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Winter dry season reproductive phenology in Bahamian dry forest and implications for conservation

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Abstract

The reproductive phenology of plants has profound influence on ecosystem dynamics including plant–animal interactions. Broad phenological patterns, especially the timing of reproduction, may result from long-term climate trends and co-evolution between plants and their pollinators, dispersers, and predators. Yet, interannual climate variation and local abiotic conditions may also affect the timing and magnitude of plant reproduction. Understanding the patterns of and controls on plant reproduction are crucial for conservation efforts under a changing global climate and rapidly expanding human development. However, phenology studies from the Neotropics are sparse. Here, we examine the relative timing and magnitude of fleshy-fruited plant reproduction during the winter dry season in subtropical dry forest on Eleuthera, The Bahamas over a nine-year period. At least 47 species were observed with some dry season reproductive activity, but only 17% showed evidence of a fruiting peak or continuous reproduction. Overall fruit abundance generally declined through the dry season, but flower production increased between mid and late dry season. Variation in fruit and flower abundance among years was related to temperature and rainfall, but local site conditions—particularly successional stage and groundwater availability—explained more variability in reproductive activity than climate variation. Groundwater availability had a particularly strong positive influence on flower and fruit abundance at the end of the dry season, a critical time for migrant frugivores preparing to return to their breeding grounds. This emphasizes the importance of protecting sites with accessible groundwater to conserve biodiversity in the archipelago and elsewhere.

KEYWORDS
bird conservation, climate variation, *Erithalis fruticosa*, freshwater lens aquifer, *Lantana involucrata*, reproductive phenology, tropical dry forest

1 | INTRODUCTION

In tropical and subtropical dry forests (TDFs), the phenology of many plants shows marked seasonality in relation to water availability (Frankie et al., 1974; Bullock & Solis-Magallanes, 1990). Different reproductive syndromes exist, with some species fruiting only in the wet season, others in the dry season, and a few continuously throughout the year (Mclaren & Mcdonald, 2005; Opler et al., 1980). These syndromes have evolved in response to long-term climate trends governing favorable conditions for reproduction and seedling

establishment combined with disperser availability and seed predation risk (Rathcke & Lacey, 1985). However, interannual climate variation and local environmental conditions can affect both vegetative and reproductive phenological processes contributing to large interannual and inter-individual variation within a population (e.g., Gunarathne & Perera, 2014; Reich, 1995; Silveira et al., 2013).

Plant reproduction variation can influence ecosystem processes and has direct consequences for consumers of nectar, fruits, or seeds (Van Schaik et al., 1993; Walker & Del Moral, 2003). Fleshy fruits are important food for many consumers, especially birds (Estrada & Fleming, 1986). Some fleshy-fruited TDF plants maximize fruit production during the wet season due to high water need (Bullock & Solis-Magallanes, 1990; Lieberman, 1982). However, other plants fruit during the dry season when seed dispersal services may be higher due to the presence of both resident and migrant avian frugivores (Almazán-Núñez et al., 2015; Howe & De Steven, 1979).

Of the world's bird species, 72% occur in tropical forests with most of those species in the Neotropics and over half in TDFs (Pillay et al., 2022). Despite the importance of plant phenological patterns to this large segment of global biodiversity, phenological studies in the Neotropics are rare, usually ≤2 years and highly concentrated in a few areas (Mendoza et al., 2017). Here, we address this knowledge gap, using dry season (winter) plant reproductive phenology data collected over a 9-year period in TDF on the island of Eleuthera, The Bahamas, an archipelago grossly underrepresented among phenology studies (Mendoza et al., 2017). Wunderle Jr. et al. (2014) reported trends in winter fruit abundance of three shrub species on Eleuthera. We expand that work by examining trends in flowering and fruiting among all fleshy-fruited species present in those study sites over a longer period.

We focus on dry season reproduction as it is a time when migrant and winter resident (hereafter "migrant") birds augment populations of resident frugivores, comprising ~47% of species detected on Eleuthera (Currie, Wunderle Jr., Ewert, Davis, & Mckenzie, 2005; Franklin & Steadman, 2013; Wunderle Jr. & Waide, 1993). Conditions are moist when migrants arrive, but are driest just before vernal migration (Sherry et al., 2005). Broad patterns of flowering and fruiting of fleshy-fruited plants over this period will have evolved in response to historical climate and biotic interactions. Nonetheless, interannual climate variation and local environmental factors may influence the relative timing and abundance of different reproductive phenophases. For example, if water availability is a major driver of the timing or amount of fleshy-fruited plant reproductive activity (Mendoza et al., 2017), it could limit dry season fruit production temporally based on recent rainfall or spatially based on the availability of, for example, groundwater.

Studies show depth to groundwater is important to primary productivity (Glanville et al., 2023) and avian habitat in arid temperate regions like Western North America (Arriana Brand et al., 2011; Merritt & Bateman, 2012). However, few studies address links between groundwater, plant reproduction, and avian habitat in TDF. These links may be especially important on islands like Eleuthera where there are no freshwater streams or lakes, but where a highly localized freshwater lens within 1–2 m of the surface may provide the only consistently moist pockets on the landscape (Sealey, 2006; USACE, 2004).

Identifying patterns of and controls on plant reproduction, especially at times when seed dispersal services are highest, is crucial for understanding plant–animal interactions in TDFs (Chapman et al., 2005) and for anticipating the impacts of global climate change or encroaching human development. Among the diverse consumers dependent on TDFs are migratory birds of conservation concern whose annual survival and reproductive success are influenced by wintering ground conditions (Rockwell et al., 2012, 2016). Understanding how climate variation interacts with local factors to influence intra- and interannual variation in TDF dry season flower and fruit production can help prioritize critical conservation areas or inform habitat restoration (Rother et al., 2022).

2 | METHODS

2.1 | Study area

Eleuthera is a subtropical island in the central Bahamas (25°15′ N, 76°20′ W). Most rainfall occurs from May through October, with a dry season from November through April, but rainfall shows high interannual variation (Figure S1). Eleuthera's undeveloped landscape is typical of central and southern Bahamian islands (Byrne, 1980), consisting of a mosaic of variably aged vegetation consequent to shifting agriculture or failed development (Helmer et al., 2010). Characteristic vegetation consists of both evergreen and deciduous broadleaf shrubs and trees (Franklin et al., 2015).

2.2 | Site selection

Like many studies examining tropical fruit phenology (Abernethy et al., 2018; Mendoza et al., 2017), our data came from investigating food resources for consumers. Our study placed particular emphasis on the near-threatened (IUCN, 2023) Kirtland's Warbler (*Setophaga kirtlandii*), a Neotropical-Nearctic migrant wintering almost exclusively in The Bahamas. Due to this focus on an avian winter resident, field personnel were only present on Eleuthera during the winter dry season, thus, precluding our ability to collect full-year phenology data. Nonetheless, the study design revealed warbler abundance was positively correlated with fruit abundance with warblers moving from fruit-poor to fruit-rich sites through the dry season (Wunderle Jr. et al., 2014).

To track reproductive activity across the landscape through the dry season, we established transects in nonhomogeneous TDF habitat "sites" broadly defined by Kirtland's Warbler use at the time of establishment and point-of-access (also see: Wunderle Jr. et al., 2010; Wunderle Jr. et al., 2014). Between 2003 and 2007, a total of 71 belt transects (20 m * 1 m) were geolocated within eight study sites on southern Eleuthera (Figure S2). Transects were placed

parallel to pre-existing roads and narrow trails established for bird surveys. A stratified random design was used to locate between 3 and 21 transects per site, depending on habitat variation within and spatial extent of the site (limited by habitat availability or access). Across all sites, transects were separated by an average distance of 175 m (minimum = 20 m).

