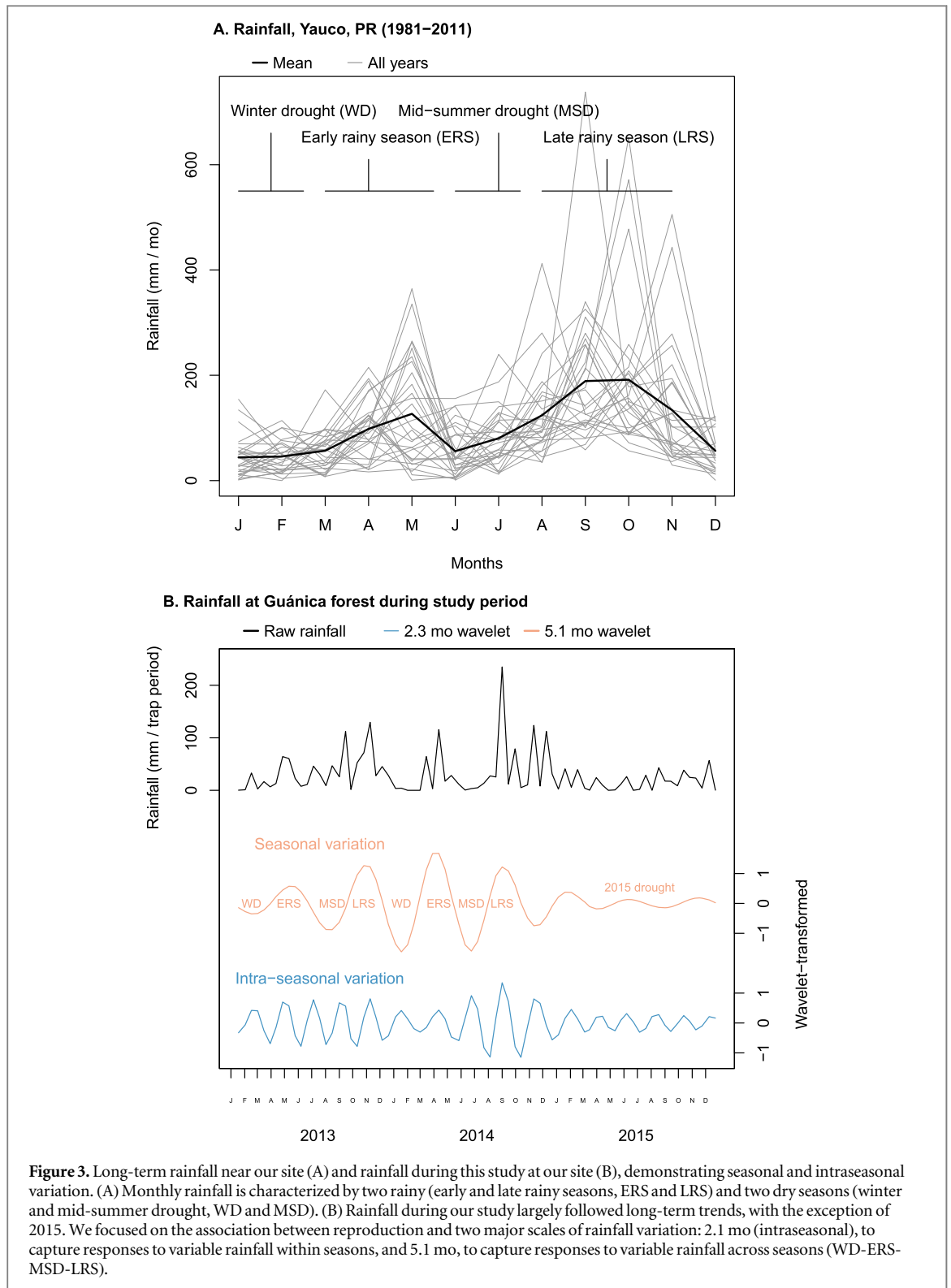
Methods

Study site

The Guánica State Forest is a semi-deciduous dry forest in southwest Puerto Rico (17 °58′ N, 65 °30′W). Mean annual temperature is 25.1 °C and annual rainfall averages 860 mm (Murphy and Lugo 1986b). Seasonal rainfall is bimodal, split between an early rainy season (ERS, April–May) and a late rainy season (LRS, August–November, figures 2, 3). Between rainy seasons is a mid-summer drought (MSD), which is expected to intensify with global climate change (Rauscher *et al* 2008). Annual rainfall was near average in 2013 and 2014 but 2015 was a remarkable year due to failure of seasonal rains (Gamble and Curtis 2008, Maldonado *et al* 2016). Climate and soil moisture data were obtained from USDA NRCS www.wcc.nrcs.usda.gov/nwcc/site?sitenum=2067, see supplemental material).

Soils are classified as mollisols on limestone, with hilly topography and rocky outcrops. Aquifer dynamics are characterized by seasonal depletion and recharge (Govender *et al* 2013). Forest canopy reaches 5 m height on south-facing slopes and ridges and 9 m in valleys with a leaf area index of ∼3 (Murphy and Lugo 1986b).

Tree data

In 2012, we established a permanent 4 ha (200 × 200 m) plot in the forest (146–193 m elevation, figure S1). All arborescent stems ⩾2.5 cm diameter at breast height (1.3 m height, DBH) were mapped, measured for diameter, and identified to species. We censused a total of 45 836 stems of 68 tree species. In 2014, we remeasured DBH in half the 20 × 20 m quadrats and assessed survival in all quadrats (see supplement for more detail).

