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ARTICLE

Insectivorous birds reduce herbivory but do not increase mangrove growth across productivity zones

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Abstract

Top-down effects of predators and bottom-up effects of resources are important drivers of community structure and function in a wide array of ecosystems. Fertilization experiments impose variation in resource availability that can mediate the strength of predator impacts, but the prevalence of such interactions across natural productivity gradients is less clear. We studied the joint impacts of top-down and bottom-up factors in a tropical mangrove forest system, leveraging fine-grained patchiness in resource availability and primary productivity on coastal cays of Belize. We excluded birds from canopies of red mangrove (Rhizophoraceae: *Rhizophora mangle*) for 13 months in zones of phosphorus-limited, stunted dwarf mangroves, and in adjacent zones of vigorous mangroves that receive detrital subsidies. Birds decreased total arthropod densities by 62%, herbivore densities more than fivefold, and reduced rates of leaf and bud herbivory by 45% and 52%, respectively. Despite similar arthropod densities across both zones of productivity, leaf and bud damage were 2.0 and 4.3 times greater in productive stands. Detrital subsidies strongly impacted a suite of plant traits in productive stands, potentially making leaves more nutritious and vulnerable to damage. Despite consistently strong impacts on herbivory, we did not detect top-down forcing that impacted mangrove growth, which was similar with and without birds. Our results indicated that both top-down and bottom-up forces drive arthropod community dynamics, but attenuation at the plant-herbivore interface weakens top-down control by avian insectivores.

KEYWORDS

field experiment, insectivorous birds, mangrove, *Rhizophora mangle*, structural equation models, top-down and bottom-up forces, trophic dynamics

INTRODUCTION

Predators have strong impacts on the structure and function of communities, and loss or removal of top predators can shift ecosystems between stable states, alter biodiversity, and degrade ecosystem services (Duffy, 2002; Estes et al., 2011). The potential primary productivity of an ecosystem has long been central to theory of top-down control (Oksanen et al., 1981); it is now commonly recognized that communities are simultaneously affected from the top-down by predators and from the bottom-up by resource quantity and quality (Abdala-Roberts et al., 2019; Östman et al., 2016). Most research now focuses on quantifying the relative importance and variability of these forces within and among systems (Burkepile & Hay, 2006; Gripenberg & Roslin, 2007; Gruner et al., 2008; Hanley & La Pierre, 2015; Vidal & Murphy, 2018). Fertilizer additions, in concert with predator removals, are used widely to test these ideas experimentally (e.g., Garibaldi et al., 2010; Gruner, 2004), but the use of natural resource gradients, which contextualize hypotheses within the observed range of variation in nature, are underutilized particularly in tropical ecosystems (but see Dyer & Letourneau, 1999; Wyckhuys et al., 2017).

Mangrove forests are ecologically and economically important tropical and subtropical habitats in which bottom-up effects of nutrients, supplied in sediments and tidal subsidies, are well-established drivers of ecosystem productivity, biomass, and diversity (Lee et al., 2014). Limiting nutrients such as nitrogen (N) and phosphorus (P) constrain mangrove forest structure and productivity, regulate mangrove growth, and alter mangrove–herbivore interactions (Feller, 1995; Feller et al., 2003; Feller & Chamberlain, 2007; Onuf et al., 1977; Reef et al., 2010). In contrast, top-down cascading effects of predators have received less attention in mangrove systems. Arguably, the importance of predators and the likelihood of cascading impacts and their strength hinge upon herbivore ability to control plant biomass growth (Shurin et al., 2002). Arthropod herbivores can have strong detrimental impacts on mangrove growth, reproduction, and survival, although most studies focus on predation of propagules or seedlings (Cannicci et al., 2008; Feller, 2002; He & Silliman, 2016; Sousa et al., 2003). In one of the few investigations of top-down effects in mangrove vegetation, Offenberg et al. (2005) found that ants on the mangrove *Rhizophora mucronata* decreased herbivore abundance and rates of herbivory, although indirect effects did not alter tree growth. However, vertebrate insectivores are often the top predators in mangrove canopies: consumers that instigate cascading indirect effects on herbivory and plant biomass in other forest systems (Mäntylä et al., 2011; Mooney et al., 2010).

