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No. 93 Caribbean Naturalist 2023

The *Caribbean Naturalist . . .*

- A peer-reviewed and edited interdisciplinary natural history science journal with a regional focus on the Caribbean (ISSN 2326-7119 [online]).
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Cover Photographs: Collection of arthropod taxa typical of foliage and ground surface samples in The Bahamas and Caribbean. Although the photographs were taken in different locations in the Caribbean and The Bahamas they represent taxa typical of those on Eleuthera. Outer photos clockwise from the top include an ant (*Pheidole megacephala*, Formicidae, Hymenoptera; photograph © Mark Yokoyama); caterpillar (Geometridae, Lepidoptera; photograph © Mark Yokoyama); weevil (Curculionoidea, Coleoptera; phtograph © Mark Yokoyama); leafhopper (Cicadellidae, Hemiptera; photograph © Mark Yokoyama); kaytdid nymph (Tettigonidae, Orthoptera; photograph © Mark Yokoyama); Cerembicid beetle (Cerembicidae, Coleoptera; photograph © Dave Currie; bee fly (Bombyliidae, Diptertodea; photograph © Dave Currie); carpenter ant (Camponotus, Formicidae, Hymenoptera; photograph © Mark Yokoyama); jumping spider (Salticidae, Aranea; photograph © Mark Yokoyama); bush cricket (Tettigonidae, Orthoptera; photograph © Dave Currie). Inner photos clockwise from top include: ant (Formicidae) attending aphids (Hemiptera; photograph © Mark Yokoyama); wall crab spider (Thomisidae, Aranea; photograph © Mark Yokoyama); and cockroach (Blattodea; photograph © Mark Yokoyama).

The ***Caribbean Naturalist*** (ISSN # 2326-7119) is published by the Eagle Hill Institute, PO Box 9, 59 Eagle Hill Road, Steuben, ME 04680-0009. Phone 207-546-2821, FAX 207-546-3042. E-mail: office@eaglehill.us. Webpage: www.eaglehill.us/cana.

Periodical postage paid in Steuben, ME and additional mailing offices. **Special issue proposals are welcome**. On-line secure subscription ordering: rate per year for Caribbean subscribers - $15 regular, $10 students, $75 organizations; for Non-Caribbean subscribers - $20 regular, $15 students, $100 organizations. **Authors**: submission guidelines are available at www.eaglehill.us/cana. **Co-published journals:** The *Northeastern Naturalist* (ISSN 1092-6194 [print], ISSN 1938-5307 [online]), the *Southeastern Naturalist* (ISSN 1528-7092 [print], ISSN 1938-5412 [online]), and the *Urban Naturalist* (ISNN #2328-8965), journals with separate Boards of Editors. The Eagle Hill Institute is a tax exempt 501(c)(3) nonprofit corporation of the State of Maine (Federal ID # 010379899).

The Effects of Rainfall on Foliage and Ground Arthropod Availability for Kirtland's Warblers and Other Gleaning Insectivores in the Late Dry Season in The Bahamas

Joseph M. Wunderle Jr.[1,*], Patricia K. Lebow[2], David N. Ewert[3], Jennifer D. White[1], and Dave Currie[1]

Abstract - Effects of dry-season rains in the tropics may vary among arthropod taxa with potential consequences for arthropod consumers. To study rainfall effects on availability of different arthropod prey for *Setophaga kirtlandii* (Kirtland's Warbler) and other surface-gleaning avian insectivores, we sampled late dry-season (March–April) arthropods over 9 years in an early succession dry forest on Eleuthera, The Bahamas. We sampled arthropods on foliage (with branch clips) and on the ground surface (with 5-min scans) to document variation in biomass and occurrence with prior rainfall for different taxa. We ran mixture models separately for foliage and ground samples with biomass or occurrence of a specified arthropod group as the response variable. Models included the covariates: sample site, year, days after 1 March, and prior cumulative rain amount or number of days with rain in periods of different lengths. Results showed that total biomass of foliage arthropods (predominantly spiders) did not vary with rainfall measures (quantities or prior periods), whereas arthropod occurrence in foliage samples decreased with increases in various rainfall measures reflecting negative response of foliage spiders to rainfall. By contrast, both total biomass and occurence of ground-surface arthropods (predominantly ants and flies) increased in ground samples with rainfall measures, reflecting positive ant biomass responses and positive fly occurrences with rainfall. As the late dry season progressed with days after 1 March, foliage arthropod biomass and occurrence increased with increases in rainfall measures, due to increases in foliage ant biomass and spider occurrences. By contrast, ground arthropod biomass varied little with days after 1 March, but occurrences in ground samples decreased with days after 1 March in models with cumulative rainfall in long-duration periods and with number of rain days in the prior 30 days. Arthropod taxa differed in availability in the late dry season depending on rainfall measure and duration of the prior period with little congruence in rainfall responses between foliage and ground arthropods. These diverse arthropod responses to rainfall are expected to change with increased frequency of heavy downpours and droughts associated with global climate change, resulting in unknown consequences for the Kirtland's Warbler and other gleaning insectivores.

Introduction

In the northern Neotropics and subtropics, the winter corresponds to the dry season, when rainfall decreases as the winter proceeds. Associated with decreased precipitation are declines in availability of arthropods (Johnson and Sherry 2001, Strong

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Manuscript Editors: Craig Layman

and Sherry 2000) and fruit (Griz and Machado 2001, Ramírez 2002, Redwine et al. 2007), which, in turn, can affect reproduction and survival of birds reliant on these resources. Often these declines in food resource are most severe when droughts occur at the end of the dry season. These late-winter droughts can be especially challenging for migrants, such as the near-threatened (IUCN 2023) *Setophaga kirtlandii* (Baird) (Kirtland's Warbler), on their wintering grounds before vernal migration when increased energy intake is needed for pre-migratory fattening (Wunderle et al. 2014). Most research and conservation efforts for the warbler have occurred on its Michigan breeding grounds, where habitat restoration and brood-parasite control have contributed to population recovery (Kepler et al. 1996, Probst 1986). Until recently, however, the warbler and its habitat were poorly studied in The Bahama's wintering grounds despite recognition that events there could compromise breeding-ground conservation efforts (USFWS 1985).

The Kirtland's Warbler overwinters in The Bahamas during the November to April dry season, which can be especially severe in March and April (Sealey 2006). Late winter droughts are exacerbated by the thin soils overlying the archipelago's limestone substrates and, consequently, fruit and arthropod biomass decline at some sites in late winter (Wunderle et al. 2014). Corresponding with winter declines in the warbler's food resources are declines in the warbler's corrected body mass (Wunderle et al. 2014). These results corroborate findings of carryover effects on the breeding grounds, which indicate that reproductive success and annual return to The Bahamas are positively associated with the preceding March rainfall in The Bahamas (Rockwell et al. 2012, 2016).

Although it has been previously demonstrated that availability of fruits favored by the warbler varies with rainfall in The Bahamas (Wunderle et al. 2014), little is known about how different arthropod prey of Kirtland's Warblers and other insectivores vary with winter rainfall. Depending on drought severity, some arthropod populations increase with drying trends, as observed in Araneae (Levings and Windsor 1984, Smith and Robertson 2008, Spiller and Schoener 2008), Coleoptera and Hymenoptera (Smith and Robertson 2008), and Homoptera (Beltrán and Wunderle 2014). Some rainfall-response differences are attributable to differences in drought tolerance among species and temporal and spatial variation in rainfall and edaphic conditions (Hilt et al. 2007, Levings and Windsor 1984, Nyeko et al. 2002). Rainfall can influence arthropod abundance both directly—via physiological effects on reproduction, development, or activity (Chaniotis et al. 1971, Pullin and Knight 1992, Tauber et al. 1998)—and indirectly by affecting food availability or risk of predation or parasitism (Janzen 1973, Spiller and Schoener 1995, Wolda 1978). We predicted arthropod taxa or guilds would differ in their responses to rainfall in the late dry season, thereby affecting availability for insectivores.

To document how late-winter (March–April) availability of various arthropods fluctuates with rainfall, we sampled arthropods from tree and shrub foliage and the ground surface for 9 consecutive years in an early succession dry-forest study site on Eleuthera, The Bahamas. We used sampling methods devised to measure arthropod availability for insectivorous birds that opportunistically glean or pick arthropods

from the ground surface (measured with ground scans; Strong and Sherry 2000) and the foliage of shrubs and trees (measured with foliage clips; Johnson 2000). We adopted these 2 methods because Kirtland's Warblers glean arthropods from surfaces on the ground and foliage of shrubs and trees in The Bahamas (Wunderle et al. 2010), as do other migrant and resident insectivorous birds (Emlen 1977). The efficacy of these 2 methods for sampling arthropod availability for surface-gleaning insectivorous birds has been supported by positive associations of avian insectivore abundance and site fidelity with arthropod biomass on foliage (Johnson 2000, Johnson and Sherry 2001) and on the ground surface (Brown and Sherry 2006, Strong and Sherry 2000) and on both foliage and the ground surface by the Kirtland's Warbler (Wunderle et al. 2014). Although appropriate for assessing availability of arthropod prey for surface-gleaning insectivorous birds foraging at these sites, the 2 methods alone do not sample the entire arthropod communities (Johnson 2000, Kent et al. 2019).