In December 2012, we set up fifty phenology traps distributed in every other quadrat across the plot. The traps have surface area of 0.50 m^2 and were constructed using 1 mm mesh mounted 80–100 cm above the ground. We collected trap contents bi-weekly between January 2013 and December 2015, for a total of 77 collection dates. At each collection, we recorded presence of flowers or flower parts and counted mature fruits and seeds in traps, identifying all to species. We converted mature fruit number to approximate seed number by multiplying by the average number of seeds/fruit, which was calculated using fruits collected at Guánica. To ensure sufficient data for robust parameter estimation, our species-specific analyses of phenology–rainfall associations were restricted to the top 27 species ranked by number of trap-flower occurrences and the top 27 species ranked

Figure 3. Long-term rainfall near our site (A) and rainfall during this study at our site (B), demonstrating seasonal and intraseasonal variation. (A) Monthly rainfall is characterized by two rainy (early and late rainy seasons, ERS and LRS) and two dry seasons (winter and mid-summer drought, WD and MSD). (B) Rainfall during our study largely followed long-term trends, with the exception of 2015. We focused on the association between reproduction and two major scales of rainfall variation: 2.1 mo (intraseasonal), to capture responses to variable rainfall within seasons, and 5.1 mo, to capture responses to variable rainfall across seasons (WD-ERS-MSD-LRS).

by number of seeds collected in traps in 2013–2014 (i.e. years when seasonal rainfall occurred, table S1). These species account for 87% and 82% of basal area, respectively.

Functional traits

We collected trait data from multiple individuals of each species (table S2) using standard methods (Cornelissen *et al* 2003). The only exception was that we used a combination of methods to measure WSG. For trees at least 10 cm DBH, we measured wood specific gravity (WSG; g cm^{-3}) using an increment borer, following Cornelissen *et al* (2003). For species that do not typically reach this size, we used branch WSG measurements, again following Cornelissen *et al* (2003). To correct for differences between these

measurements, we regressed branch and core samples from the same individuals and used this regression to estimate core WSG for trees lacking core measurements (supplemental material).

We collected three fully expanded, sun-exposed leaves from individual mature trees during July-September, with 1–11 individuals/species (mean = 7.5). We used a flatbed scanner to measure leaf area (cm^2) on freshly collected leaves. We measured mass of dried leaves to calculate specific leaf area (SLA; $cm^2\ g^{-1}$). Leaf area and SLA were measured on entire leaves (including petiole) of fully expanded, sun-exposed foliage of mature trees. We pooled, ground, and shipped all leaves of each species to the Agricultural Analytical Services Lab at Pennsylvania State University to determine leaf N and P (% dry mass). We assessed if species had taproots based on reports in Little *et al* (1974), Howard (1988), and Liogier (1997). Dry seed weight was taken from locally-collected data (Castilleja 1991), the Kew global seed database (Royal Botanic Gardens Kew 2015), and botanical references (Little *et al* 1974, Howard 1988, Liogier 1997). For each species, we calculated maximum height as the larger value between (i) heights estimated at our study site and (ii) the maximum height reported by Little and Wadsworth (1964). Deciduous, semideciduous (i.e. substantial but partial leaf shedding within an individual, or variation among individuals or among years in deciduousness), or evergreen status was taken from Little *et al* (1974), Howard (1988), and Liogier (1997) and expert opinion (pers. comm. Marcos Caraballo) and was converted to a numeric variable where semideciduous was halfway between evergreen and deciduous.

Demography

We calculated growth and survival from 2012 to 2014, i.e. mean change in diameter and proportion surviving for individuals of each species. Although trunks of individual trees may swell or shrink in response to rain events, we found evidence for significant interspecific variation in our measured growth and survival (growth: Kruskal-Wallis chi-squared = 1897.4, df = 69, $p < 10^{-16}$; survival: chi-squared = 1012.3, df = 69, $p < 10^{-16}$, see table S1 for species sample sizes). Seed germination, measured as percent of seeds germinating, was aggregated across similar germination experiments conducted by Castilleja (1991) at our site (Guánica), by Ray and Brown (1994) at dry forests in St. John, and by Carvajal Velez (2002) at dry forests in the region around our site (supplemental material). Though we attempted to control for environmental differences among these germination studies, we acknowledge that they provide a limited view of interspecific variation in germination at our study site, due to potential species × environment interactions (Soriano *et al* 2011).

Data analysis

We used wavelet transforms to quantify scale-specific correlations in reproduction among species (multivariate) and between individual species and rainfall (bivariate). Wavelets allow a spectral decomposition of a signal, similar to Fourier transforms, with the important exception that wavelets can characterize time-localized, non-stationary, signals (Keitt and Fischer 2006). Scale-specific and non-stationary patterns are likely to occur in dry forest phenology because drivers of phenology may act over multiple scales and time points. Temporal rainfall patterns are variable and irregular especially in semiarid regions like dry forests. We used the widely employed Morlet wavelet basis function (Keitt 2008, Vasseur *et al* 2014), which gives a reasonable tradeoff between resolving frequency versus location (in time) of signals. In wavelet transforms, this basis function is dilated (to represent different frequencies, or scales) and shifted in time (to represent different points in time) to capture variability in the original signal (Goupillaud *et al* 1984). We show an example transform with a Morlet wavelet of rainfall at our study site for two major scales (frequencies) of variation (figure 3).

Community phenology: from synchronous to compensatory dynamics

To answer question (1), we asked whether reproduction showed synchronous, asynchronous, or compensatory dynamics, and if these patterns changed across temporal scales, suggesting multiple processes acting at distinct scales. We estimated each species' flowering phenology by calculating the number of traps with flowers in each trap period. Variation in seed investment among species was estimated by multiplying the number of seeds by average seed mass. We square root transformed flower and seed data as a tradeoff between representing the dominance of common species versus allowing them to overwhelm analyses. For comparison, we conducted additional analyses on untransformed data and on normalized data (supplemental material).

We characterized community phenology as synchronous, asynchronous, or compensatory using the community-wide wavelet modulus ratio (WMR) (Keitt 2008). WMR quantifies the ratio of variance in aggregate community-wide reproduction relative to the variance in species-level reproduction (Keitt 2008, 2014). WMR tends to unity under synchrony, i.e. when both aggregate community- and species-level variation are high. WMR tends to zero under compensatory dynamics, i.e. when species-level variation is high but community-level variation is low (because species compensate for each other). Asynchronous dynamics have a WMR between these extremes. Significance of WMR as high (synchrony) or low (compensatory dynamics) was assessed at each point in time and scale using 1000 non-parametric

bootstraps of species (Keitt 2008, 2014). We used the 'mvcwt' R package for these calculations (Keitt 2014).