2.3 | Phenological surveys

Transects were surveyed each dry season from November 2003 through April 2012. Not all transects were surveyed in all years due to transect loss to development and later establishment of some study sites (Table S1). Each year, most transects were surveyed three times: (1) early (November–December), (2) mid (January–February), and (3) late dry season (March–April). The numbers of flowers (except in 2003), unripe fruit, and ripe fruit present within the 20 m^2 transect were counted separately for each fleshy-fruited plant species at each survey. For our purposes, fleshy-fruited plants included four classes (Van Der Pijl, 1982): (1) seeds with fleshy seed coats; (2) arilloid fruits; (3) fruits with a fleshy endocarp inside a hard pericarp; (4) pericarp fruits or drupes and berries.

2.4 | Phenology data reduction and environmental variables

Within and across species on a transect, we quantified abundance of various reproductive phenophases: (1) total reproductive activity as the combined number of flowers, unripe, and ripe fruit; (2) total fruit abundance as the number of unripe plus ripe fruit; (3) separate abundances of flowers and ripe fruits; and (4) the percentage of all fruit that were ripe (percentage ripe fruit).

From Lynden Pindling International Airport (Nassau) climate data (https://www.ncei.noaa.gov/access), we derived: (1) total precipitation occurring 21–50 days before the survey date, and (2) the average daily minimum temperature recorded between December through February, typically the coolest months. We believe Nassau rainfall (~96 km west) is a reasonable proxy for our sites because most winter rainfall in The Bahamas is derived from cold fronts from the northwest (Sealey, 2006). From maps, we derived local environmental variables expected to influence reproduction, which varied within and among our loosely defined sites: (1) a binary variable representing approximate groundwater availability based on categorical mapping by the US Army Corps of Engineers (USACE, 2004; low = USACE "scarce," or moderate to high = USACE "generally" or "locally plentiful"); (2) relative transect age based on number of years since last disturbance in 2005 (range = 0–37 year; see Helmer et al., 2010); (3) a binary variable representing relative latitudinal position (north or south, Figure S2); and (4) minimum distance to the east coast of Eleuthera. We expected ground water availability would positively influence reproductive activity, but increasing age would negatively influence reproduction, since younger sites have lower resource competition. Relative latitude often correlates with broad differences in precipitation and temperature regimes (Sealey, 2006), while some of our personal observations suggested locations closer to the east coast might have more late dry season reproductive activity.

2.5 | Qualitative and statistical analyses

We first qualitatively examined general trends in how total reproductive activity and the relative contributions of different phenophases to total activity varied within and among dry seasons. We also examined which species contributed most to total reproductive activity and phenophase abundance by calculating, across all transects, the median percentage of a metric (e.g., flower abundance) attributable to a given species. Because we did not have information on canopy cover of species within transects, which might limit the relative contribution of less abundant species, our analysis emphasized the consistency of a species' contribution to dry season reproduction across transects and years. We assumed species with consistent interannual contributions to a given phenophase at a particular dry season period were reflective of responses evolved to long-term climate trends. To minimize transect-specific stochasticity, we focused our attention on species showing reproductive activity on at least three transects within a survey period and, across those transects, a median contribution greater than the grand median across all species and transects in at least 5 of the 9 years. However, we also looked for possible masting indicated by species with very large contributions to reproduction across at least three transects in just 1 or 2 years.

To examine how interannual climate variation and local environmental conditions influenced reproductive phenophase abundances, we employed hierarchical cross-classified models (HCM), a generalized linear mixed model for nested data when lower-level units are cross-classified by two or more higher-level units (Doedens et al., 2022; Raudenbush & Bryk, 2002). Using HLM 7 software (Scientific Software International, Inc.) and full maximum likelihood, HCM estimated the fixed effects of climate (precipitation, temperature) and environment (groundwater, etc.), while also allowing partitioning of the total variance in phenophase abundance into components associated with surveys nested within transects and among transects cross-classified by years.

Separate HCM models were built for started-log transformed values of: (1) flower abundance, (2) fruit abundance, and (3) the percentage ripe fruit. Models were built up progressively according to three "levels": surveys, transects, and years. Each abundance metric was a random response variable with variance estimated at all three levels. At the survey level, we examined whether phenophase abundance across surveys varied as a function of time of dry season (quantified as number of days since 1 October, centered around the grand mean), the total precipitation occurring 21–50 days before a survey, or their interaction since prior rainfall usually declined between the early and late dry season. The effect of time was treated as random in the model for the fruit abundance but, to ease

estimation procedures, as non-randomly varying based on environment (see below) in the other two models where polynomials were used to estimate nonlinear trends in activity through time.

At the transect level, we examined whether average phenophase abundance or its trend through the dry season varied among transects as a function of age, groundwater resources, or geographic position. We also examined whether presence of *Erithalis fruticosa* or *Lantana involucrata* influenced phenophase abundance given (1) the high contribution of these two species to dry season reproduction (see Results) and (2) our interest in the species due to Kirtland's Warbler preference for their fruits (Wunderle Jr. et al., 2010). Finally, we examined whether phenophase abundance through the dry season varied among years as a function of the average minimum temperature during December–February. Temperature was not used at the survey level because (a) it showed a strong nonlinear association with time of dry season and (b) given the relatively mild winter temperatures in the Bahamas, we expected the minimums encountered at the coldest time of year would have the greatest effect on subsequent trends.

Within each level, variables were entered successively according to theoretical prioritization and retained or removed based on significant model improvement indicated by reductions in Akaike's information criterion ($\Delta AIC \geq 2$) and likelihood ratio tests ($p \leq .05$). In order to retain statistical power and produce the most parsimonious model, a variable entered at an early stage could be removed at a later stage if a univariate *t*-test indicated its model coefficient did not significantly ($p < .05$) differ from zero and changes in model deviance and AIC indicated removal of the variable did not significantly decrease model fit.

3 | RESULTS

3.1 | Qualitative trends in dry season reproduction

Total reproductive activity across all species varied substantially within and among years. Within years, reproductive activity generally declined from early through late dry season, but individual species showed various patterns (Figure 1). Across all transects and years, at least 47 (excluding incompletely identified species) fleshy-fruited species were observed with some dry season reproductive activity (Table S2). Regardless of the year or dry season period, most species made small contributions to total reproductive activity within transects, possibly reflecting their local canopy cover. However, ~70% of species were observed with above average reproductive activity on at least one transect during at least one survey, though we did not see evidence suggestive of masting. Only eight species made above average contributions to total reproductive activity across at least three transects and 5 years (Figure 1), though five additional species made sizeable contributions to particular reproductive phenophases, as described below or shown in Figures 2 and 3. There were few distinct species-specific within-dry season trends for total reproductive activity except *Chiococca* spp. and *Lasiacis divaricata* typically made their highest contributions to reproductive activity in the early or mid-dry season. *Bursera simaruba* made its highest contribution in the mid or late dry season.

Overall, dry season reproductive activity was dominated by unripe fruit. Across all transects and surveys, flower abundance averaged (grand median) less than 1% of total reproductive activity, but often showed an increase between mid and late dry season (Figure 2, grand median % of late dry season reproductive activity = 4.8). Only five species made consistent (≥5 years) above average contributions to flower abundance (Figure 2). The sizeable relative contributions of *Lantana bahamensis*, *L. involucrata*, and *Erithalis fruticosa* were partly a function of their multi-small-flowered inflorescences, but their contributions were also consistently high across all years. *E. fruticosa* and *L. involucrata* made large contributions to flower abundance throughout the dry season, while *L. bahamensis* was more variable.

Ripe fruit averaged ~6.7% of total reproductive activity across all transects and surveys. Its greatest relative contribution typically occurred during the mid-dry season (Figure 3; median % of reproductive activity = 13.3) when five species made consistently high contributions to ripe fruit counts: (1) *Bourerria ovata*, (2) *Lasiacis divaricata*, (3) *Erithalis fruticosa*, (4) *Lantana involucrata*, and (5) *Psychotria* spp. (Figure 3). However, the latter three species also made sizeable contributions to ripe fruit counts in other dry season periods in at least 5 survey years, particularly in late dry season when *Eugenia axillaris* also showed consistently high contributions.