Here, we investigated the joint impacts of avian top predators and resource availability on arthropods and plants on offshore mangrove islands in Belize. Specifically, we quantified how predators and resources affected arthropod abundance in mangrove canopies, herbivory on mangrove leaves and buds, and mangrove growth. Over a period of 13 months, we excluded birds from the canopies of *R. mangle* in immediately adjacent zones of strong and relaxed nutrient limitation in island interiors. At our study sites, low-stature, slow-growing stands of *R. mangle* are limited severely by P (Feller, 1995) and are directly adjacent to patches of rapidly growing plants where substantial accumulation of flocculent detritus alleviates P limitation (Faust & Gulledge, 1996). We took advantage of this fine-grained, natural variation to manipulate the presence of insectivorous predators (birds) in neighboring stands of stunted and fast-growing plants separated by distances as small as 5 m. We asked the following questions: (1) Does natural variation in resource availability affect arthropod densities and herbivory? (2) Do birds impact arthropod densities and herbivory and do these effects cascade to plant growth? And (3) do resource conditions mediate the impacts of birds? Our experimental design allowed an investigation into how intraspecific variation of nutrient-limited plant traits may ramify to influence top-down trophic interactions.

METHODS

Study system

Rhizophora mangle is a woody halophyte that grows in tidal wetlands along tropical and subtropical coastlines of the Americas and the Caribbean (Spalding et al., 2010). The stature and productivity of *R. mangle* can vary substantially within and among forests due to abiotic factors such as disturbance and nutrient limitation (Feller, 1995; Feller et al., 2003; Lovelock et al., 2004). In nutrient-poor conditions, *R. mangle* forms stands of stunted individuals (hereafter "dwarfs") <1.5 m tall, whereas in more favorable conditions heights >20 m can be attained (Gill & Tomlinson, 1977; Lugo, 1997). Tall and dwarf stands of *R. mangle* are common in natural systems, constituting an estimated 28% and 55% of mangrove habitat area in Belize, respectively (Murray et al., 2003).

Rhizophora mangle is attacked by an array of arthropod herbivores, including folivores, wood borers, root borers, bud feeders, and tissue miners (Brooks & Bell, 2002; Feller, 2002; Feller & Chamberlain, 2007). In some forests, the arboreal crab, *Aratus pisonii* (Sesarmidae) is responsible for the majority of leaf feeding damage on *R. mangle* leaves (>80%), while non-crab damage to leaves is mostly caused by moth larvae, crickets, and katydids (Feller, 1995; Feller & Chamberlain, 2007). Bud feeding by moth larvae in the genus *Ecdytolopha* (Tortricidae) can result in a loss of 10%–36% of leaf area by impacting leaf expansion from buds (Feller & Chamberlain, 2007), and wood-boring beetle larvae have been observed to kill over 50% of *R. mangle* canopies by girdling, pruning, and hollowing branches (Feller, 2002). The role of predators in suppressing herbivores on *R. mangle* has rarely been examined, although one study observed that predators and parasitoids jointly inflicted a mortality rate of 89% on a leaf-mining gracillariid moth (Feller & Chamberlain, 2007).

Study sites

We established our field experiment on Twin Cays, Belize (16.82° N, 88.10° W), a 92-ha archipelago of peat-based mangrove islands located approximately 12 km from the mainland. Island vegetation is dominated by mangroves, the majority of which are *R. mangle*. Black mangroves (*Avicennia germinans* [L.]) are locally common in some areas, while white mangroves (*Laguncularia racemosa* [L.] C.F. Gaertn.) are scattered and relatively rare. A narrow 5–20 m band of large, productive *R. mangle* mangroves (5–6 m tall) lines the island perimeters, while interior ponds are inhabited by old-growth stands of dwarf *R. mangle* (<1.5 m tall) that are short statured, primarily due to P limitation (Feller, 1995; Feller et al., 2003). In the shallow, carbonate-rich waters on the Belize barrier reef, typical benthos communities are limited primarily by P, except where seabird rookeries deposit guano (Lapointe et al., 1993). No such rookeries are evident historically on Twin Cays (Mitten et al., 2004).

Within the island interiors of Twin Cays, microbial mats that include N-fixing cyanobacteria form on sediment and peat within the benthos of permanently inundated ponds (Lee & Joye, 2006). Gasses generated within these mats during the day can lift them, along with associated sheets of detritus, to the water's surface (Faust & Gulledge, 1996; Lee & Joye, 2006). Prevailing winds blow the floating flocculent material downwind toward pond edges (usually edges to the south/west), creating localized deposits of decaying organic matter (hereafter "floc"). Where floc deposits occur, *R. mangle* exhibits vigorous growth uncharacteristic of nearby (∼5 m distant) P-limited dwarf stands. Thus, we hypothesized that the floc contributes a subsidy that alleviates P limitations on growth. Indeed, experimental P fertilization of dwarf *R. mangle* induced vigorous growth rates similar to that of trees growing in floc accumulation zones, whereas floc trees are co-limited by N and P (Feller et al., 2003). Vigorous *R. mangle* stimulated by floc account for about 7% of land area of Twin Cays, while dwarf stands of *R. mangle* cover about 25% of the landscape (Rodriguez & Feller, 2004).