Understanding how arthropod availability varies with rainfall is important for understanding how various taxa will respond to a changing climate with predicted increases in the frequency of extreme rainfall events and intense droughts (Knutson et al. 2010, McLean et al. 2014, Neelin et al. 2006). These extreme weather events are expected to influence arthropod availability (Chen et al. 2019), which, in turn, will have consequences for insectivores, some of which are of conservation concern.

Field-site Description

This study was conducted on Eleuthera (24.9314°N, 76.1900°W), a low-elevation (51 m max) island of 518 km^2 in The Bahamas. Eleuthera's annual rainfall is seasonal, with most of its mean annual rainfall (1090 mm/yr) occurring in the May–October wet season (Sealey 2006). Although variable, rainfall tends to decline during the winter (Sealey 2006). The winter dry season (November–April) and limestone substrate contribute to a dry broadleaf evergreen formation, locally known as coppice, which includes both evergreen and deciduous broadleaf trees and shrubs (Correll 1979, Mooney 1905). Dominant trees include *Vachellia choriophylla* (Cinnecord), *Bursera simaruba* (L.) Sarg. (Gumbo Limbo), *Coccoloba diversifolia* (Pigeon Plum), and *Metopium toxiferum* (L.) Krug. & Urb. (Poisonwood), which are found in mature coppice stands as well as lower-stature early succession stands. Like most Bahamian islands (Byrne 1980), Eleuthera's current undeveloped landscape consists of a mosaic of variably aged vegetation primarily as a consequence of shifting agriculture, fire, or failed development (Helmer et al. 2010, Larkin et al. 2012). Similar disturbances affected our study site bordering the southeastern edge of the Rock Sound settlement, in southern Eleuthera. We selected this study site because of the presence of Kirtland's Warblers (Wunderle et al. 2014) during all winters of the study. The 18.7-ha study site had a gently rolling topography attributable to 2 Pleistocene ridges and associated swales with a north–south alignment. The average age after disturbance on the study site was 18.7 ± 1.2 SE years, resulting in an average canopy height of 2.2 ± 0.5 SE m (Wunderle et al. 2014).

Methods

We sampled arthropods in the foliage and on the ground at the Rock Sound study site during late winter (25 March–15 April) for 9 years (2004–2012). Only a brief overview of the arthropod sampling methods is provided here as the details are found in Wunderle et al. (2014). We established 2 grids on the study site and used a stratified random design to space arthropod sample stations in the grids, independently for foliage and ground arthropods. The 24 sample stations were located >15 m apart along east–west grid trails, and we used a coin toss during each sampling visit to determine the side of the trail for sampling. Starting in 2010, coppice vegetation at the western end of the big grid was cleared for gardens and, therefore, sampling stations were substituted along the east–west grid trails to replace the original stations lost to clearing (2 substitutes in 2010 and 4 substitutes each in 2011 and 2012).

The abundance of ground arthropods was measured during a 5-min interval by a kneeling observer who watched the surface of the ground substrate for arthropods within a 0.25-m^2 quadrat (Strong and Sherry 2000). Upon detection, the observer made attempts to remove individual arthropods (with forceps, aspirators, or fingers) from the quadrat to prevent recounting. We estimate that ~50–70% of individuals were successfully removed from the quadrat during a timed scan. This method samples only the ground-surface arthropod availability and not the total above-ground or leaf-litter availability and is therefore appropriate only for assessing prey availability for birds that pick arthropods from the surface (Strong 2000).

We sampled the abundance of foliage arthropods on 16 species of small trees and shrubs (Table 1) between 0.5 and 3.0 m above the ground based on a species' availability at each sample station. All sampled plant species were evergreen and

Table 1. Number of individuals of each tree or shrub species sampled for foliage arthropods by the foliage-clipping method in late winter (March–April). Sampling was conducted over 9 winters (2004–2012) in Rock Sound, Eleuthera, The Bahamas. Methods are described in the text.

Plant species	Individuals
Cocoloba diversifolia Jacq. (Pigeon Plum)	33
Piscidia piscipula (L.) Sarg. (Jamaican Dogwood)	22
Bourreria ovata Miers (Bahama Strongback)	19
Vachellia choriophylla (Benth.) Seigler & Ebinger (Cinnecord)	15
Eugenia axillaris (Sw.) Willd. (White Stopper)	13
Guapira obtusata (Jacq.) Little (Broadleaf Blolly)	13
Reynosia septentrionalis Urb. (Darling-plum)	13
Ateramnus lucidus (Sw.) Rothm. (Oysterwood)	11
Guapira discolor (Spreng.) Little (Blolly)	10
Sideroxylon salicifolia (L.) Lam. (White Bully)	6
Chiococca alba (L.) Hitch. (Snowberry)	3
Psychotria nervosa Sw. (Wild Coffeee)	2
Crossopetalum rhacoma Crantz (Maidenberry)	1
Erithalis fruticosa L. (Black Torch)	1
Exostema caribaeum (Jacq.) Schult. (Caribbean Princewood)	1
Phyllanthus epiphyllanthus L. (Swordbush)	1

maintained their foliage for the duration of the study, although some nearby tree species (e.g., *Bursera simaruba*) were deciduous and lost leaves in late winter. We used the branch-bagging and clipping methods of Schowalter et al. (1981) and Johnson (2000) as modified by Wunderle et al. (2014). Our method involved placing an open cloth bag, contained within a canvas sweep-sample insect net (38 cm in diameter) over a branch then enclosing the branch and foliage within the cloth bag by quickly closing the bag about the branch. Once surrounded and the bag closed, the branch was cut, sealing the enclosed clipping inside the bag. After cutting the sample branch, we weighed the bag and its enclosed clipping with a Pesola spring scale (±5 g), and obtained the sample clipping weight by subtracting the bag weight. Next, we shook the closed bag, then opened it carefully to allow inspection and capture of arthropods visible on the bag or vegetation. Following the inspection and capture of arthropods in the bag, we made a smaller clipping from the enclosed branch and removed the small clipping. We then placed the small clipping on a light gray cloth on the ground for inspection to capture the remaining arthropods. After inspection and arthropod removal, we lightly beat the smaller clipping sample against the cloth on the ground to dislodge any remaining arthropods and then repeated the clipping and inspection process until the bag was emptied. We tallied all arthropods found on the smaller clippings and the inside of the bag to obtain the total value of arthropods for the original sample clipping. The branch-clipping method inadequately samples flying insects such as large Diptera, Hymenoptera, and Odonata (Johnson 2000), but all of which were poorly (<10%) represented in Kirtland's Warbler fecal samples and foraging observations (J.M. Wunderle, unpubl. data; Wunderle et al. 2014).

We identified all arthropods (insects and spiders) at least to level of order and recorded Formicidae (ants) separately from other Hymenoptera. We measured the length of captured arthropods in the field with a ruler (±0.5 mm), but just estimated the lengths of those individuals that escaped before they could be measured (<10% of individuals). We used the length data in length–weight regressions of Jamaican arthropods (Johnson and Strong 2000) to calculate biomass obtained separately for taxa found above ground (henceforth foliage) or on the ground surface. Biomass of foliage arthropods is reported as milligrams per gram of foliage clip (hereafter "mgm/gm foliage clip" in figures and "mgm/100 gm foliage clip" in text) and biomass of ground arthropods as milligram per 5-min scan of 0.25-m^2 quadrat (hereafter "mgm/0.25 m^2"). Two people worked together to obtain each arthropod sample (i.e., a ground scanner/counter and scribe and a foliage scanner/counter and scribe/scanner). Although different observers were responsible for arthropod identifications and measurements (3 for foliage and 5 for ground arthropods), no significant differences ($P >$ 0.10) were found among observers for arthropod identifications.

We obtained rainfall data from the National Climatic Data Center of the National Oceanographic and Atmospheric Administration for the Nassau International Airport, located 96.6 km west of the Rock Sound study site. Because most rainfall in The Bahamas is derived from cold fronts from the northwest during November through April (Sealey 2006), we believe that the Nassau rainfall represents a reasonable proxy for our study site. To explore the effects of prior rainfall on arthropod

abundance, we used both prior cumulative amount of rainfall (mm) and number of days with rain because differences in responses (arthropod presence/absence or biomass) might vary with rainfall measures (Spiller and Schoener 1995). We used a number of different prior rainfall periods including 30, 60, 90, and 120 days before arthropod sampling to document rainfall response, which may vary with the prior period (Spiller and Schoener 1995).

Statistical analyses

To study the effects of late-winter (March-April) rainfall on arthropod availability in foliage or the ground in samples obtained over 9 winters, we used lognormal-logit (zero-augmented or hurdle) models with mixed effects (Hilbe et al. 2017, Rodrigues-Motta et al. 2015). We ran the models separately for foliage and ground samples with the response variable set as the total biomass of the specified arthropod group at a particular grid station on a specified date. We modelled Araneae (spiders), herbivore/detritivore arthropods, Formicidae, and the total arthropods from the foliage samples, and Araneae, Formicidae, Diptera, and the total arthropods from the ground samples. The foliage herbivore/detritivores guild (henceforth herb/detritivores) consisted of the orders Blattidae, Coleoptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Orthoptera, and Thysanura. The analyses excluded stinkbugs (Pentatomidae) because of their absence in warbler fecal samples from Michigan (Deloria-Sheffield et al. 2001) and Eleuthera, and also their absence from Eleuthera foraging observations (Wunderle et al. 2014).