3.2 | Factors influencing dry season phenophase abundance

HCM models of average flower and fruit abundance across all years and transects supported qualitative within-dry season trends described above. Flower abundance was similarly high during the early and late dry season and lowest during the mid-dry season (Table 1, π_{1jk} π_{2jk}; Figure 4), while fruit abundance (ripe + unripe) showed a near-constant decline through the dry season (Table 2, π_{1jk}; Figure 5). The separate abundances of ripe and unripe fruit were highly correlated across all surveys (Spearman's rho = .69), but the percentage ripe fruit generally showed a peak in the mid-dry season (Table 3, π_{1jk} π_{2jk}; Figure 6).

Variance partitioning in HCM models indicated the bulk of variation in flower and fruit abundance was within transects through the dry season. However, of the total variation observed in flower abundance among surveys, ~2% was attributed to variation among years (i.e., interannual climate variation) while 47% was variation among transects (i.e., local environmental conditions). For fruit abundance, 9% of the total variation was among years and 14% was among transects.

For both phenological stages, increasing precipitation 21–50 days before a survey had a positive influence on abundance, but the effect was most pronounced in the late dry season (Table 1, π_{4jk}; Table 2, π_{3jk}). Average minimum temperature during December–February also influenced flower abundance such that years with

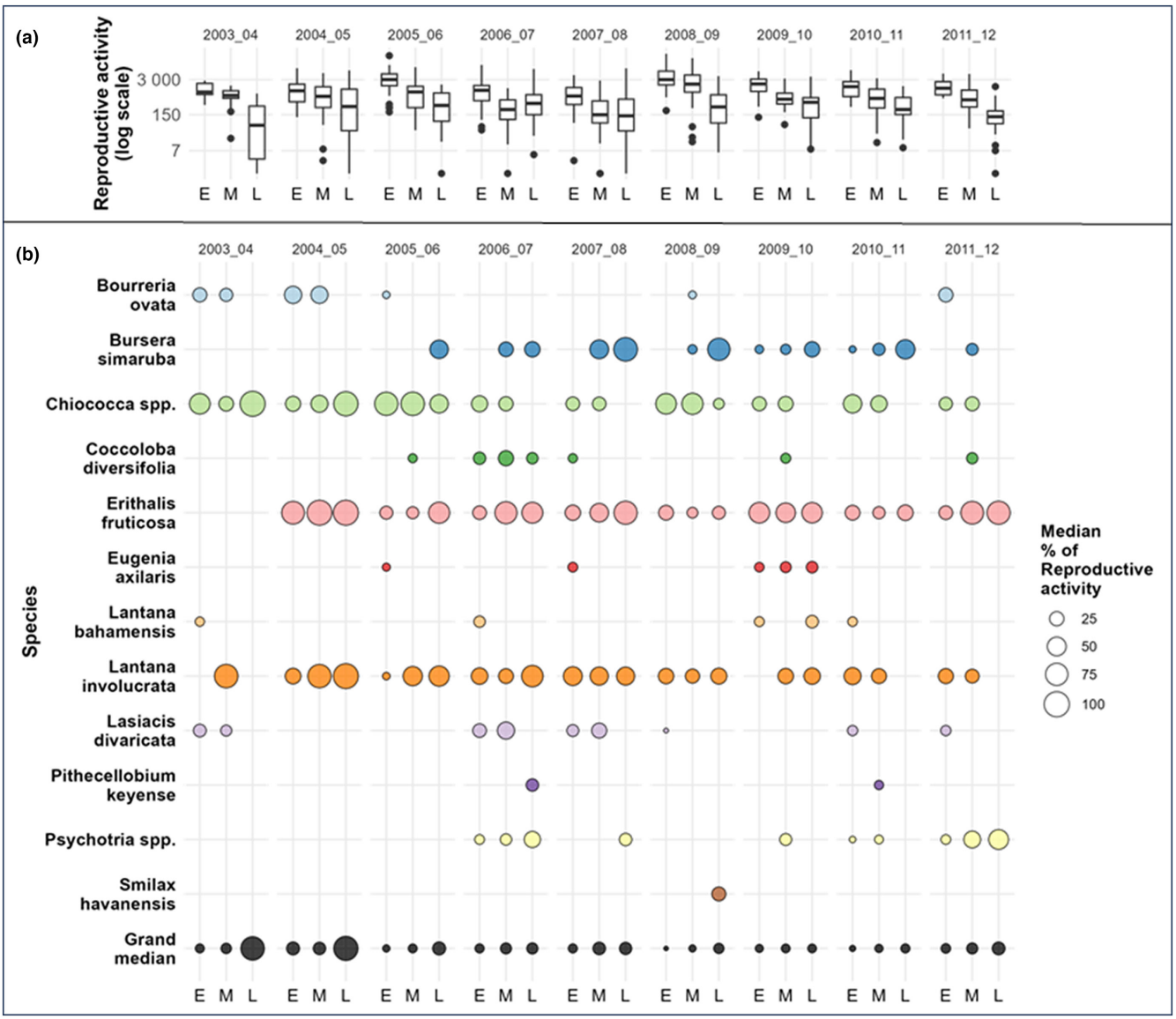

FIGURE 1 Temporal variation in total reproductive activity (a) and relative species-specific contributions (b). Total reproductive activity is the combined number of flowers, unripe fruit, and ripe fruit across all transects surveyed during the early (E, November–December), mid (M, January–February), and late (L, March–April) dry season over 9 years (2003–2011) on Eleuthera, The Bahamas. Species-specific contributions reflect the median percent of total reproductive activity comprised by that species across all transects where it was reproductively active during that survey. With the exception of *Pithecelobium keyense* (see Discussion), species-specific contributions are shown only for species with above average contributions (relative to the grand median across all reproductively active species) by at least one phenophase (see Figures 4 and 5) across at least three transects in a survey period in at least 5 years.

higher minimum mid-dry season temperatures had higher late dry season flower abundance (Table 1: β_{01}, β_{11}, and β_{21}). We did not find strong evidence for effects of precipitation or mid-dry season minimum temperatures on the percentage ripe fruit. However, time of dry season alone explained only 7% of the variance in the percentage ripe fruit among surveys within transects, while time and precipitation together explained 13% and 45%, respectively, of the among-survey variation in flower and total fruit abundance.

Local environmental conditions influenced flower abundance, fruit abundance, and the percentage ripe fruit. Compared to older transects or those with low groundwater, younger transects (Table 1: γ_{02}) and those with moderate to high groundwater resources (Table 1: γ_{01}) had more flowers throughout the dry season (Table 1: γ_{02} and Table 1: γ_{01}, respectively; Figure 4a,b) and showed a lower rate of decline in the fruit abundance through the dry season (Table 2: γ_{12} and Table 2: γ_{11}, respectively; Figure 5a,b). The percentage ripe fruit was also generally higher on younger transects throughout the dry season (Table 3: γ_{02}; Figure 6a), but transects with higher groundwater did not necessarily show an advantage until the late dry season (Table 3: γ_{01}, γ_{11}, γ_{21}; Figure 6b).

Compared to the northernmost transects, the southernmost transects showed an almost linear increase in flower abundance through the dry season (Table 1: γ_{13} and γ_{23}) due to lower flower abundance in the early dry season but less difference by the late