Species-specific reproduction in relation to rainfall

To address question (2), we quantified the temporal scales of greatest rainfall variation (Supplemental Material), and then asked how phenology was related to rainfall at two of these scales (2.3 and 5.1 mos). We focus on rainfall–reproduction association at the 2.3 mo period to capture responses to variable rainfall within seasons ('intraseasonal') and at the 5.1 mo period ('seasonal') to capture responses to variable rainfall across seasons (figure 3).

To characterize phenological relationships with rainfall, we calculated the bivariate wavelet coherence (akin to correlation) between rainfall and species reproduction (Grinsted *et al* 2004). First, we calculated the wavelet coherence between rainfall and reproduction at the two focal scales (2.3 and 5.1 mos) (figure S2). Coherence ranges from 0 (no correlation) to 1 (perfect correlation). The scale-specific coherence allowed us to identify species with strong responses to seasonal rainfall variation but lacking intraseasonal responses to rainfall. Note that strong coherence may occur independent of the rainfall–reproduction phase, allowing us to model species with strong responses but differing lags. Next, we calculated the phase of species responses to seasonal rainfall at the 5.1 mo scale (figure 3), representing whether species reproduce in rainy or dry seasons (figure S2). Because there was no rainy season in 2015, we used only 2013 and 2014 data in wavelet calculations of rainfall–reproduction phenology. To improve normality, we square root transformed flower and seed observations. We performed calculations using the 'biwavelet' package in R (Gouhier 2014).

We assessed how the 2015 drought influenced intensity of species flowering and fruiting. To do so, we calculated total flower-trap occurrences for each species in 2013 and 2014 (years with roughly normal rainfall) and compared with total flower-trap occurrences in 2015. For seed rain, we calculated total seed count for each species in 2013 and 2014 and compared with total seed count in 2015.

Species phenology and functional traits

We next asked if species differences in responses to rainfall were associated with functional traits and demography (Question (3)). We tested for associations between traits and demographic rates versus phenology–rainfall correlations (the latter of which were calculated to answer question (2) above, figure S2). First, to understand ecological strategies associated with the strength of a species rainfall response (coherence), we calculated Pearson's correlation coefficient for traits and demographic rates versus the rainfall–reproduction coherence at each of the two time scales, i.e. we made a series of bivariate tests.

Second, we tested trait associations with reproduction in rainy versus dry seasons, i.e. the phase of rainfall–reproduction correlations (figure S2). The reproduction of some species was weakly related with rainfall, a pattern we expected would characterize species with conservative strategies. To preserve this information (signal of weak coherence) we aimed to conduct an analysis accounting for both phase and coherence of the rainfall–reproduction relationship. Traditional circular statistics (i.e. the association between reproduction–rainfall phase versus a trait) would consider only the phase for each species, discarding information about the strength of the relationship. To account for phase and coherence associations with traits, we multiplied rainfall–reproduction phase by coherence at the seasonal scale (5.1 mo) to obtain a vector, which we converted to Cartesian coordinates as

$$x = \text{coherence}^* \cos(\text{phase})$$
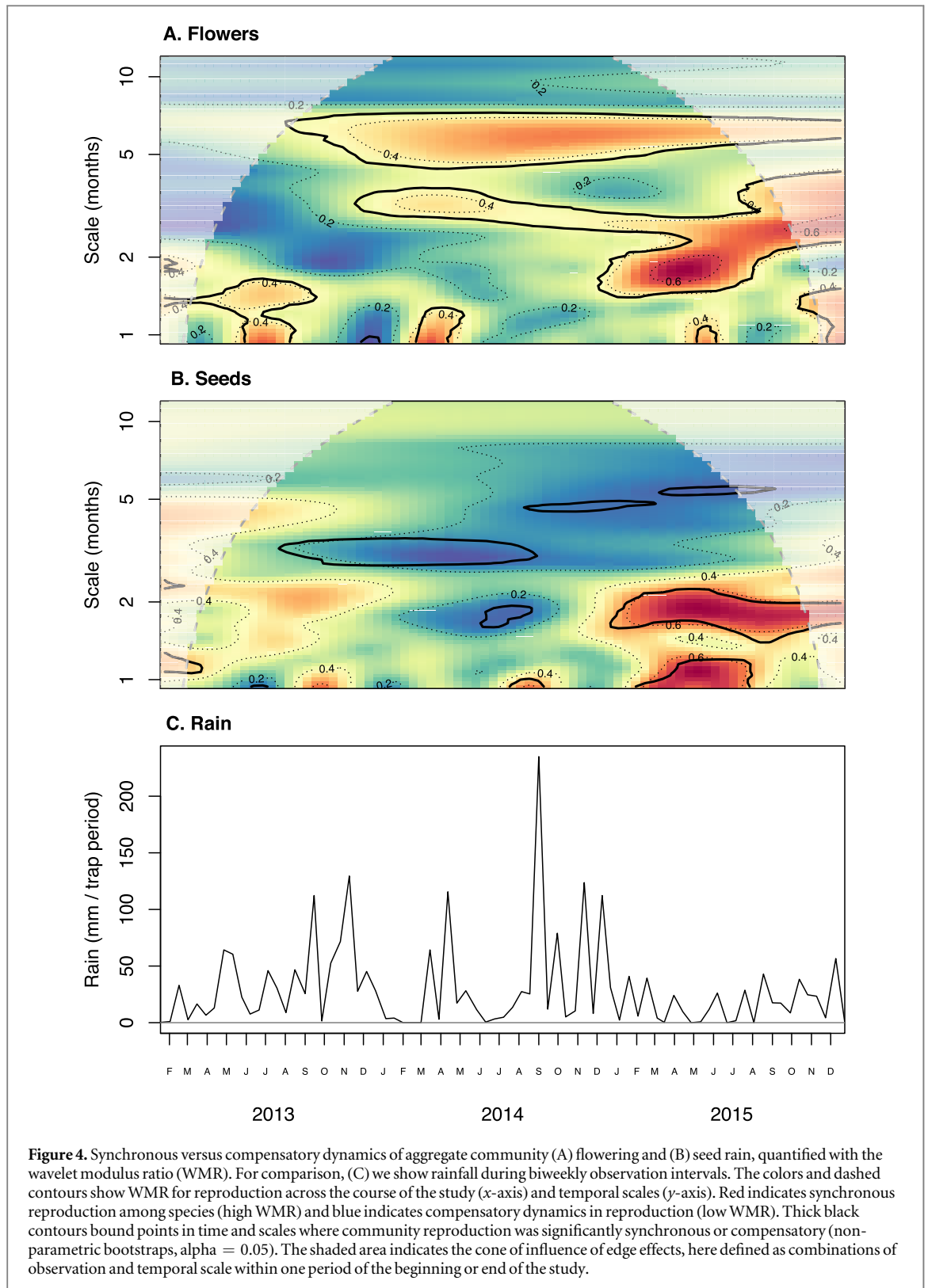
and