The lognormal-logit model is a mixture model that assumes the population follows a mixing of 2 populations, one portion that has positive biomass values which follow a lognormal distribution and another portion that models the non-occurrence of arthropods (zero biomass). We fit models with SAS® V9.4 (Cary, NC) software general-purpose Bayesian modeling procedure (SAS/STAT proc MCMC; SAS Institute 2015). Models included days after 1 March and an indicator of amount or occurrence of prior rain period (i.e., prior 30, 60, 90, or 120 days) as covariates for both the biomass and occurrence of arthropods. We considered a covariate to be significant, i.e., it is a likely contributor, if its 95% highest posterior density credible interval (HPD CI) for the covariate's coefficient (β) did not contain zero or if the posterior probability that the coefficient falls in the opposing direction was small ($P_\beta < 0.05$, i.e., the probability the coefficient falls away from zero is high). Note the second criterion is less stringent. Random effects for foliage arthropod samples included winter (year), location (sample station), tree species, and winter*tree species (i.e., interaction of winter by tree species), whereas random effects for ground-surface arthropod samples included winter and location (sample station in the grid). We eliminated random effects following a backward stepwise method until effective sample sizes (for the fitting cycle) were considered sufficient. Before fitting the lognormal-logit models, we fit similar linear mixed effect models to shifted and transformed biomass values to also study effects of winter, location (sample station), and tree species.

For traditional frequentist statistical tests, raw or unadjusted *P* values are reported. For Bayesian modeling, posterior probabilities and credible intervals are used.

We did not consider adjustments for simultaneous testing because failing to detect important potential associations is a much greater concern to us than identifying a potentially false association. The tradeoff between the frequentists' Type I error rate control at the expense of the Type II error rate control can have negative consequences in exploratory studies such as ours (Hurlbert and Lombardi 2003, Moran 2003, Roback and Askins 2005). Correspondingly, there are methods for adjusting posterior probabilities in Bayesian studies (Westfall et al. 2011), but for similar reasons as with frequentists' tests, we have not adjusted our posterior probabilities or credible intervals.

Results

Arthropod biomass and absence

Over the 9 winters (2004–2012) of sampling of foliage arthropods in late winter (March–April; Fig. 1), we found an annual sample mean for all foliage arthropods of 2.607 ± 0.369 SE mgm/100g foliage clip, of which nearly half consisted of Araneae (1.124 ± 0.140), followed by Orthoptera (0.481 ± 0.162), Coleoptera (0.223 ± 0.062), Lepidoptera (0.142 ± 0.048), Homoptera (0.112 ± 0.027), Formicidae (0.073 ± 0.018), Hemiptera (0.031 ± 0.021), Diptera (0.009 ± 0.003), and Hymenoptera excluding Formicidae (0.003 ± 0.003).

In contrast to the ranking of taxa by biomass in foliage samples, over half of the annual late-winter sample mean for ground-surface arthropod biomass of 1.229 ± 0.363 SE mgm/0.25m^2 (Fig. 2) consisted of Formicidae (0.671 ± 0.180), followed by Diptera (0.382 ± 0.148), Coleoptera (0.050 ± 0.038), Araneae (0.033 ± 0.1.35), Orthoptera (0.015 ± 0.010), Hymenoptera excluding Formicidae (0.005 ± 0.005), Colembolla (0.002 ± 0.001), and Homoptera (0.002 ± 0.002).

The arthropod groups differed substantially in the percentage of foliage samples in which different taxa were absent from a sample: e.g., no arthropods = 3.33% (7/210), no Araneae = 11.43% (24/210), no herb/detritivores = 32.38% (68/210), and no Formicidae = 65.71% (138/210). As with foliage arthropods, various arthropod groups differed markedly in the percentage of samples in which various taxa were absent in ground-surface samples: e.g., no arthropods = 2.80% (6/214), no Araneae = 86.91% (186/214), no Diptera = 67.76% (145/214), and no Formicidae = 8.88% (19/214).

Random effects

Foliage arthropod variation with winter, location, and tree species. Winter, grid location (grid sample station), tree species, and winter*tree species were included as random effects in lognormal-logit models run separately for each foliage arthropod biomass response variable (total foliage arthropods, foliage Araneae, foliage herb/detritivores) and separately for each prior rainfall covariate (i.e., prior 30, 60, 90, 120 days). Winter, location (grid sample station), and tree species were substantial components of variation in most models, whereas winter*tree species did not explain attributable variation. Although location and tree species were in all models, winter was a component in only 2 of 8 models in explaining Formicidae, 4

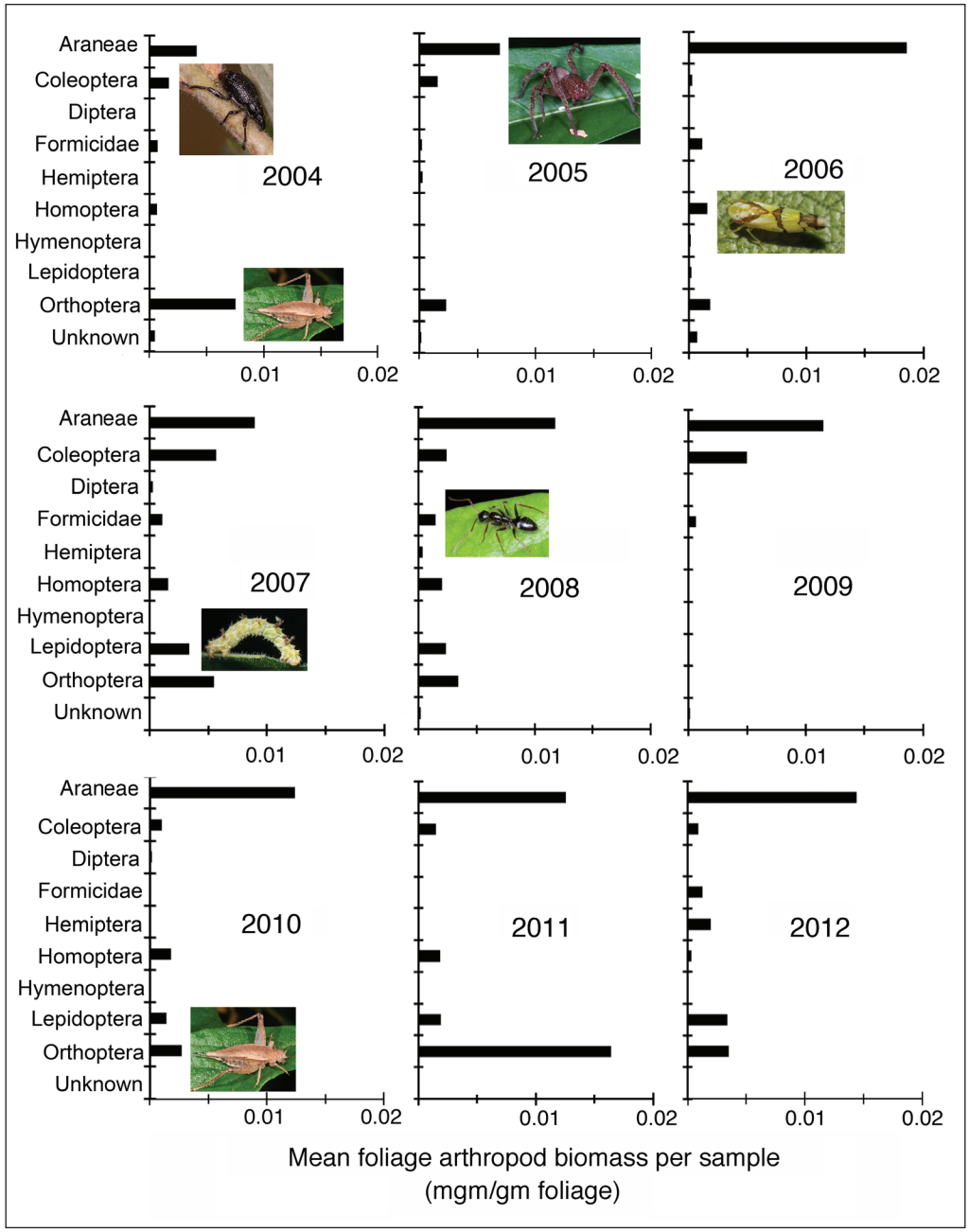

Figure 1. Bar graphs of mean biomass of foliage arthropod taxa (mgm/gm foliage clip) sampled over 9 years (2004–2012) in late winter (25 March–15 April) on 2 grids in second-growth dry forest at Rock Sound, Eleuthera, The Bahamas. Arthropod taxa are shown by order, except for the family Formicidae shown separately from Hymenoptera, which are displayed here without Formicidae. Arthropods were sampled on foliage with a bag and clip technique (Johnson 2000) at 24 sample stations in the 2 grids as summarized in methods and Wunderle et al. (2014). Photographs © Mark Yokoyama.