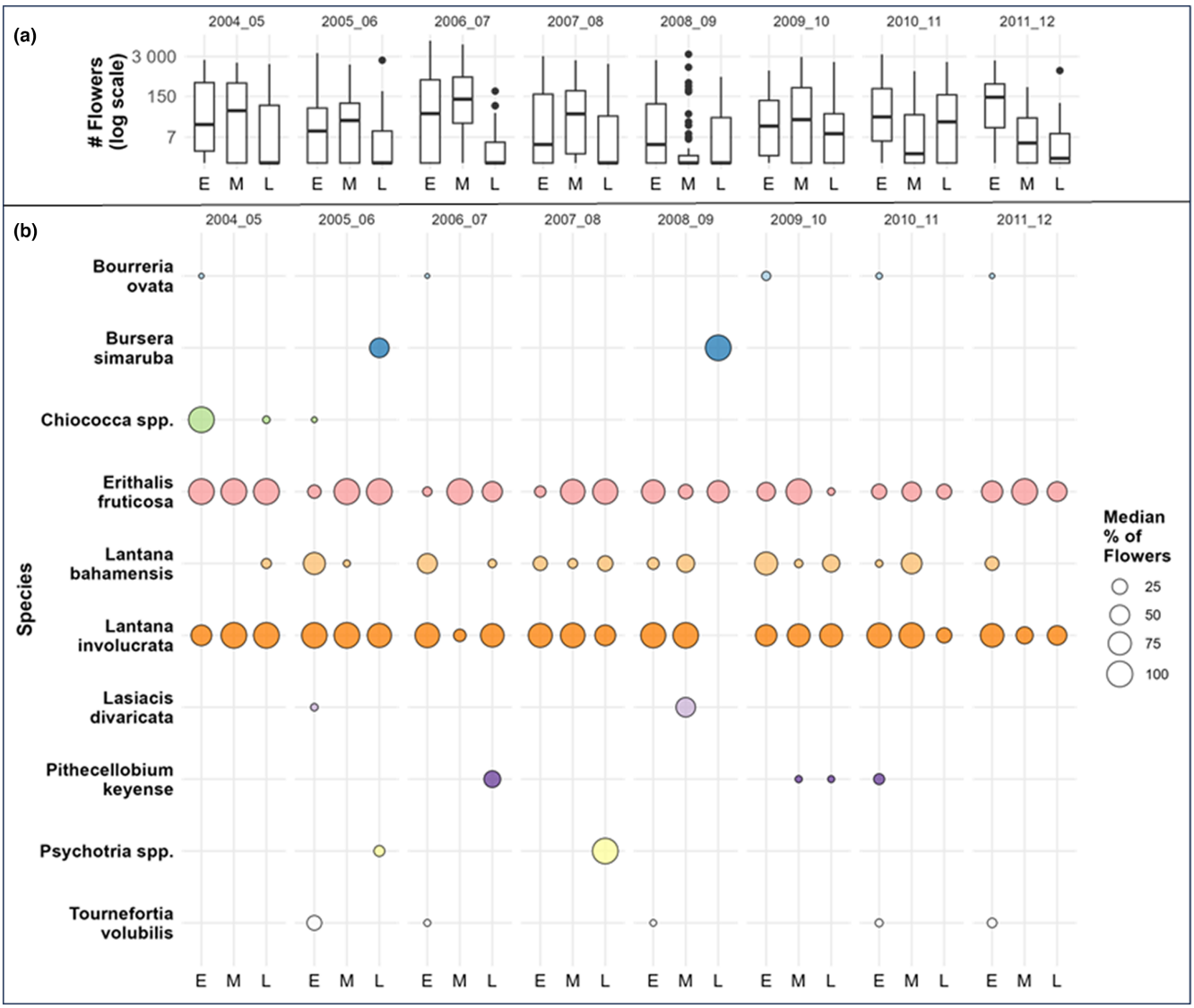

FIGURE 2 Temporal variation in flower abundance (a) and relative species-specific contributions (b). Flowers were counted during the early (E, November–December), mid (M, January–February), and late (L, March–April) dry season on Eleuthera, The Bahamas between 2003 and 2012. Species-specific contributions reflect the median percent of total flower abundance comprised by that species across all transects where it was flowering during that survey. With the exception of *Pithecelobium keyense* (see Discussion), species-specific contributions are shown only for species flowering on at least three transects in a survey period and which had above average contributions to at least one reproductive phenophase in at least 5 years.

dry season (Figure 4d). Latitude did not appear to influence the fruit abundance or percentage ripe fruit, but transects closest to the east coast had a lower average fruit abundance than plots further away (Table 2: γ_{01}; Figure 5d). This latter finding was driven by transects in one site (DD) averaging 238 m to the coast, whereas all other transects were over 1 km from the coast. Removal of the DD transects from the analysis removed the effect of distance, suggesting a site effect driven by local conditions (e.g., substrate—see Wunderle Jr. et al., 2014).

Local species composition also contributed to variation in dry season flower and fruit abundance. Transects supporting *Lantana involucrata* generally had higher average flower abundance (Table 1: γ_{03}; Figure 4c), while transects with either *L. involucrata* or *Erithalis fruticosa* had less decline in flower abundance between the early and mid-dry season (Table 1: γ_{11} and γ_{21}; Figure 4c). Transects with *L. involucrata* also had higher fruit abundance on average (Table 2: γ_{01}; Figure 5c).

4 | DISCUSSION

Though focused on early- to mid-successional habitat during the dry season, our study begins to address the scant information on plant phenology patterns in Bahamian subtropical dry forests, elucidating potential reproductive syndromes and environmental drivers of the timing and abundance of fleshy-fruited species' dry season

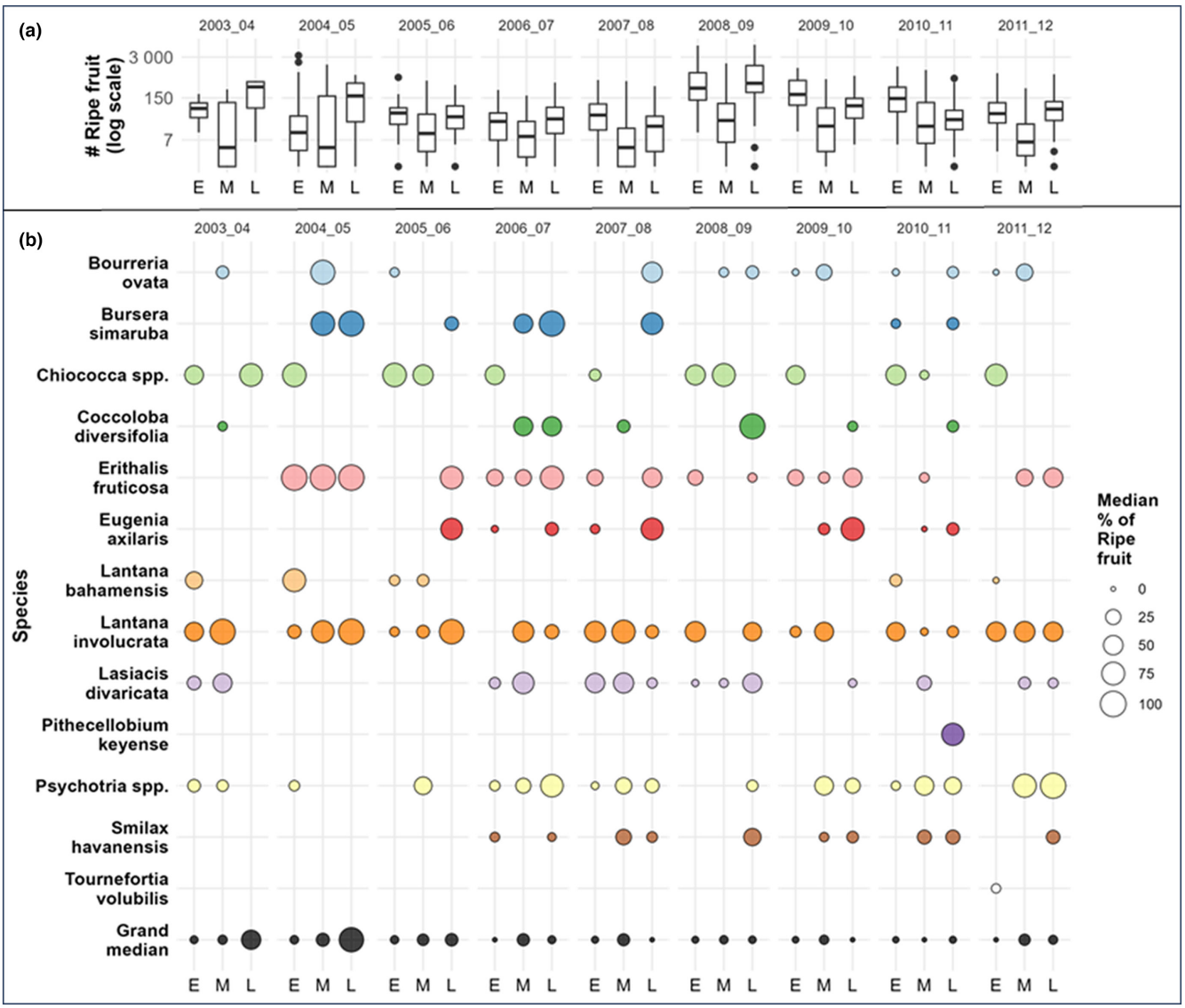

FIGURE 3 Temporal variation in ripe fleshy fruit abundance (a) and relative species-specific contributions (b). Fruit was counted during the early (E, November–December), mid (M, January–February), and late (L, March–April) dry season on Eleuthera, The Bahamas between 2003 and 2012. With the exception of *Pithecelobium keyense* (see Discussion), species-specific contributions are shown only for species with above average contributions to at least one reproductive phenophase (relative to the grand median across all species and transects) across at least three transects in a survey period in at least 5 years.