$$y = \text{coherence}^* \sin(\text{phase}).$$

This vector represents the phase of reproduction with respect to seasonal rainfall, weighted by the strength of the relationship (figure S2). Because this was a multivariate measure of phenology (as opposed to simply rainfall–reproduction coherence), we fit linear models where species traits were a function of $x + y$. We chose this formulation for convenience; we do not mean to imply that phenology causes variation in traits. The fitted coefficients of x and y gave a vector representing the association between each species trait and species reproduction with respect to seasonal rainfall. We assessed the statistical significance of the trait association with phenology by testing the joint hypothesis that the x and y coefficients equaled zero using a Wald test (implemented in the R package 'aod', Lesnoff and Lancelot 2012). For comparison, we also conducted analyses relating traits to the reproduction–rainfall phase, ignoring rainfall–reproduction coherence. We calculated the Johnson–Wehrly–Mardia correlation coefficient (JWM $R^2_{x\theta}$) between phase and traits, and assessed significance by permuting trait values among species (Pewsey *et al* 2013).

Third, we tested whether response to the 2015 drought was associated with traits and demography. We calculated the ratio of 2015 reproduction to 'normal' flowering and fruiting (average of 2013 and 2014) and tested their Spearman's rank correlation with species traits.

Results

Soil moisture was closely related to rainfall, highlighting the importance of rainfall for potential drought stress (Pearson's $r = 0.71$, figure 2(A)). We collected and identified 45 species in 2064 species-by-trap flower occurrences. We identified a total of 42 species, collected 29 374 mature fruits (then converted

Figure 4. Synchronous versus compensatory dynamics of aggregate community (A) flowering and (B) seed rain, quantified with the wavelet modulus ratio (WMR). For comparison, (C) we show rainfall during biweekly observation intervals. The colors and dashed contours show WMR for reproduction across the course of the study (*x*-axis) and temporal scales (*y*-axis). Red indicates synchronous reproduction among species (high WMR) and blue indicates compensatory dynamics in reproduction (low WMR). Thick black contours bound points in time and scales where community reproduction was significantly synchronous or compensatory (non-parametric bootstraps, alpha = 0.05). The shaded area indicates the cone of influence of edge effects, here defined as combinations of observation and temporal scale within one period of the beginning or end of the study.

to estimated seed counts), and 10 168 additional seeds (apart from seeds in fruits).

Species phenology: from synchronous to compensatory dynamics

Among all species observed as flowers, we found synchrony in flowering that was significant (i.e. greatest WMR) and most consistent at the ∼6 mo time

scales (see red bounded by black, indicating bootstrap significance, figure 4(A)). This ∼6 mo scale roughly corresponds to the twice yearly rainy/dry seasons. We also observed bursts of significant synchrony each year in May or June at the ∼1 mo scale, the shortest we analyzed, signifying synchrony among species in the initiation of flowering at the start of the ERS. At other scales, community flowering was indistinguishable

from the null expectation, i.e. essentially asynchronous.

Consistent with multiple species releasing seeds in the dry season (figure 2(B)), seed rain was not significantly synchronous and instead asynchronous at time scales of seasonal rainfall (no red across top of figure 4(B)). For most of the normal years (2013–2014), seed rain at ~3 mo scales exhibited significant compensatory dynamics (i.e. low WMR) among species (blue bounded by black, indicating bootstrap significance, in middle of figure 4(B)). This scale indicates compensatory dynamics occurred within rainy or dry seasons but does not correspond to a major scale of rainfall variability (figure 2(D)). Results were qualitatively consistent, but with minor differences, when we considered species seed output as the number of traps present (i.e. as done with flowering phenology), or when we used alternate data transformations (figures S3–S5).

Species-specific reproduction relative to rainfall

Species-specific wavelet rainfall–reproduction correlations revealed a diversity of phenological patterns. Consistent with the synchrony we observed among species at seasonal time scales (figure 4(A)), most species peaked in flower-trap counts at the peak of seasonal rains or within ~2 mos (i.e. most species located in top of figure 5(A)). Thus, most species had lower flower production during middle to late dry seasons. In contrast to flowering, the relationship between seed rain and rainfall showed greater variation among species, with several species peaking in seed rain in dry seasons (figure 5(B)).

In general, species showed a wide range of reproduction–rainfall coherence at our focal scales (figures 6(A) and (B)). Coherence at one scale was not closely related with coherence at the other scale (i.e. points are scattered in figures 6(A) and (B)), signifying the presence of species with strong associations with seasonal rainfall (*y*-axis of figure 6) but weak associations with intraseasonal rainfall (*x*-axis of figure 6) and vice versa.