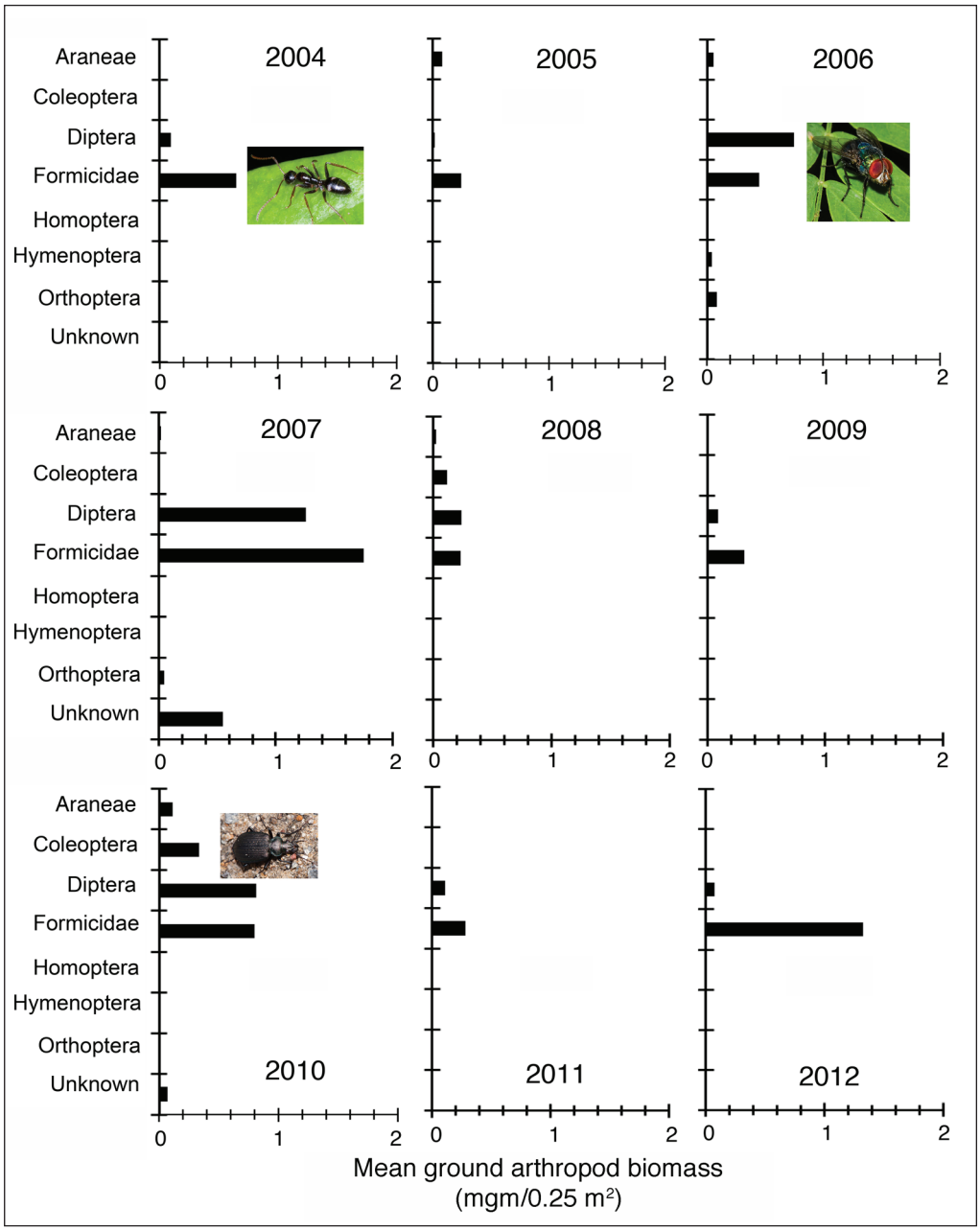

Figure 2. Bar graphs of mean biomass of ground-surface arthropod taxa (mean mgm/0.25 m^2 during 5 min. scan) sampled over 9 years (2004–2012) in late winter (25 March–15 April) on 2 grids in second-growth dry forest at Rock Sound, Eleuthera, The Bahamas. Arthropod taxa are shown by order, except for the family Formicidae shown separately from Hymenoptera, which are displayed here without Formicidae. Arthropods were sampled by scanning the ground surface in a 0.25 m^2 quadrat for 5 minutes (Strong and Sherry 2000) at 24 sample stations as summarized in methods and Wunderle et al. (2014). Photographs © Mark Yokoyama.

of 8 models for total arthropods, 6 of 8 Araneae models, and all of the herb/detritivore models. When winter did occur, it was typically a more substantial component of variation than either location or tree species. Initial linear mixed-effect models based on shifted, transformed biomass (that did not accommodate zero values) indicated that winter had a significant effect on all arthropod response variables in all model runs (total arthropods, log-transformed: $P < 0.0003$; Araneae, square-root transformed: $P < 0.0365$; herb/detritivores, log-transformed: $P < 0.0006$). These models, regardless of the specific arthropod response variable or prior rain period, indicated neither tree species nor winter*tree species had significant effects ($P > 0.380$, $P > 0.140$, respectively) on any arthropod response variables. Similarly, location (sample station) had no significant effect on the arthropod response variables, although it had a marginal effect on square-root transformed biomass of Araneae ($0.0894 < P < 0.0997$).

Ground-surface arthropod variation with winter and location. Winter and location (sample station) were included as random effects in lognormal-logit models run separately for biomass of each response variable for arthropods collected on the ground (total ground arthropods, ground Formicidae, and ground Diptera). Winter and location were both important components of variation in the Formicidae and total ground arthropod models, with winter usually the dominant component. Location was an important component of variation in 7 of 8 models of Diptera, whereas winter contributed to the variation in 4 of 8 models. Araneae were only present in a small number of ground-surface samples, and their models tended to have fewer variance components. In initial linear mixed models on the shifted and transformed biomass, winter had a significant effect on biomass of total ground arthropods and ground Diptera in all model runs with the different prior rain periods ($P < 0.005$), but no significant effect on biomass of ground Formicidae in all model runs ($P > 0.200$). In those models, location had no significant effect in runs with any prior rain period for biomass of total ground arthropods, ground Formicidae, or ground Diptera (all tests $P > 0.20$).

Rainfall effects

Foliage arthropods and rainfall. Contrary to expectations, biomass of foliage arthropods did not change with prior rainfall, either cumulative amount or number

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Figure 3 (following page). Coefficients (β) and 95% highest posterior density credible intervals (HPD CI) for covariates indicating foliage arthropod amount (biomass) or occurrence (samples with zero presence) associated with cumulative rainfall or number of days with rain in the prior rain period (i.e., 30, 60, 90, or 120 days) sampled in late winter (March–April) over 9 years at Rock Sound, Eleuthera, The Bahamas. Analyses involved lognormal-logit (zero-augmented or hurdle) models with mixed effects that also included days after 1 March as a covariate, results of which are shown in Figure 5. A covariate was judged significant if its 95% HPD CI for the covariate's β did not contain zero or the probability that the coefficient was in an opposing direction was below 0.05 ($P_\beta < 0.05$). P_β values for models with covariate coefficients with low opposing probabilities are shown to the right side of each corresponding β in each panel. See methods for foliage arthropod sampling methods and model details.

of days with rain for all prior rainfall periods, as indicated by β values that overlapped zero with higher probabilities (Fig. 3). Moreover, the number of foliage samples without arthropods significantly increased with cumulative rainfall ($P_\beta < 0.05$) in the prior 30-, 90-, and 120-day periods, and increased with number of