phenophases. A large proportion of TDF plant species flower or fruit synchronously one or two times per year, though timing of peak activity varies (Mclaren & Mcdonald, 2005; Opler et al., 1980). Although at least 47 fleshy-fruited species in our study showed some dry season reproductive activity, only ~13% showed patterns indicative of dry season peaks in reproductive phenophases, while ~4% demonstrated non-synchronous or continuous dry season flowering and fruiting. The latter are likely important resources for consumers particularly toward the end of the dry season. Regardless of reproductive syndrome, however, the magnitude of reproductive activity during the dry season was driven by climatic variation and, especially, local environmental factors. Consideration of these local factors in the selection of conservation areas may improve long-term outcomes for the approximately 25 avian species consuming fruit in Bahamian TDF (Currie, Wunderle Jr., Ewert, Anderson, et al., 2005; Currie, Wunderle Jr., Ewert, Davis, & Mckenzie, 2005; Emlen, 1977; Franklin & Steadman, 2013), including the near-threatened White-crowned Pigeon (*Patagioenas leucocephala*) and Kirtland's Warbler (IUCN, 2023), plus the endemic Bahama Yellowthroat (*Geothlypis rostrata*).

4.1 | Phenology patterns

Of the species encountered on our study sites (Table S2), 79% are described as reproducing throughout the year (Correll & Correll, 1996), but our results suggest greater seasonality in TDFs on Eleuthera. Consistent with Wunderle Jr. et al. (2014), we found

TABLE 1 Results from hierarchical cross-classified linear models estimating flower abundance (log scale) on a transect during winter.

Fixed effects	Coefficient	SE	Df	*p*
Model for average number flowers: $\pi_{0jk}=\theta_0+\gamma_{01}+\gamma_{02}+\gamma_{03}+\beta_{01}$				
Average log flower number in mid-winter, θ_0	0.890	0.303	866	.003
Difference in log flower number for transects with moderate to high groundwater, γ_{01}	0.902	0.371	68	.018
Incremental change log flower number with change in transect age, γ_{02}	−0.081	0.017	68	<.001
Difference in log flower number for transects with *Lantana involucrata*, γ_{03}	1.356	0.401	68	.001
Incremental change log flower number with change in average minimum temperature during Dec-Feb, β01	−0.357	0.138	6	.041
Model for instantaneous rate of change in log flower number with days since 1 October: $\pi_{1jk}=\theta_1+\gamma_{11}+\gamma_{12}+\gamma_{13}+\beta 11$				
Average rate of change in mid-winter, θ_1	0.017	0.004	866	<.001
Difference in rate for transects with *Erithalis fruticosa*, γ_{11}	0.006	0.002	866	.014
Difference in rate for transects with *Lantana involucrata*, γ_{12}	−0.011	0.002	866	<.001
Difference in rate for northern v. southern transects, γ_{13}	−0.015	0.004	866	<.001
Incremental change in rate with change in average minimum temperature during Dec-Feb, β_{11}	0.005	0.001	866	<.001
Model for acceleration in rate of change in log flower number with square of days since 1 October: $\pi_{2jk}=\theta_2+\gamma_{21}+\gamma_{22}+\gamma_{23}+\beta_{21}$				
Average acceleration, θ_2	0.00003	0.0001	866	.681
Difference in acceleration for transects with *Erithalis fruticosa*, γ_{21}	−0.0001	0.0001	866	.022
Difference in acceleration for transects with *Lantana involucrata*, γ_{22}	0.0001	0.0001	866	.317
Difference in acceleration for northern v. southern transects, γ_{23}	0.0003	0.0001	866	.001
Incremental change in acceleration with change in average minimum temperature during Dec-Feb, β_{21}	0.0002	0.00003	866	<.001
Model for rate of change in log flower number with change in precipitation 21–50 d prior: $\pi 3jk=\theta_3$				
Average rate of change in log flower number with change in precipitation 21–50 d prior to mid-winter survey, θ_3	0.010	0.002	866	<.001
Model for moderation of precipitation effect by time of winter: $\pi 4jk=\theta_4$				
Change in precipitation effect for precipitation multiplied by days since 1 October, θ_4	0.0001	0.00005	866	.021
Random Effects: Final estimation of variance components	**Variance**	**chisq**	**d.f.**	***p***
Variation among surveys, e	2.870			
Variation among transects, b_{00j}	1.505	543.83	65	<.001
Variation among years, c_{00k}	0.081	35.58	3	<.001

Note: Coefficients for fixed effects of variables are used to estimate log flower number (Y) at time *i* on transect *j* in year *k* according to the model: $Y_{ijk}=\pi_{0jk}+\pi_{1jk}{}^{*}X_{1ijk}+\ldots.+\pi_{njk}{}^{*}X_{nijk}+e_{ijk}$. A parameter π_{njk} may be further defined by a sub-model incorporating variables differing among transects (W) or among years (Z), for example, $\pi_{njk}=\theta_n+\gamma_{n1}{}^{*}W+\beta_{n1}{}^{*}Z+b_{00j}+c_{00k}$. Random variation in flower number is partitioned among the survey level (*e*), transect level (b_{00j}), and year level (c_{00k}). Only fixed effects associated with a significant reduction in Akaike's information criterion ($\Delta AIC>2$) and model deviance (likelihood ratio test, $p<.05$) were retained, but the significance (*p*-value) of effects based on univariate *t*-tests is also shown.

overall reproductive activity of fleshy-fruited plants generally declined across the dry season, primarily as a consequence of reduced fruiting, while flowering increased in the late dry season. This is consistent with patterns seen for trees in Jamaican TDF on limestone substrate (Mclaren & Mcdonald, 2005) and with late dry/early wet season flowering typical of TDFs elsewhere (e.g., De Lampe et al., 1992; Frankie et al., 1974). We are unaware of community-level reproductive phenology studies in The Bahamas, but these patterns suggest peak flowering on Eleuthera occurs in the late dry to early wet season.

The majority of reproductive species on our transects were likely supporting fruit with variable development and ripening times initiated after wet season flowering peaks. Among the few species displaying a consistent dry season phenological pattern was *Chiococca alba*, with ripe fruit abundance peaking in the early to mid-dry season as also observed in Puerto Rico (Acevedo-Rodríguez et al., 1985). By contrast, fruits of *Bursera simaruba* typically showed the highest relative abundance in the mid to late dry season, with ripe fruits most pronounced in the late dry season. In other tropical regions, *B. simaruba* is known to flower in the late