Total rainfall for 2015 was 45% of the mean of the previous two normal years and was associated with lower flowering in 17 of the top 27 most frequent flowering species and lower seed rain in 22 of the top 27 most common seed rain species. Flowering was not as strongly reduced in the drought as was seed rain (figure 2), with the median species reproductive output in 2015 at 61% of 2013–2014 levels for flowering but only 15% for seed rain, indicating median species seed rain showed stronger than linear declines associated with drought, i.e. rainfall at 45% of normal translated into only 15% of normal seed production. The reproductive nadir of the entire study period was in May 2015, the time of year when the early rainy season typically occurs.
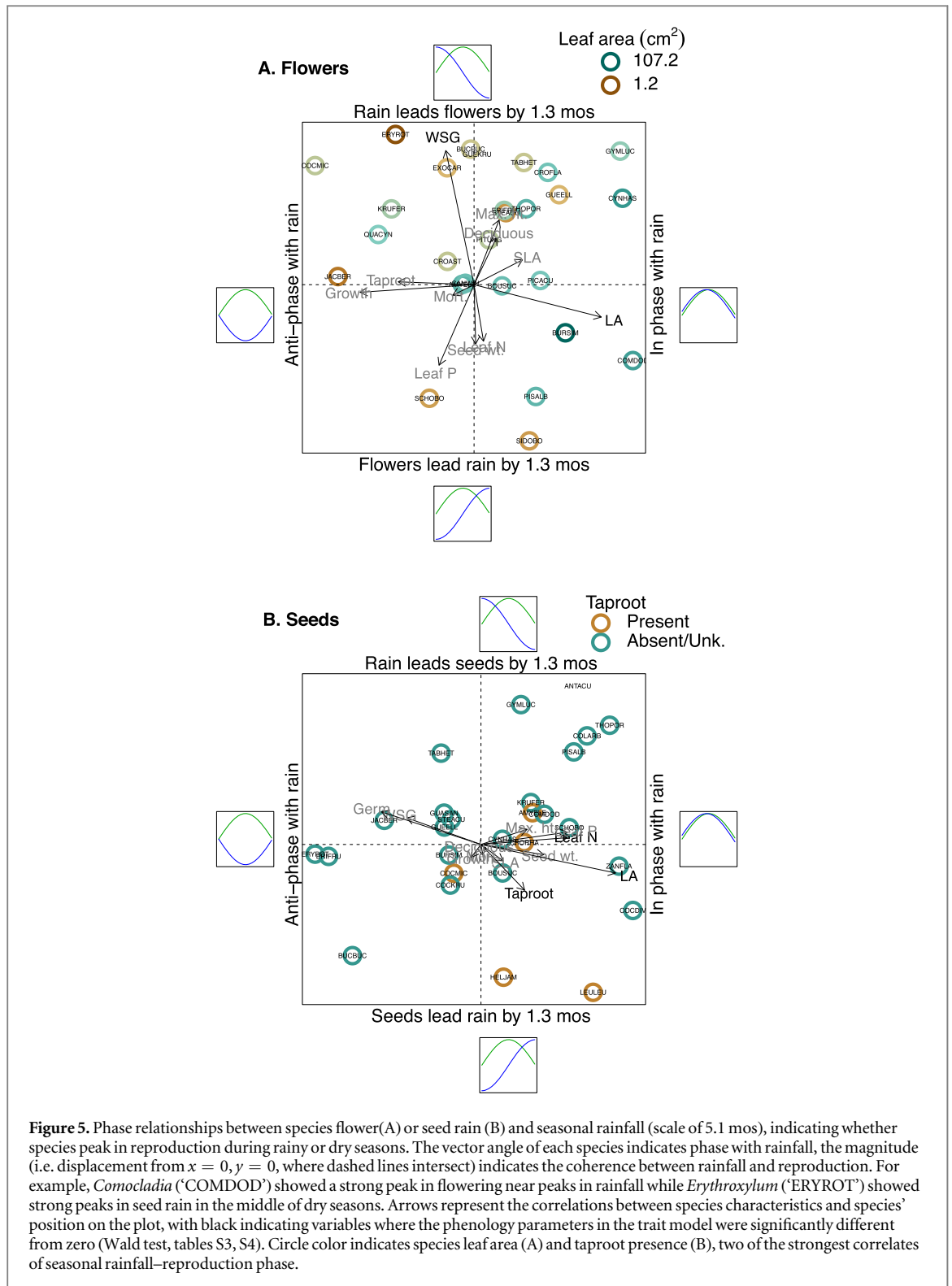
Interspecific phenological variation and species traits

Species flowering phase relationships with seasonal rainfall (5.1 mo scale) were most strongly related with leaf area ($N = 26$, log leaf area $\sim x + y$, $R^2_{adj} = 0.23$, Wald test $p = 0.0084$; JWM $R^2_{x\theta} = 0.19, p = 0.0909$, table S3) with larger-leaved species flowering closer to peaks in seasonal rainfall (figure 5(A)). Additionally, species with high WSG ($N = 26$, $R^2_{adj} = 0.23$, Wald test $p = 0.0085$; JWM $R^2_{x\theta} = 0.45$, $p = 0.0020$) tended to peak in flowering closer to the nadir of seasonal rainfall. Average mortality, growth and other traits (leaf N and P, taproots, SLA, maximum height, deciduousness, and seed mass) were more weakly related to phase of flowering with respect to seasonal rainfall (table S3).

Species seed rain phase relationships with precipitation were most strongly related with leaf area ($N = 26$, $R^2_{adj} = 0.36$, Wald test $p = 0.0003$; JWM $R^2_{x\theta} = 0.26$, $p = 0.0400$, table S4, figure 5) and leaf N ($N = 23$, $R^2_{adj} = 0.22$, Wald test $p = 0.0174$; JWM $R^2_{x\theta} = 0.21$, $p = 0.1069$). Species with higher leaf area and leaf N (correlation $r = 0.42$ among seed rain species) peaked in seed rain close to the peak of rainy seasons. Additionally, species with taproots ($N = 26$, $R^2_{adj} = 0.17$, Wald test $p = 0.0309$; JWM $R^2_{x\theta} = 0.19$, p = 0.0939) tended to peak in seed rain prior to the peak of seasonal rainfall. Average growth, mortality, and other traits were weakly related to phase of seed rain with respect to rainy versus dry seasons (table S4).