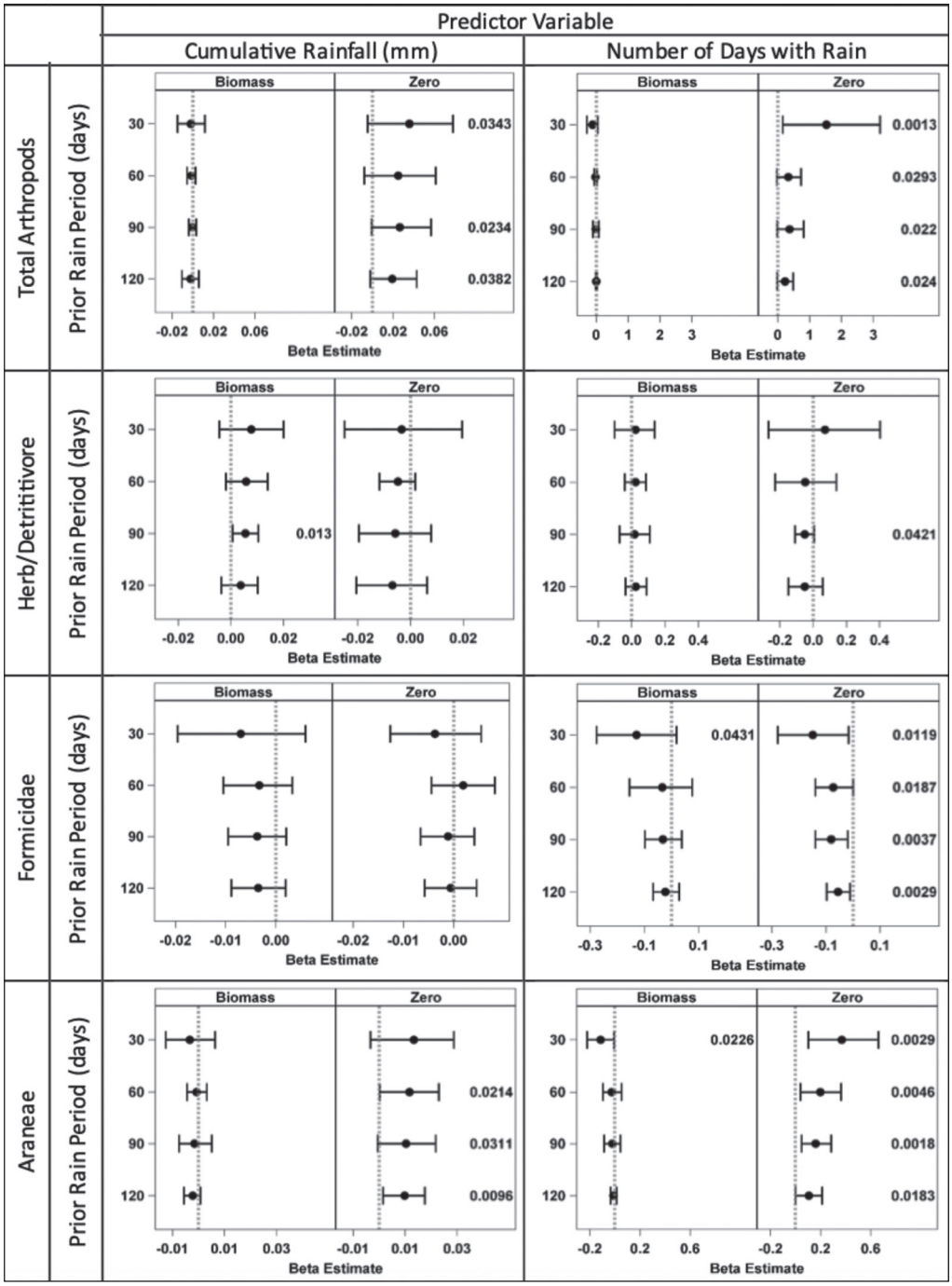

Figure 3. [Caption provided on previous page.]

days with rain for all prior rain periods (Fig. 3). The arthropod absence with rainfall largely reflected the response of Araneae, which were especially sensitive to rainfall and were likely to be absent from foliage samples, as number of days with rain increased for all prior rainfall periods and with cumulative rainfall in the prior 60-, 90-, and 120-day periods. In addition, Araneae biomass decreased with an increase in number of days with rain in the prior 30 days. By contrast, foliage herb/detritivore biomass increased with an increase in cumulative rainfall in the prior 90 days, and herb/detritivore absence in foliage samples decreased with number of days with rain in the prior 90-day period. Formicidae, which were included with the foliage herb/detritivores, showed a significant decrease in biomass with rainfall in the number of days with rain in the 30-day prior period, whereas the probability of foliage samples without Formicidae decreased with an increase in number of days with rain for all prior periods.

Ground arthropods and rainfall. As expected, biomass of total ground arthropods increased with cumulative rainfall in models with the prior 60-, 90-, and 120-day periods (Fig. 4). In addition, ground-surface samples without arthropods decreased as cumulative rainfall increased in the prior 90- and 120-day periods, and number of samples without arthropods also decreased as number of days with rain increased in all prior rain periods. Formicidae, the largest constituent of the ground arthropod biomass, increased in biomass with cumulative rainfall in prior 30- and 60-day periods, but biomass of Formicidae did not change with number of days with rain in any of the prior rain periods. Moreover, the number of ground samples without Formicidae did not change with cumulative rainfall or number of days with rain in any of the prior periods. Araneae biomass in ground samples did not vary significantly with rainfall (amount or number of days), nor did samples without Araneae vary significantly with cumulative rainfall in any of the prior rain periods. However, samples without Araneae decreased with number of days with rain in the prior 60 days. Diptera biomass increased with the 60- and 120-day cumulative rainfall and the number of rain days in the prior 120-day period. Samples without Diptera decreased with the 60-, 90-, and 120-day prior periods of cumulative rainfall and prior number of days with rain; however, the samples without Diptera increased with the prior 30-day period of cumulative rainfall.

Figure 4 (following page). Coefficients (β) and 95% highest posterior density credible intervals (HPD CI) for covariates indicating arthropod amount (biomass) or occurrence (samples with zero presence) on the ground associated with cumulative rainfall or number of days with rain in the prior rain period (i.e., 30, 60, 90, or 120 days) sampled in late winter (March–April) over 9 years at Rock Sound, Eleuthera, The Bahamas. Arthropods were sampled with 5-min ground scans of 0.25 m^2 in March and April of each year. Analyses involved lognormal-logit (zero-augmented or hurdle) models with mixed effects. Models also included days after 1 March as a covariate, results of which are shown in Figure 6. A covariate was judged significant if its 95% HPD CI for the covariate's β did not contain zero or the probability that the coefficient was in an opposing direction was below 0.05 ($P_\beta < 0.05$). P_β values for models with covariate coefficients with low opposing probabilities are shown to the right side of each corresponding β in each panel. See methods for ground-surface arthropod sampling methods and model details.

Arthropod change with days after 1 March

Change in foliage arthropods after 1 March. Total foliage arthropod biomass increased with days after 1 March in models with cumulative rainfall and number of days with rainfall in the prior 30, 60, 90, and 120 days (Fig. 5). The probability of a

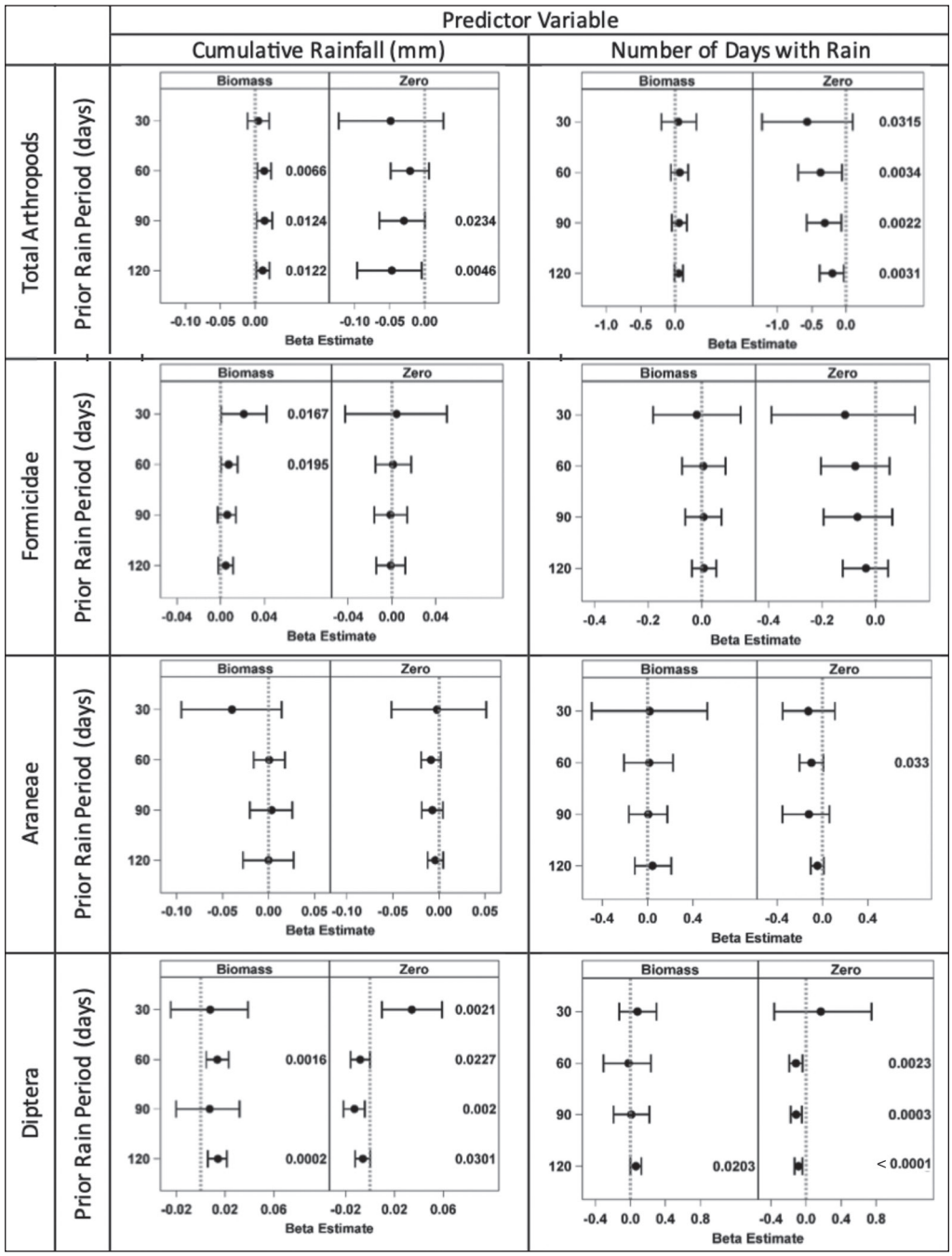

Figure 4. [Caption provided on previous page.]