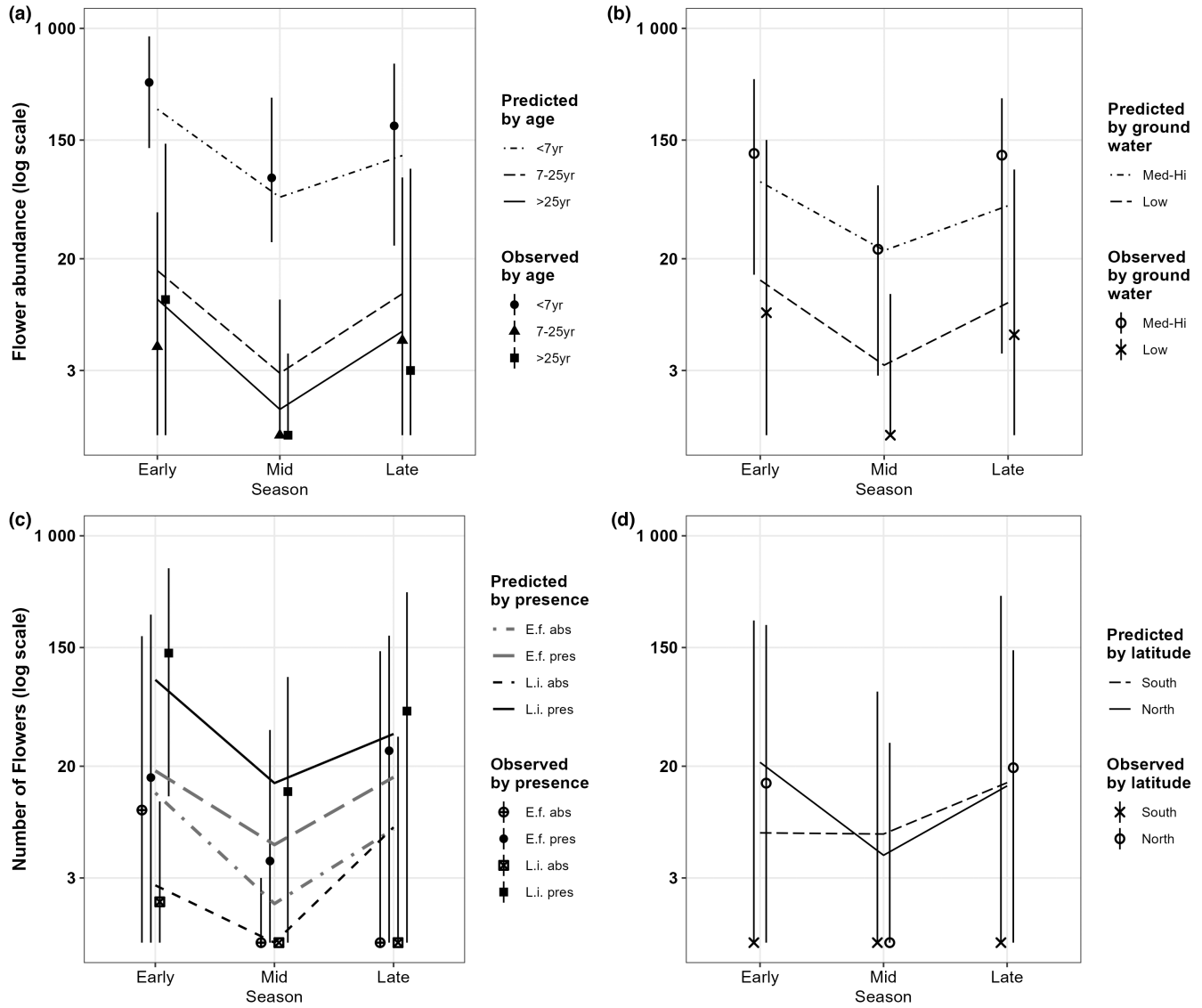

FIGURE 4 Temporal dry season variation in flower abundance (natural log scale) as a function of environmental factors: (a) relative transect age; (b) groundwater resources; (c) absence (abs) or presence (pres) of *Lantana involucrata* (L.i.) or *Erithalis fruticosa* (E.f.); or (d) relative latitude (southernmost *v.* northernmost transects). Flower abundance was measured during the early (November–December), mid (January–February), and late dry season (March–April) between 2004 and 2011. Lines show model predictions adjusting for the influence of all other relevant variables (Table 1) using their average values across the specific transects included in each time of season by environmental condition combination. Point symbols and vertical whiskers show the median and interquartile range, respectively, of flower abundance within each combination.

dry/early wet season. Fruits ripen asynchronously over long durations up to the onset of the next flowering period when any remaining fruit is dropped *en masse* (Greenberg et al., 1995; Hulshof et al., 2012).

Asynchrony in fruit ripening at the individual or population level may be advantageous for seed dispersal by providing a predictable food source for seed dispersers. *B. simaruba* fruits have been observed in abundance during even the driest seasons in TDFs (Almazán-Núñez et al., 2015; Cortés-Flores et al., 2019), and steady availability of asynchronously ripening *Bursera* fruit can support the establishment and defense of territories by avian seed dispersers (Greenberg et al., 1995). *Bursera* fruits on our study sites were consumed by multiple bird species, which could have kept the observed standing crop of ripe fruit low until the late dry season just prior to a mass shedding of remaining fruit.

While continuous reproduction (i.e., individuals flowering/fruiting year-round) is less common among TDF plants (Murphy & Lugo, 1986), two species on our study sites showed evidence of continuous, or at least multi-episodic, reproduction. *Lantana involucrata* and *Erithalis fruticosa* produced both flowers and fruit throughout the dry season and showed consistently high contributions to the overall reproductive activity on individual transects. Because we did not track individual plants in our study, we cannot be certain the reproductive activity we observed reflected continuous individual

TABLE 2 Results from hierarchical cross-classified linear models estimating the fruit abundance (number of unripe and ripe fruits, log scale) on a transect during winter.

Fixed effects	Coefficient	SE	Df	*p*
Model for average fruit abundance: $\pi_{0jk}=\theta_0+\gamma_{01}+\gamma_{02}$				
Average log fruit abundance in mid-winter, θ_0	5.896	0.270	854	<.001
Incremental change log fruit abundance with change distance (km) to the east coast, γ_{01}	0.001	0.0002	68	<.001
Difference in log fruit abundance for transects with *Lantana involucrata*, γ_{02}	0.440	0.177	68	.016
Model for rate of change in log fruit abundance with days since 1 October: $\pi_{1jk}=\theta_1+\gamma_{11}+\gamma_{12}$				
Average rate of change, θ_1	−0.022	0.002	854	<.001
Difference in rate for transects with moderate to high groundwater, γ_{11}	0.007	0.002	68	.005
Incremental change in rate with change in transect age, γ_{12}	−0.001	0.0001	68	<.001
Model for rate of change in log fruit abundance with change in precipitation 21–50 d prior: $\pi_{2jk}=\theta_2$				
Average rate of change in log fruit abundance with change in precipitation 21–50 d prior to mid-winter survey, θ_2	0.005	0.002	854	.03
Model for moderation of precipitation effect by time of winter: $\pi_{3jk}=\theta_3$				
Change in precipitation effect for precipitation multiplied by days since 1 October, θ_3	0.0001	0.00004	854	.004

Random Effects: Final estimation of variance components	Variance	chisq	d.f.	*p*
Variation among surveys, *e*	1.483			
Variation among transects in the average fruit abundance, b_{00j}	0.418	306.00	68	<.001
Variation among transects in the rate of change, b_{10j}	0.00003	115.04	68	<.001
Variation among years in the average fruit abundance, c_{00j}	0.468	378.77	6	<.001
Variation among years in the rate of change, c_{10j}	0.00002	27.74	6	<.001

Note: Coefficients for fixed effects of variables are used to estimate the log fruit abundance (Y) at time *i* on transect *j* in year *k* according to the model: $Y_{ijk}=\pi_{0jk}+\pi_{1jk}{}^{*}X_{1ijk}+....+\pi_{njk}{}^{*}X_{nijk}+e_{ijk}$. A parameter π_{njk} may be further defined by a sub-model incorporating variables differing among transects (W) or among years (Z), for example, $\pi_{njk}=\theta_n+\gamma_{n1}{}^{*}W+\beta_{n1}{}^{*}Z+b_{00j}+c_{00k}$. Random variation in the average abundance and its rate of change through winter is partitioned among the survey level (e), transect level (b_{00j}, b_{10j}), and year level (c_{00k}, c_{10k}). Only fixed effects associated with a significant reduction in Akaike's information criterion ($\Delta AIC>2$) and model deviance (likelihood ratio test, $p<.05$) were retained, but the significance (*p*-value) of effects based on univariate *t*-tests is also shown.

flowering or fruiting rather than reproductive asynchrony within the local population. However, dry season surveys of individuals of both species by Wunderle Jr. et al. (2014) showed they supported fruit throughout the dry season even if abundance generally declined. Furthermore, our analyses showed both an early and late dry season peak in flowering on transects supporting these species (Figure 4). This suggests some individuals may reflower in the late dry season after shedding a fruit crop derived from early dry season flowering—a phenomenon we have anecdotally observed for both species on Eleuthera.