We found that the species with strong flowering responses to intra-seasonal rainfall variation (2.3 mo scale) had significantly greater leaf area ($N = 26$, Pearson's $r = 0.42$, $p = 0.0349$) and maximum height ($N = 26$, $r = 0.43$, $p = 0.0277$, figure 6(A), table S5) and lower mortality ($N = 27$, $r = -0.39$, $p = 0.0415$). Average growth and other traits were not significantly related to rainfall-flower coherence at the 2.3 mo scale. For seed rain, we found no significant trait associations with responses to intra-seasonal rainfall variation. The strongest pattern was that species with taproots had non-significantly weaker seed rain responses to intra-seasonal rainfall variation ($N = 26$, $r = -0.35$, $p = 0.0812$, figure 6(B), table S6) and species with high leaf N had non-significantly stronger seed rain responses to intra-seasonal rainfall variation ($N = 23$, $r = 0.37$, $p = 0.0816$). No trait was significantly related to seasonal rainfall–reproduction coherence (5.1 mo scale, tables S5 and S6).

Surprisingly, no traits or demographic variables were strongly associated with species reproductive response to the 2015 drought (all trait associations with change in flowering or seed rain had $p > 0.05$, tables S7 and S8). For flowering, species with greater leaf area (Spearman's rho = 0.34, $p = 0.0895$) and lower average mortality rates (Spearman's
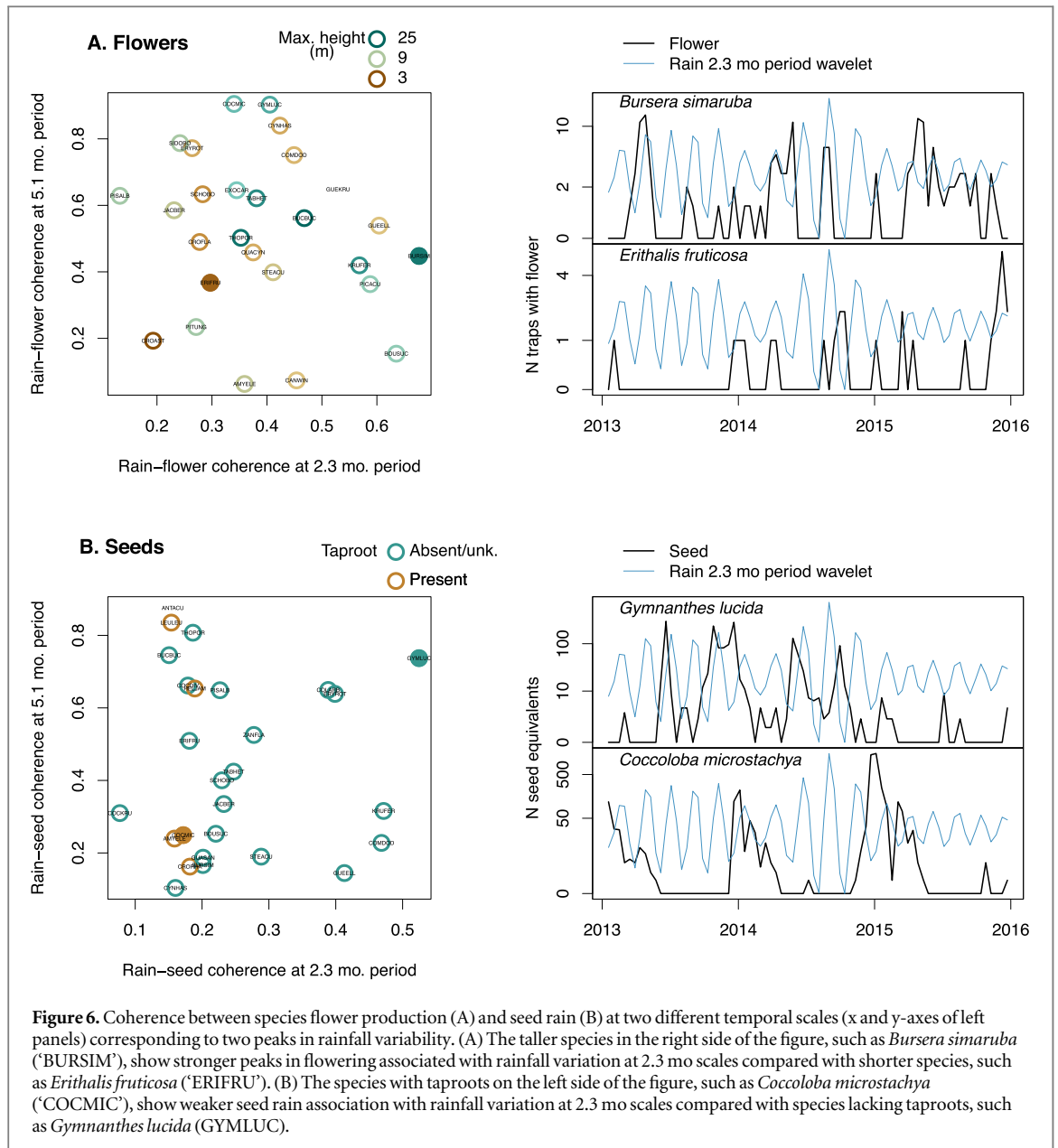
Figure 5. Phase relationships between species flower(A) or seed rain (B) and seasonal rainfall (scale of 5.1 mos), indicating whether species peak in reproduction during rainy or dry seasons. The vector angle of each species indicates phase with rainfall, the magnitude (i.e. displacement from $x = 0$, $y = 0$, where dashed lines intersect) indicates the coherence between rainfall and reproduction. For example, *Comocladia* ('COMDOD') showed a strong peak in flowering near peaks in rainfall while *Erythroxylum* ('ERYROT') showed strong peaks in seed rain in the middle of dry seasons. Arrows represent the correlations between species characteristics and species' position on the plot, with black indicating variables where the phenology parameters in the trait model were significantly different from zero (Wald test, tables S3, S4). Circle color indicates species leaf area (A) and taproot presence (B), two of the strongest correlates of seasonal rainfall–reproduction phase.

rho $= -0.33$, $p = 0.0971$) were non-significantly less sensitive to the 2015 drought.