foliage sample without arthropods consistently decreased with days after 1 March with models that included cumulative rainfall in all prior periods or with number of days with rain in all prior periods. Correspondingly, the likelihood of a foliage sample without Araneae decreased with days after 1 March for all models that also included cumulative rainfall in all prior periods or with number of days with rainfall for all prior periods. Foliage Araneae biomass, however, did not change significantly with days after 1 March, except for an increase with the model that also included the number of days with rainfall in the prior 30 days. Foliage herb/detritivore biomass did not vary significantly with days after 1 March (for rainfall amount or days), and herb/detritivore absence in foliage samples did not vary significantly with days after 1 March. Similarly, foliage samples without Formicidae did not vary significantly with days after 1 March in models with rainfall amounts or days with rain in any of the prior rain periods. Formicidae biomass, however, increased after 1 March with models with cumulative rainfall in the prior 90 and 120 days and with number of rain days in the prior 30 days.

Change in ground-surface arthropods after 1 March. Biomass of total ground arthropods did not vary significantly with days after 1 March in models with prior cumulative rainfall or in models with the prior number of days with rainfall ($P_\beta > 0.20$; Fig. 6). However, there was a significant increase in the number of ground-surface samples without arthropods for days after 1 March in models with cumulative rainfall in the prior 90 days and 120 days and the number of days

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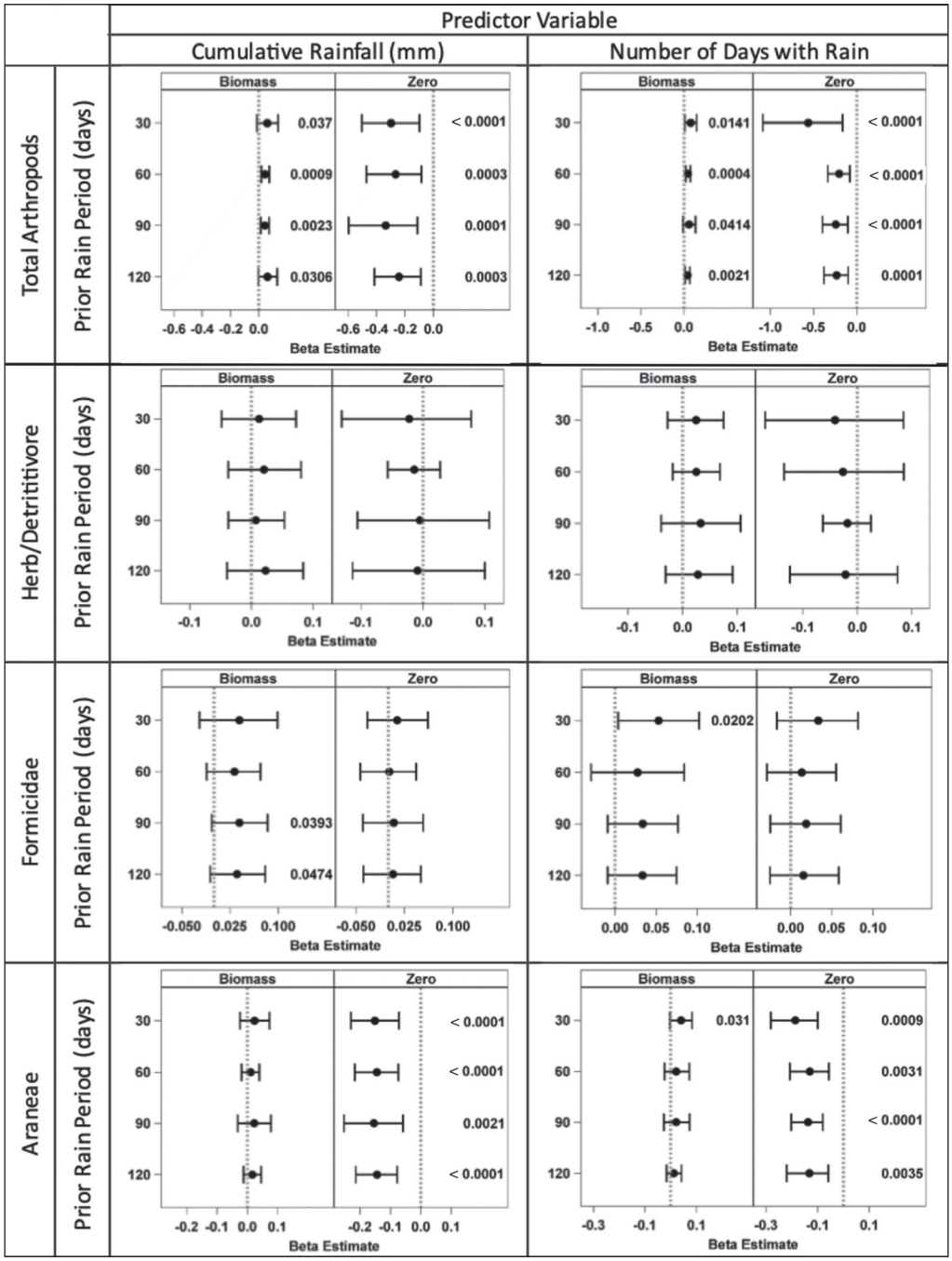
Figure 5 (following page). Coefficients (β) and 95% highest posterior density credible intervals (HPD CI) for covariates indicating arthropod amount (biomass) or occurrence (samples with zero presence) in the foliage associated with days after 1 March in models that also included cumulative rainfall or number of days with rain in the prior rain period (i.e., 30, 60, 90, or 120 days) sampled in late winter over 9 years at Rock Sound, Eleuthera, The Bahamas. Arthropods were sampled with branch clipping in March and April of each year. Analyses involved lognormal-logit (zero-augmented or hurdle) models with mixed effects. A covariate was judged significant if its 95% HPD CI for the covariate's β did not contain zero or the probability that the coefficient was in an opposing direction was below 0.05 ($P_\beta < 0.05$). P_β values for models with covariate coefficients with low opposing probabilities are shown to the right side of each corresponding β in each panel. See methods for foliage arthropod sampling and model details.

Figure 6 (see p. 16). Coefficients (β) and 95% highest posterior density credible intervals (HPD CI) for covariates indicating arthropod amount (biomass) or occurrence (samples with zero presence) on the ground associated with days after 1 March in models that also included cumulative rainfall or number of days with rain in the prior rain period (i.e., 30, 60, 90, or 120 days) sampled in late winter over 9 years at Rock Sound, Eleuthera, The Bahamas. Arthropods were sampled with 5-min ground scans in March and April of each year. Analyses involved lognormal-logit (zero-augmented or hurdle) models with mixed effects. A covariate was judged significant if its 95% HPD CI for the covariate's β did not contain zero or the probability that the coefficient was in an opposing direction was below 0.05 ($P_\beta < 0.05$). P_β values for models with covariate coefficients with low opposing probabilities are shown to the right side of each corresponding β in each panel. See methods for ground-surface arthropod sampling and model details.

with rainfall in the prior 30 days. For ground Formicidae and Araneae, each separately, there were no significant ($P_\beta > 0.40$) changes in biomass after 1 March in models with prior rainfall (amount or days), nor did samples without Formicidae or Araneae change significantly after 1 March with prior rainfall (amount or days)



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in the model. However, occurrence of samples without Diptera decreased after 1 March when models included the 30-day prior cumulative rainfall.