Continuous or asynchronous reproduction can be advantageous for early successional shrub species such as *Erithalis fruticosa* and *Lantana involucata*. Seeds of both species can germinate relatively soon after dispersal during both dry and wet seasons, though germination is highest in bare soil and open canopy conditions (Fleming et al., 2015). Year-round reproduction by individuals or the population can aid colonization of newly disturbed sites as they appear on the landscape. Asynchronous and multi-episodic reproduction can also reduce intraspecific competition for resources, including pollinators and dispersers (Rathcke & Lacey, 1985; Schubert & Walters, 2022), which may be important during the dry season given spatial and temporal variability in insect abundance (Wunderle Jr. et al., 2014).

4.2 | Environmental drivers

Long-term climate trends and biotic interactions (i.e., pollinators, dispersers, and predators) are viewed as the main drivers of phenological patterns in tropical systems (Mendoza et al., 2017). The consistent temporal patterns of dry season reproductive activity we observed are indicative of such long-term co-evolutionary processes, yet our study also shows that near-term events and, especially, local abiotic conditions exert substantial influence on the abundance of flowers and fruit present at any given time of dry season within TDF on Eleuthera. Both timing and quantity of reproduction are

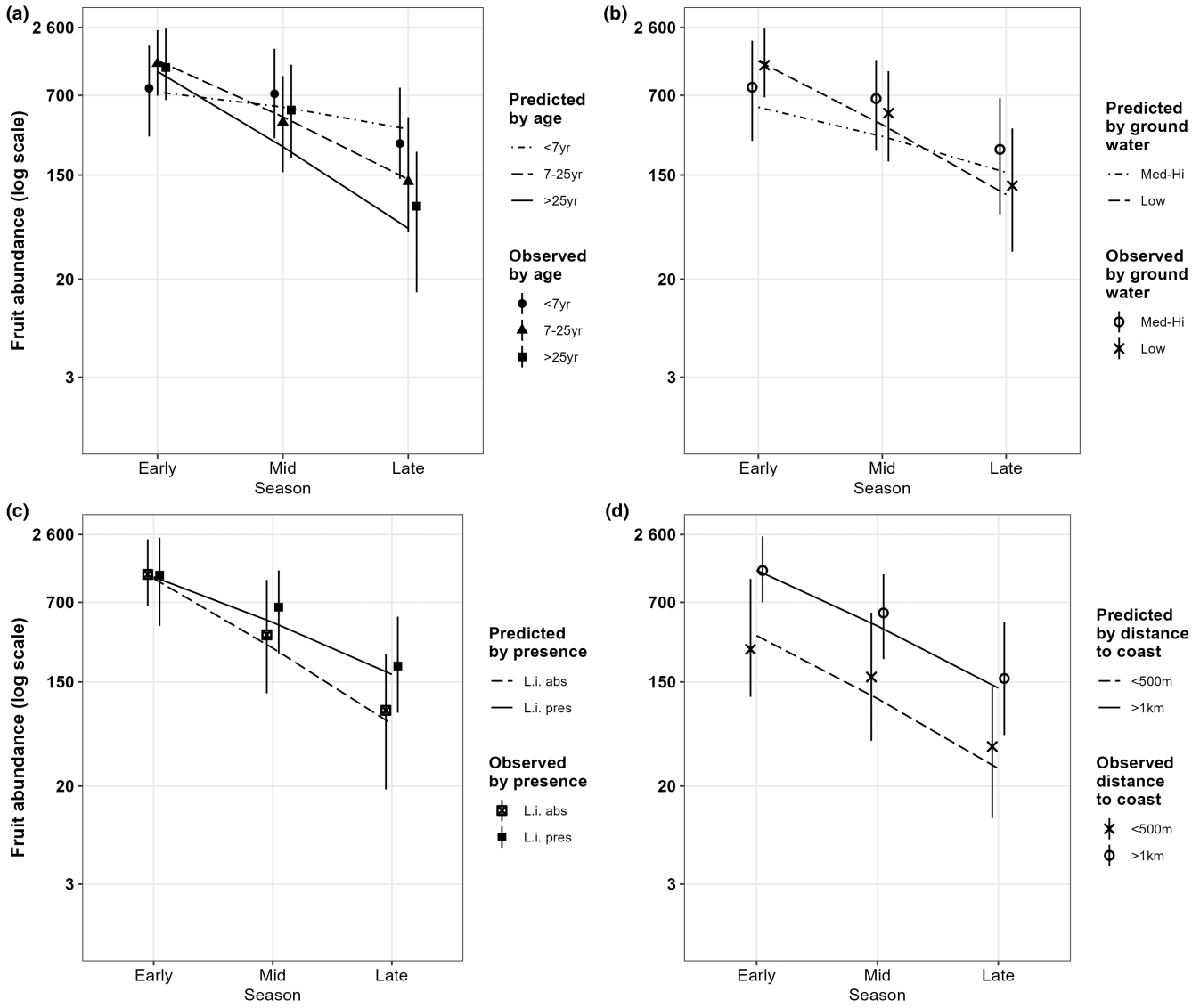

FIGURE 5 Temporal dry season variation in total fruit abundance (ripe + unripe; natural log scale) as a function of environmental factors: (a) relative transect age; (b) groundwater resources; (c) presence of *Lantana involucrata*; or (d) distance to the east coast of Eleuthera, The Bahamas. Fruit abundance was measured during the early (November–December), mid (January–February), and late (March–April) dry season between 2003 and 2011. Lines show model predictions adjusting for the influence of all other relevant variables (Table 2) using their average values across the specific transects included in each time of season by environmental condition combination. Point symbols and vertical whiskers show the median and interquartile range, respectively, of fruit abundance within each combination. Note the differing slopes of the lines in (c) are not a function of model coefficients but of the particular set of plots included in each of the categories. Also, the effect in (d) is driven by a group of plots at one site very near the east coast; see text for discussion.

important to ecosystem processes, but they are rarely studied together (Mendoza et al., 2018).

Although flowering of some tropical species is triggered by a sustained drop in air temperatures (Gunarathne & Perera, 2014), the number of flowers produced may be higher in warmer years (Sakai & Kitajima, 2019). We found less extreme mid-dry season temperatures were associated with a greater abundance of flowers several weeks later. Rather than simply enhancing activity of common late dry season flowering species, however, the warmer temperatures appeared to stimulate flowering of species not typically observed with significant late dry season flowering activity on our transects. For example, *Pithecellobium keyense* and *Psychotria* sp. showed unusually high contributions to late dry season flower abundances following the warm winter dry seasons of 2006–2007 and 2007–2008, respectively (Figure 2). Because mild winter temperatures may also facilitate activity of insect pollinators (Pascarella, 1998; Rathcke, 2001), fruit abundance during the wet season could also be enhanced.

The positive relationship we observed between dry season flower and fruit abundance and prior rainfall, especially toward the end of the dry season, is consistent with other work demonstrating the importance of water availability to fleshy-fruited plant

TABLE 3 Results from hierarchical cross-classified linear models estimating the percentage of all fruit that were ripe (log scale) on a transect during winter.