Two main islands constitute most of Twin Cays' landmass and we established one study site on each of these islands (Dock and Boa sites on West and East Island, respectively). Site locations were chosen based on accessibility and on the co-occurrence of fast-growing floc-associated *R. mangle* on pond edges and dwarf *R. mangle* within ponds. The two sites we selected were ∼0.7 km apart (Appendix S1: Figure S1).

Mitten et al. (2004) documented 14 species of insectivorous birds on Twin Cays, of which the two most commonly observed at our study sites were the yellow warbler *Setophaga petechia* (Parulidae) and the Yucatan vireo *Vireo magister* (Vireonidae). Both of these species are year-round residents of Twin Cays. Yucatan vireos will excavate mangrove branches to extract food and are likely the only local bird species that forages on *R. mangle* wood borers (Mitten et al., 2004). Yellow warblers glean insects in mangrove canopies at Twin Cays but have also been observed feeding on the mangrove tree crab *Aratus pisonii*, which is an abundant and omnivorous non-insect folivore of *R. mangle* (Mitten et al., 2004). Green herons *Butorides virescens* (Ardeidae) were commonly observed at our sites; this species may also opportunistically feed on mangrove tree crabs (Yeager et al., 2016). We did not observe arboreal vertebrate insectivores other than birds in the interior ponds where our experimental units were located. Brown anoles, *Anolis sagrei* (Dactyloidae), were abundant in tall stands of *R. mangle* fringing the exterior of the islands.

Experimental design

Experimental manipulations were established 7–12 January 2010 (Appendix S1: Figure S2). At each of two sites, we selected 20 experimental units with two levels of mangrove growth form (sensu Cornelissen et al., 2003): 10 *R. mangle* dwarf plants (low resource treatment) and 10 branches on different *R. mangle* trees near floc deposits (high resource treatment, hereafter "floc"). Vigorous floc trees were much larger than the dwarf *R. mangle* in interior ponds. Therefore, we manipulated only portions of the floc trees of similar size to dwarfs, in order to standardize the size of our experimental units. We built 1-m^3 frames of three-quarter inch PVC (1 inch = 2.54 cm) around each experimental unit and randomly selected half of the frames around dwarfs and floc trees to be covered in polypropylene netting (2 × 2 cm openings; Dalen Deer-X netting) to exclude vertebrates but not arthropods. Thus, each combination of resource treatment (growth form: floc vs. dwarf) by bird access treatment (no net vs. net) had a total replication of $n = 10$ (five per site, 40 plants in total). Nets did not extend underwater to the sediment surface, rather they stopped at the height of high tide so that they allowed floating detritus movement but not bird access. The mean tidal range at Twin Cays is slight, with a maximum of 21 cm (Wright et al., 1991). Experimental units were chosen so that they were all at least 5 m apart, had 10–20 terminal shoots, and could be oriented within frames so that they would not contact net coverings. Three terminal stems in the outer canopy were haphazardly chosen on each experimental unit and marked with aluminum tags (Feller et al., 2003). These stems were later used to quantify plant growth and rates of herbivory (see *Assessing growth and plant traits*). Nets and frames were checked and repaired if needed at 2, 4, and 8 months after initiation of treatments. After 13 months (10–16 February 2011), we measured all final response variables, except in the case of two experimental units: a floc tree, to which birds had access, that died between months 8 and 13 and a dwarf tree, assigned to the bird exclusion treatment, whose frame and netting were blown off during the same timeframe.

Measurements of flocculent detritus

The depth of the floc near the base of each experimental unit was measured repeatedly; once at the start of the experiment and again after 2, 4, and 8 months. At each time point, an extending ruler was used to measure the depth of floc at five locations within the base of each frame. All floc depth measures were averaged to create a single floc depth value for each tree.

At four sites (two on each island) where accumulations of floc were present and associated with margins of rapidly growing *R. mangle*, we collected three floc samples and three peat substrate samples. Floc samples were collected every 5 m along a pond edge with floc accumulation, and peat was collected 10 m toward the pond's interior from each floc sample (where only trace amounts of floc were present). Substrate percent P by mass was determined by placing a known mass (~2 mg) of dried, ground material in a muffle furnace at 550°C for 2 h (Miller, 1998), followed by colorimetric analysis using the ammonium molybdate method (Clescerl et al., 1999).