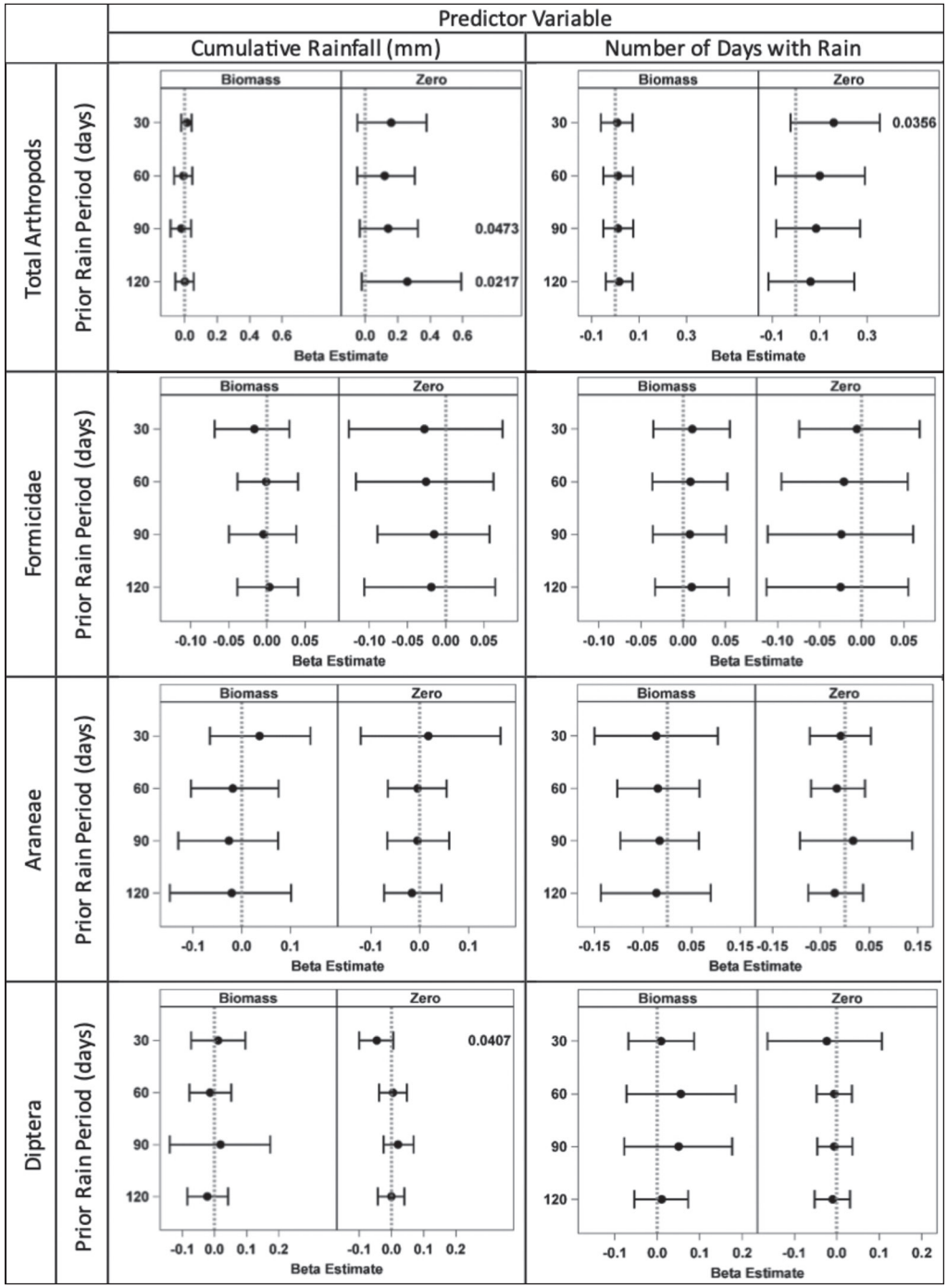

Figure 6. [See p. 14 for caption.]

Discussion

We detected more arthropod responses to rainfall (cumulative or days and prior periods) with measures of occurrence than with biomass. Occurrence, the simpler measure, represents a measure of site occupancy (presence or absence). Biomass, however, includes both a measure of abundance and body mass, the latter of which can vary because a taxa's mass or body size may change during development in response to a variety of factors including moisture (Chown and Gaston 2010). For example, the larger lengths of ants, spiders, beetles, and Lepidoptera larvae in a dry forest in Puerto Rico during the wet season compared to the dry season, was attributed by Beltrán and Wunderle (2014) to greater food availability in the wet period allowing larval instars to grow bigger than during the dry period with fewer available food resources. By contrast, they found that Homopterans were larger on average in the dry period compared to the wet period because of a higher abundance of the smaller nymphs in the wet period. Besides moisture, other factors might contribute to body size, including temperature and predation pressure (Berger et al. 2006, Chown and Gaston 2010), which may affect biomass or availability for arthropod predators. Therefore, biomass of some arthropod taxa might vary independently of changes in moisture, which may contribute to some of the discrepancies in results between biomass and occurrence.

Rainfall measured as number of days with rain enabled us to detect more foliage arthropod rainfall responses (15) than when measured as cumulative amounts for foliage arthropod rainfall responses (7). These findings are consistent with the suggestion of Spiller and Schoener (1995) that days with rainfall provide a better measure of the effects of precipitation in The Bahamas because water delivered by heavy downpours during a few days may be mostly lost via runoff from the limestone substrate in contrast to more continuous rain during many days leaving less time for desiccation. On the ground surface, however, we tallied more arthropod rainfall responses with cumulative rainfall (13) than with number of days with rain (9). The differences between foliage and ground in effectiveness of rainfall measures used to detect arthropod responses may result from position differences in desiccation susceptibility. Desiccation appeared to be more severe in the canopy foliage than on the ground where sample plots were shaded by the canopy and moisture was retained in leaf litter and soil, suggesting that cumulative amount of rainfall may be an appropriate measure for detecting ground-surface arthropod responses to rainfall.

Foliage arthropods

The late dry-season decreases in occurrence of foliage arthropods with rainfall was attributable primarily to the response of spiders, which constituted the greatest proportion (47%) of any taxa in the foliage arthropod biomass. The likelihood that spiders were absent from foliage samples increased with cumulative rainfall in the prior 60-, 90-, and 120-day periods and as the number of days with rain increased in all prior periods. Moreover, foliage spider biomass decreased with an increase in rainfall in the prior 30 days. These negative responses by foliage

spiders (mostly Salticidae, Sparassidae, and Thomisidae) to rainfall are consistent with studies documenting spider declines with rainfall due to an indirect effect of increased predation by spider predators (e.g., wasps and centipedes), which benefit from increased rainfall (Lensing et al. 2005, Polis et al. 1998, Spiller and Schoener 2008; but see Spiller and Schoener 1995 for positive rainfall effects on spiders). The negative correlation of spider abundance with rainfall found by Spiller and Schoener (2008) strengthened with the duration of the prior period in which rainfall was measured before spider sampling. By contrast, we found an opposite trend; the predictor values (β) for calculating the likelihood of foliage samples without spiders increased as the duration of the prior rain period decreased. The negative response of spiders to prior 30-day rainfall suggests a direct effect of rainfall on foliage spiders (e.g., mortality from rain or shift to refugia elsewhere), which may weaken over longer time intervals. Our results are consistent with findings indicating that heavy downpours might dislodge arthropods from plants (Chen et al. 2019, Kobori and Amano 2003) and change microclimatic conditions, which may retard development rates (Dobkin et al. 1987, Kamata and Igarashi 1994), thereby reducing adult abundance. On the other hand, as the late dry season progressed with days after 1 March, the probability of foliage spider occurrence increased, given increased cumulative rainfall or rain days regardless of prior rain-period duration. The temporal response of foliage spider occurrence with advancement toward the wet season was expected because of the increased availability of arthropod prey in the wet season (Tanaka and Tanaka 1982, Wolda 1978).

In contrast to the negative rainfall response of foliage spiders in the late dry season, the foliage herb/detritivore guild showed a positive response to rainfall, at least with rainfall measured in the prior 90 days. Following this prior rain period, guild biomass increased with increased cumulative rain amount, whereas guild occurrence displayed an increase with number of days with rain. Much of the guild increase reflected an increase in Coleoptera (mostly weevils, Curculionidae), which were one of the most common taxa in the herbivore/detritivore guild in foliage (after Orthoptera). Ants, a minor constituent of the herb/detritivore guild in the foliage, increased in occurrence with number of days with rain in all prior periods, but ant biomass decreased with days with rain in the prior 30 days. Thus, rainfall had mixed effects during March–April or the late dry season on the availability of foliage arthropods.

Both foliage arthropod biomass and occurrence increased with the progression of days after 1 March in all models with rainfall (cumulative amount or rain days) in all prior periods. Contributing to this increase with days after 1 March were foliage spider occurrences (with rain amounts or days in all prior periods) and ant biomass (with rain amounts in prior 30, 90, 120 days, and with rain days in prior 30 days). Corresponding with this temporal progression in foliage arthropod abundance as the wet season (spring) approached was an increase in day length and mean temperature, which together with rain stimulated reproduction and development in some insects (Beck 1980, Tauber et al. 1986). Our results are consistent with previous findings of increased arthropod abundance associated with rainfall during the

transition from the dry to wet season in tropical dry forests with distinct wet and dry seasons (Pinheiro et al. 2002, Silva et al. 2011, Tanaka and Tanaka 1982, Wolda 1978). During this seasonal transition, the arthropod numerical response may lag behind rainfall by 3–5 weeks (Tanaka and Tanaka 1982; Wolda 1977, 1978). Overall, foliage arthropod abundance was expected to increase with increased rainfall as the wet season commenced in May.