Fixed effects	Coefficient	SE	Df	*p*
Model for log percentage ripe fruit: $\pi_{0jk}=\theta_0+\gamma_{01}+\gamma_{02}$				
Average log % ripe fruit in mid-winter, θ_0	2.634	0.118	907	<.001
Difference in log % ripe fruit for transects with moderate to high groundwater, γ_{01}	−0.539	0.161	69	.001
Incremental change log % ripe fruit with change in transect age, γ_{02}	−0.020	0.005	69	<.001
Model for instantaneous rate of change in log percentage ripe fruit with days since 1 October: $\pi_{1jk}=\theta_1+\gamma_{11}$				
Average rate of change in mid-winter, θ_1	−0.001	0.001	907	.363
Difference in rate for transects with moderate to high groundwater, γ_{11}	0.005	0.002	907	.001
Model for acceleration in rate of change in log percentage ripe fruit with square of days since 1 October: $\pi_{2jk}=\theta_2+\gamma_{21}$				
Average acceleration, θ_2	−0.0002	0.00002	907	<.001
Difference in acceleration for transects with moderate to high groundwater, γ_{21}	0.0001	0.00004	907	.015
Random effects: Final estimation of variance components	**Variance**	**chisq**	**d.f.**	***p***
Variation among surveys, e	1.148			
Variation among transects, b_{00j}	0.064	123.10	68	<.001
Variation among years, c_{00k}	0.074	79.64	6	<.001

Note: Coefficients for fixed effects of variables are used to estimate the log percentage ripe fruit (Y) at time *i* on transect *j* in year *k* according to the model: $Y_{ijk}=\pi_{0jk}+\pi_{1jk}{}^{*}X_{1ijk}+....+\pi_{njk}{}^{*}X_{nijk}+e_{ijk}$. A parameter π_{njk} may be further defined by a sub-model incorporating variables differing among transects (W) or among years (Z), for example, $\pi_{njk}=\theta_n+\gamma_{n1}{}^{*}W+\beta_{n1}{}^{*}Z+b_{00j}+c_{00k}$. Random variation in percentage ripe fruit is partitioned among the survey level (*e*), transect level (b_{00j}), and year level (c_{00k}). Only fixed effects associated with a significant reduction in Akaike's information criterion ($\Delta AIC > 2$) and model deviance (likelihood ratio test, $p < .05$) were retained, but the significance (*p*-value) of effects based on univariate *t*-tests is also shown.

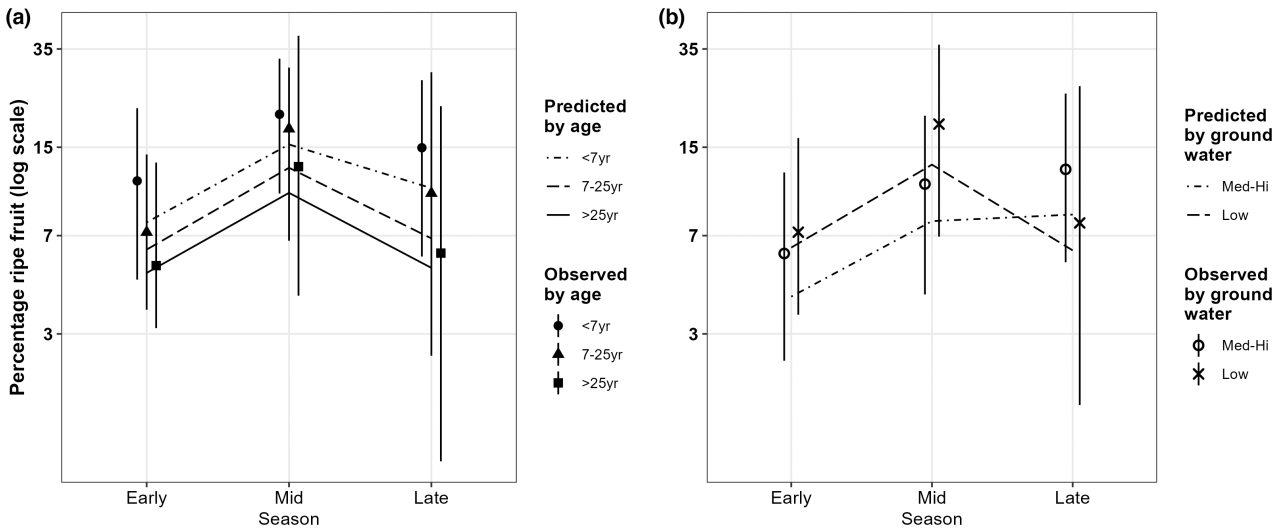

FIGURE 6 Temporal dry season variation in the percentage of fruit that were ripe (natural log scale) as a function of environmental factors: (a) relative transect age or (b) groundwater resources. Percentage ripe fruit abundance was measured during the early (November–December), mid (January–February), and late (March–April) dry season between 2003 and 2011 on Eleuthera, The Bahamas. Lines show model predictions adjusting for the influence of all other relevant variables (Table 3) using their average values across the specific transects included in each time of season by environmental condition combination. Point symbols and vertical whiskers show the median and interquartile range, respectively, of fruit abundance within each combination.

reproduction (e.g., Chen et al., 2017). However, climate is not the only determinant of water availability, and variance partitioning in our models indicates local abiotic conditions can be more influential than interannual climate variation. Some local conditions may arise from geographically driven climate variation. For example, conditions generally become warmer and drier moving southward through the archipelago (Sealey, 2006). This could explain the latitudinal difference we observed in the early dry season flower abundance if

such conditions lead to an earlier end to the late summer/fall flowering period at more southerly locations. Geographic position can also influence local edaphic conditions. Low fruit abundance on our group of east coast transects was likely reflective of low water availability given the well-drained sandy soils at the DD site. Regardless of latitude or longitude, however, accessibility of groundwater was favorable for flower and fruit abundance within transects, especially in the driest period of the year. Wunderle Jr. et al. (2014) found late season fruit abundance was positively related to arthropod abundance, which indicates localized groundwater patches on Bahamian islands support multiple late dry season resources important to birds preparing for vernal migration (see also Akresh et al., 2019). Thus, greater attention to the links between consumer food resources and water table depth in TDF systems is warranted.

Successional stage also influences local abiotic conditions, especially light availability. The increased flower and fruit abundance we observed on more recently disturbed transects has been found in younger seres elsewhere (Blake & Loiselle, 1991; Levey, 1988; Martin, 1985). Second growth species reproduce over longer periods and produce larger fruit crops relative to species that grow in the shaded understory of mature forests (Denslow et al., 1986; Opler et al., 1980). Light limitation contributes to these differences, because open-grown individuals of many species produce more fruit than shaded conspecifics (Clark & Clark, 1987; Jordano, 1982). On our study sites, we generally observed *Chiococca alba* shrubs present in the shaded understory of tall TDF (>37 years since disturbance) rarely produced flowers or fruit in contrast to the species' more abundant reproduction on our younger transects.

4.3 | Conclusions

The fleshy fruits produced during the winter dry season in Bahamian TDF provide critical resources for both resident and migratory frugivorous birds (Currie, Wunderle Jr., Ewert, Anderson, et al., 2005; Wunderle Jr. et al., 2010). While overall abundance of fleshy fruits declines through the dry season, certain sites (e.g., close to the freshwater lens) and certain species (e.g., *Lantana involucrata* and *Erithalis fruticosa*) are the most likely to support these fruit resources, as well as pollinator attracting flowers, in the late dry season. Wunderle Jr. et al. (2014) observed banded Kirtland's Warblers moving from fruit-poor to fruit-rich sites in the late dry season and an unusually high late dry season concentration of birds at one study site with high groundwater resources and abundant *L. involucrata* fruit. This and other similar habitat patches likely function as a "keystone habitat" (Levey, 1990) for frugivores during a period of fruit scarcity driven by "typical" climate and phenological patterns. In the face of global climate change, which may increase the incidence of droughts and other extreme weather events (Neelin et al., 2006), such habitats should be prioritized for conservation to help maintain biodiversity in both the Bahamian landscape and the breeding grounds of Bahamian winter migrants.

AUTHOR CONTRIBUTIONS

JMW and DE conceived and obtained funding for the study. DC and JDW assisted with study design. EH developed remote sensing-based habitat maps. DC, JDW, and GF supervised data collection and management. GF conducted all analyses and lead the writing of the manuscript with critical input from all authors. All authors approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data supporting the findings in this work will be made openly available through the US Forest Service Research Data Archive: https://www.fs.usda.gov/rds/archive/.

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SUPPORTING INFORMATION

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

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