Discussion

Patterns of spatial community diversity have received a great deal more study compared to diversity along temporal axes. Reproductive phenology has long been hypothesized to be an axis of niche partitioning, especially in tropical forests (Janzen 1967, Gentry 1974, Stiles 1977, Wheelwright 1985, Murali and Sukumar 1994, Sakai 2001, Botes *et al* 2008). However, a persistent challenge has been that multiple opposing processes may drive phenology at distinct scales, obscuring each other's effects (Elzinga *et al* 2007, Keitt 2008). A predictive, integrative understanding of phenology will require quantifying links with interspecific variation in life history and physiology across

Figure 6. Coherence between species flower production (A) and seed rain (B) at two different temporal scales (x and y-axes of left panels) corresponding to two peaks in rainfall variability. (A) The taller species in the right side of the figure, such as *Bursera simaruba* ('BURSIM'), show stronger peaks in flowering associated with rainfall variation at 2.3 mo scales compared with shorter species, such as *Erithalis fruticosa* ('ERIFRU'). (B) The species with taproots on the left side of the figure, such as *Coccoloba microstachya* ('COCMIC'), show weaker seed rain association with rainfall variation at 2.3 mo scales compared with species lacking taproots, such as *Gymnanthes lucida* (GYMLUC).

temporal scales (Visser *et al* 2010). Here, we used multi-scale wavelet analysis to demonstrate that tropical dry forest tree species exhibit synchronous, asynchronous, *and* compensatory dynamics in reproduction, depending on temporal scale and stage of reproduction. Trait differences corresponded to phenological diversity in ways supportive of acquisitive versus conservative tradeoffs in drought response (Markesteijn *et al* 2011, Sterck *et al* 2011). However, traits were poor predictors of reproductive response to the 2015 drought, suggesting limits to species flexibility to reproduce in the face of years with extreme drought events.

Synchrony versus compensatory dynamics
We found significant evidence for community-wide synchrony in flowering across multiple time scales. Two lines of evidence suggest that shared responses to

rainfall or moisture drive this synchrony (Borchert 1983). First, flowering synchrony was particularly strong at time scales similar to rainfall seasonality (i.e. 5–6 mos) and at the shortest time scales (~1 mo) during the early rainy season. Second, species tended to flower in conjunction with or soon after seasonal rainfall peaks (figure 5). However, in addition to rainfall, biotic interactions, e.g. with pollinators, may also favor flowering synchrony (Janzen 1967, Elzinga *et al* 2007).

We found community peak flowering in rainy seasons, distinct from patterns reported from other tropical dry forests, where dry seasons peaks in flowering often occur (e.g. Frankie *et al* 1974, McLaren and McDonald 2005, Singh and Kushwaha 2006, Selwyn and Parthasarathy 2006). In a multi-site neotropical study, peak flowering during the dry season occurred at wetter sites, while the strongest flowering in

synchrony with rains occurred at the driest site (Borchert *et al* 2004). Our study site does not have extremely low rainfall for a dry forest, but is found on karst and as a result soil moisture may be particularly limiting during dry seasons.

By contrast, community seed rain was often asynchronous and was significantly compensatory at ~3 mo scales. The fact that compensatory dynamics occurred at scales distinct from abiotic fluctuations suggests that co-occurring species may differ in phenological niches for reasons other than abiotic responses (Wolkovich *et al* 2014a). These compensatory dynamics may be linked to biotic interactions, e.g. with frugivores (Gentry 1974, Stiles 1977), or to trade-offs associated with risk and reward of seedling establishment (Khurana and Singh 2001, Venable 2007). However, inference of compensatory phenology has been controversial, and patterns have often been indistinguishable from null expectations (Rathcke and Lacey 1985, Wheelwright 1985, but see Botes *et al* 2008). Our study is the first to apply multi-scale WMR analysis to this question (Keitt 2008, Vasseur *et al* 2014), allowing us to resolve scale-specific and non-stationary patterns. Our finding of compensatory dynamics suggests that previous analyses might have overlooked these patterns because they are scale-specific and possibly obscured by patterns at other scales. Further research is required to demonstrate the proximate and ultimate causes of the compensatory dynamics we observed, for example via direct study of biotic interactions (Murali and Sukumar 1994, Selwyn and Parthasarathy 2006, Botes *et al* 2008).

Compensatory dynamics were stronger for seed rain than for flowering (Lechowicz 1995), potentially due to differences in the ecology of each process. It is likely that some species exhibit a substantial lag between seed production, seed release, and animal dispersal. As a result, timing of seed rain might be less constrained (compared with flower fall) by abiotic conditions such as seasonal drought, allowing for wider partitioning of seed phenology niches. The stronger synchrony in flowering compared to seed rain might signify that species differentially abort reproduction following flowering (Jones and Comita 2010). Interspecific variation in abortion may result from variation in flowering strategies, breeding systems, pollination rates, and sensitivity to unexpected post-flowering drought (Stephenson 1981).

Drought

Severe weather events like the 2015 drought may have dramatic influences on tropical forest ecosystems (Butt *et al* 2015). We found substantial community-wide declines in reproduction during the 2015 drought. This pattern stands in contrast to increases in productivity and reproduction observed from wetter forests during drought years, presumably due to increased light availability (Wright *et al* 1999, Wright

and Calderón 2006, Pau *et al* 2010). However, Wright and Calderón (2006) speculated that extreme droughts could reduce reproduction and Curran *et al* (1999) found dramatic reductions in viable seed of Dipterocarps (despite initiation of fruit production) during extended or severe droughts. The reproductive impact of extended droughts is not well known for dry forests, although researchers have documented physiological responses (Borchert *et al* 2002), increases in mortality, and decreases in recruitment (Maza-Villalobos *et al* 2013). If the reduced reproduction we observed during 2015 leads to lower recruitment for sensitive species, such droughts may contribute to stand and community changes (Curran *et al* 1999, Fauset *et al* 2012, Maza-Villalobos *et al* 2013, Uriarte *et al* 2016).