Early wet-season showers may trigger production of young leaves, flowers, and fruits in many plants (van Schaik et al. 1993, Williams et al. 1997), which, in turn, stimulates an increase in herbivore abundance (Connahs et al. 2011, Richards and Coley 2007). Ants, a minor biomass constituent of the foliage herb/detritivore guild, fit this expectation with an increase in foliage ant biomass with days after 1 March. The guild of foliage herb/detritivores, however, did not fit expectations of increased biomass or occurrence with the progression of days after 1 March, despite increased rainfall amounts or days with rain. Perhaps we would have observed a temporal response by the herb/detritivore guild had our study extended beyond 15 April when leaf-out appeared to accelerate with the onset of the wet season (J.M. Wunderle et al., unpubl. data). In addition, the absence of a temporal response at the guild level may have occurred because certain herb/detritivore taxa require more rainfall or are slower to respond than ants to the onset of the wet-season rains. Moreover, as noted by Grimbacher and Stork (2009), analyses of seasonality conducted at high taxonomic levels (order or family) can sometimes obscure differences in seasonal patterns of arthropod abundance within lower taxonomic levels or ecological groups. For instance, among herbivorous insects, sucking herbivores (e.g., Curculionidae, Homoptera, Hemiptera) were most abundant in the dry season, whereas chewing herbivores (e.g., Lepidoptera larvae) were most abundant in the wet season in agroforestry plantations (Nyeko et al. 2002). Similarly, mealybugs (sucking insects; Homoptera) infested leaves of *Plumeria alba* L. (White Frangipani) during the dry season, whereas sphinx moth caterpillars (chewing insects; Lepidoptera) fed on leaves during the wet season (Sloan et al. 2007). Our observations align with the pattern of sucking-insect abundance in the dry season; we rarely observed leaf damage by chewing insects in our sample trees during the March–April period (J.M. Wunderle, unpubl. data).

We found no evidence for shrub or tree-species preferences by any arthropod group or differences among plant species in abundance of various arthropod taxa as documented in tropical or subtropical forests elsewhere (Beltrán and Wunderle 2013, Greenberg and Bichier 2005). Failure to detect differential use of plant species by arthropod taxa may be attributable to several factors, including a large variance in arthropod biomass among branch-clip samples, small sample sizes, and low arthropod abundance per tree as noted by Schowalter and Ganio (2003). Nonetheless, evidence for tree-species preferences comes from our field observations, which documented an abundance of small flies on or associated with the foliage of the tree *Lysiloma latisiliquum* (L.) Benth. (False Tamarind) in late April after wet winters (J.M. Wunderle et al., unpubl. data).

Ground-surface arthropods

The response of ground-surface arthropods to rainfall was consistent with previous studies indicating increased abundance following rain during the dry season (Brown and Sherry 2006). This finding primarily reflected the rainfall response of ants on the ground, which increased in biomass with increased cumulative rain in the prior 30 and 60 days. Diptera biomass increased with prior 60- and 120-day rainfall amounts, and Diptera occurrence increased with an increase in number of days with rain in the prior 120 days. For many Diptera, rainfall is necessary for initiating breeding (Bates 1945, Chaniotis et al. 1971, Mullens and Peterson 2005) and for stimulating development of aestivating eggs in dry soils (Spielman 1962). The Dipterans tallied during our ground scans (e.g., Muscidae, Tabanidae) were also observed perched on the foliage of nearby shrubs (J.M. Wunderle et al., unpubl. data). The presence of Dipterans on nearby foliage coincident with their presence in ground scans suggests that they may have also displayed a similar positive rainfall response in foliage but were absent from our foliage samples because they eluded capture.

The response of ground-surface arthropods to days after 1 March given prior rain differed markedly from the foliage arthropod temporal response. Whereas total foliage arthropod biomass and likelihood of occurrence increased with days after 1 March in models with increased rainfall (cumulative or days) in all prior periods, the total arthropod biomass on the ground did not change with days after 1 March (regardless of rain measure or prior period). In addition, likelihood of arthropod occurrence in ground-surface samples decreased (rather than increased as in foliage occurrences) with days after 1 March with cumulative rainfall in the prior 90 and 120 days and with number of days with rain in the prior 30 days. Only the occurrence of Diptera in ground scans increased with days after 1 March with increased cumulative rainfall in the prior 30 days.

We attribute some ground-arthropod responses to rainfall and days after 1 March to arthropod movements into or out of the leaf litter or openings in the exposed ground in response to changes in moisture or other microclimatic conditions. Within the leaf litter, rainfall differences can affect the vertical stratification of some arthropod taxa in markedly different ways (Lensing et al. 2005), but how this relates to activity on the surface is unknown. Some vertical shifts within the leaf litter may be unrelated to arthropod surface activities if species composition differs between the surface and within the leaf litter below. For example, leaf-litter arthropod composition, as sampled with Berlese funnels, had a higher proportion of Coleoptera and holometabolous larvae relative to the leaf-litter surface where ants predominated in ground scans in Jamaican dry limestone forest (Strong 2000). Some ground-surface arthropods, especially ants, appeared to move in and out of openings in the porous limestone, facilitating rapid response to rainfall and to fallen fruits and flowers on the ground surface (J.M. Wunderle et al., unpubl. data).

As social insects, ants can respond quickly to daily and seasonal changes in the environment, reflecting behavioral responses of ant colonies to favorable physical conditions and local food abundance (Levings 1983). Quick responses were evident in our finding of increased ant biomass on the ground with increased rainfall in the

prior 30 and 60 days and consistent with rapid responses of ants in the leaf litter to changes in dry-season soil moisture in Panama (Levings 1983, Levings and Windsor 1984). For intervals of longer duration, however, such as throughout the dry season, ant colonies may respond to leaf-litter moisture content by shifting to wetter sites (Levings and Windsor 1984). These colony shifts in responses to drought may have contributed to the significant random effects of sample-station location and year in our lognormal-logit models run on ground ants. In contrast to ants on the ground, however, ant biomass in the foliage decreased with an increase in the number of days with rain in the prior 30 days, suggesting ant loss due to displacement by heavy showers (e.g., Chen et al. 2019).

Implications for Kirtland's Warblers

The diverse responses to rainfall by various arthropod taxa in the late dry season as found in our study would undoubtedly favor insectivores with opportunistic foraging behavior and a broad diet. The ability to offset declines in one diet item for another may be especially important for migrants preparing for vernal migration, assuming that the alternative food items are adequate for migration (McKinnon et al. 2015). Adjustments to fluctuations in availability of different arthropod taxa are made by Kirtland's Warblers by opportunistically foraging on diverse prey on the ground and foliage in addition to consuming fruit (Wunderle et al. 2010, 2014). A variety of arthropod prey is consumed by the warbler on both the breeding (Deloria-Sheffield et al. 2001) and wintering (Wunderle et al. 2014) grounds, where the taxa most commonly present in fecal samples (n = 96) included Coleoptera (35%), Formicidae (30%), and Araneae (31%).

Some of the common arthropod taxa found in the warbler diet showed diverse rainfall responses, which, as found by Brunner et al. (2022), lacked congruence between the foliage and the ground. For instance, in our study, Coleoptera was most likely captured by the warbler in the foliage where they were an important component of the herb/detritivore guild, which increased in biomass and occurrence with prior 90-day rainfall measures (cumulative amount and days with rain, respectively). Spiders, the predominate prey by biomass in the foliage, were most common during dry periods in the absence of rainfall, but following increased rainfall (cumulative or rain days), spider occurrence declined in foliage (all prior periods, except 30 days) and spider biomass decreased with an increase in days with rain in the prior 30 days. By contrast, on the ground, ants, the predominant prey there, increased in biomass after increased cumulative rainfall in the prior 30 and 60 days, whereas spider occurrence increased with number of days with rainfall in the prior 60 days. Therefore, as the rainfall amounts and periods over which precipitation varies, the foraging warblers may respond by tracking the differential availability of late dry-season arthropod prey by switching between foliage and ground. How the Kirtland's Warbler and other gleaning insectivores adapt to changes in arthropod availability with extreme weather events, including increased frequency of heavy downpours and extensive droughts expected with global climate change, remains to be studied.

Acknowledgments

This research, as part of the Kirtland's Warbler Research and Training Project, benefited from the enthusiastic contributions of Bahamian student interns including Ancilleno Davis, Scott Johnson, Everton Joseph, Samara Lawrentz, Zeko McKenzie, Ingeria Miller, Keith Philippe, Montara Roberts, and Jasmine Turner. We also appreciate the dedicated assistance provided by Rudy Badia, Peter Bichier, Elise Corliss, Alana Demko, Stephanie Dolrenry, Rudy King, Laurie Porth, Javier Mercado, Jennifer Thieme, and Sarah Wagner. Eric Carey, Executive Director of the Bahamas National Trust, supported the project from its initiation and assisted in many ways for which we are most grateful. The government of The Bahamas provided the research permits for the study, and permission to work on the Rock Sound site was granted by Mrs. van Oldham of the Rock Sound Commonage Committee, Eleuthera. Constructive comments and suggestions from Ancilleno Davis, Craig Layman, and 2 anonymous reviewers were helpful. Assistance with the figures was provided by D. Jean Lodge. Funding was provided by International Programs of the US Department of Agriculture Forest Service to The Nature Conservancy and the Puerto Rican Conservation Foundation working in cooperation with the Bahamas National Trust, the University of the Bahamas, the University of Puerto Rico, and the Kirtland's Warbler Recovery Team.

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