Functional basis of phenological diversity

We observed substantial phenological diversity among species, and functional trait correlates suggest that alternate strategies for dealing with abiotic constraints partly underlie this diversity. In general, we found that resource acquisitive traits were associated with rainy season reproduction (i.e. phase relationship with rainfall at 5.1 mo scale) and with rainfall–reproduction coherence at an important intraseasonal scale (2.3 mos), suggesting that moisture limitation constrains phenology of these species most strongly (Venable 2007, Markesteijn *et al* 2011, Wolkovich *et al* 2014a). For example, high leaf area and leaf N species tended to flower and drop seed near the peak of rainfall. On the contrary, species with high WSG flowered and dropped seeds in the late rainy/early dry season. High WSG, and small leaves may be key traits for maintaining activity, e.g. reproduction or seedling growth, during dry periods by allowing trees to avoid cavitation (Poorter and Markesteijn 2008, Kushwaha *et al* 2010, Méndez-Alonzo *et al* 2012).

We also found evidence that resource acquisitive strategies are associated with sensitivity to intraseasonal-scale rainfall dynamics. Species with high maximum height and large leaf area (correlation between traits $r = 0.13$), exhibited the strongest flowering–rainfall coherence, while shorter stature, smaller leaved species showed weaker relationships with rainfall at this scale (2.3 mo). This finding may signify that the tallest or largest leaved species at our site operate close to the margin of hydraulic safety (Ryan and Yoder 1997, Markesteijn *et al* 2011), such that flowering is safest in the weeks following rainfall (Borchert 1983), or that the tallest species are better able to simultaneously exploit rainfall and light due to their dominant position. Additionally, we found that species with taproots were non-significantly less sensitive to intraseasonal rainfall variation (seed rain) and significantly more likely to release seeds late in the dry season. If trees can access groundwater then drought may weakly affect tree water balance and performance

(Rundel *et al* 1995, Poorter and Markesteijn 2008, Guan *et al* 2014). Future work is required to uncover community impacts of interspecific differences in groundwater access and spatiotemporal heterogeneity in groundwater availability (Borchert 1994, Govender *et al* 2013, Guan *et al* 2014).

Despite hypotheses that phenology should be associated with life history tradeoffs, e.g. growth versus survival (Wolkovich *et al* 2014a), we did not find strong phenology associations with species average growth and survival. In general, our inferences about community phenology and dynamics are limited by the duration of this study (3 yrs). The limited timespan of observed growth and survival (2 yrs) may have been insufficient to identify leading axes of demographic variation due to the slow growth and turnover in dry forests. Masting phenology, i.e. synchronous, supra-annual reproduction within a species, is common in Malesian Dipterocarpaceae and co-occurring canopy trees (Ashton *et al* 1988). However, masting is less well-known in neotropical (mostly known from Lecythidaceae, which were absent from our site) and dry forests, partly due to a lack of long-term studies (Janzen *et al* 1978, van Schaik *et al* 1993). It is unclear how important masting may be in neotropical dry forests, given that masting is more common among Malesian dipterocarps of moist forests compared to seasonally dry forests (Ashton *et al* 1988).

Deciduous species may be more likely to flower in the dry season as the evaporative demand of leaves disappears (Borchert 1994, Selwyn and Parthasarathy 2006). We did not find reproductive phenology and drought response were associated with deciduousness, though deciduous classification is non-trivial due to extensive intraspecific variation among sites and individuals. Contrary to previous findings (Borchert 1994, Selwyn and Parthasarathy 2006), we observed some larger-leaved species known to be deciduous (e.g. *Bursera, Comocladia*) reproducing in synchrony with rainy seasons, indicating that deciduousness may have a more complex relationship with reproductive phenology than previously suggested. Janzen (1967) proposed that dry season flowering might be favored if the division of flowering and vegetative growth periods improves efficiency, and vegetative growth should be more reliant on moisture available in rainy seasons. Drivers of leaf and root phenology may interact with reproductive phenology to affect organismal and species level patterns; these aspects of resource allocation require further integration with reproductive phenology (Borchert 1983, Borchert *et al* 2004, Kushwaha *et al* 2010, Méndez-Alonzo *et al* 2012, Doughty *et al* 2014). Finally, dry season reproduction may improve pollination and dispersal for deciduous trees using wind (Janzen 1967, Frankie *et al* 1974), although a minority of our community is deciduous and there are few dominant wind-pollinated or dispersed species.

It is surprising that traits were not associated with drought response, given recent findings that the same traits are associated with response to extended drought (i.e. longer than seasonal dry period) in tropical trees (Fauset *et al* 2012, Uriarte *et al* 2016). However, we note our study species might respond differently to even more extended droughts. Previous work across Puerto Rico (including Guánica) has shown strong trends in community mean traits (WSG, SLA, and maximum height) along spatial precipitation gradients (Muscarella and Uriarte 2016). Nevertheless, the ecophysiological mechanisms that determine organismal level responses to environment may be due to complex, poorly known, interactions of traits, limiting the utility of univariate, phenomenological analyses (Laughlin and Messier 2015, Muscarella and Uriarte 2016).

Conclusions

Phenology is shaped by processes that act at multiple time scales. Previous studies (Borchert 1994, Selwyn and Parthasarathy 2006) have found functional group associations with dry forest phenological categories. Here we make inferences about drivers of phenology in a quantitative, continuous, multi-scale framework, which is less subject to problems of discretization of complex continuous patterns of phenological and trait variation. Here, we showed evidence that community phenology is characterized by synchronous, asynchronous, and compensatory dynamics, depending on temporal scale, partly due to seasonal fluctuations in abiotic constraints. Furthermore, we found that dry forest phenological diversity is associated with divergent ecological strategies for dealing with seasonal moisture constraints. However, these responses exhibit limits in response to extreme drought events. Change in seasonality is a major feature of global climate change. To better predict climate impacts on dry forest ecosystems, ecologists should build a community-level understanding of multi-scale phenological diversity and its functional basis.

Acknowledgments

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