Assessing growth and plant traits

We assessed the growth of experimental units throughout the experiment by quantifying the length and the number of leaves present for three marked twigs in apical positions, and by recording the total number of live terminal stems present (Feller et al., 2003). As marked twigs branched, we summed the lengths of all shoots and shoot segments distal to a marked point to calculate length values. Measurements of total twig length and overall terminal shoot abundance were taken 0, 2, 4, 8, and 13 months after treatments were imposed, while leaf abundances were measured 2, 4, 8, and 13 months after treatments were imposed. To create a single value summarizing the rate of change in each of these variables, we subtracted the last collected measure from the earliest collected measure for each variable and then divided these differences by the elapsed time. Data collection errors led 3/120 marked twigs to have earliest measures later than the start of the experiment while twig death led to 6/120 marked twigs to have their latest measures before the end of the experiment. Means for each experimental unit were calculated for the following plant growth metrics (1) total length of marked branches, (2) total number of leaves, and (3) total number of live buds. A correlation matrix revealed high collinearity (all $r > 0.74$), therefore we performed a principal component analysis (PCA) on the three growth rate variables, first centered and scaled to unit variance, to create a composite variable representing the overall growth of each plant (PCA axis 1). The first PCA axis captured 87.9% of the total variance in the growth-related measurements, and loadings were similar across measured variables (0.54–0.60).

To assess the toughness and nutrient content of leaves on our manipulated trees, we collected three leaves from different terminal stems growing in full sun and members of the newest fully expanded pair of leaves on each stem. We used a penetrometer (Wagner Instruments, Greenwich, CT) to measure the amount of force required to punch through each leaf. The penetrometer was pushed through the leaf at the midpoint between a leaf edge and the midrib halfway down the length of the leaf. The leaves were oven-dried at 60°C to constant mass and the three leaves from each plant were ground and homogenized individually. Leaf percent P was determined using the protocol outlined above for substrate samples. We measured leaf percent C and percent N by packing tin cups with known masses of dried ground leaf material (~4 mg) and using a Flash EA series 1112 NC soils analyzer. Internal lab standards measured along with experimental leaf samples were used to confirm the accuracy and precision of nutrient analyses.

To compare leaf morphology (leaf mass per area, or LMA [mg/cm^2]) of dwarf and floc plants, we collected single leaves from 20 nonexperimental plants at the Boa site. The leaves were in full sun and were part of the newest fully expanded pair of leaves on a terminal stem. We took digital photographs of each leaf, used ImageJ v.1.49 (Schneider et al., 2012) to measure their surface area, oven dried the leaves to constant mass at 60°C, and measured leaf biomass.

Quantifying arthropod density and herbivory

We used exhaustive visual searches of each experimental unit without collection to quantify arthropod abundances at 2, 4, and 8 months (Appendix S1: Section S1). Following visual searches at 13 months, we collected all arthropods that were discovered using handheld aspirators and identified them to order. Half of the foliage and branches on each experimental unit were clipped into plastic bags and searched again in the lab. We counted terminal shoots in clipped foliage, dried tissues to constant mass, and used linear regression to quantify the relationship between the two methods.

To quantify herbivory rates on leaves, one of the newest fully expanded leaves and one of the oldest fully expanded leaves were randomly selected from each of the three marked stems on all experimental units and digitally photographed. We used ImageJ v.1.49 (Schneider et al., 2012) to measure the area damaged by herbivores and averaged the percent damage values for the six leaves from each tree. Leaf lifespan in *R. mangle* is ∼18 months (Feller, 1995), thus the oldest leaves likely originated before the start of our experiment and were present for the duration of our experiment treatments. The young leaves likely originated during our experimental treatments and were exposed to varying durations of our bird access treatments. Both young and old leaves were included to provide measurements of herbivory integrated over time. Insect herbivores tend to feed upon younger leaves, while the dominant folivore of *R. mangle*, *A. pisonii*, feeds on older leaves (Feller & Chamberlain, 2007).

To quantify rates of herbivory on buds, we counted the number of buds with herbivore damage on each experimental unit and the number of leaf pairs in which both leaves were symmetrically damaged and/or deformed, indicating damage occurred prior to budburst. We summed the number of damaged buds and symmetrically damaged leaf pairs as an index of bud herbivory. Dead buds were not counted as "damaged" if cause of death could not be determined.

Statistical analyses

All statistical analyses were performed in R v. 4.1.1 (Forde et al., 2022b; R Development Core Team, 2021). To test hypotheses about the effect of floc buildups on mangrove growth and nutrient limitation, we modeled the interrelationships between floc depth at the base of plants, growth form (floc or dwarf), plant growth (PCA axis 1, see *Assessing growth and plant traits*), and foliar percent P using a structural equation model (SEM). We fit our model using the *lavaan* package (Rosseel, 2012). The *a priori* hypotheses built into our SEM structure were that growth form and floc depth affect plant growth, and that floc depth and plant growth affect leaf percent P. This SEM did not include additional predictors such as bird access treatment, levels of herbivory, etc. due to limitations imposed by our sample size ($n = 40$). An SEM approach was used to model direct and indirect effects of floc subsidies and to manage collinearity among growth, floc depth, and plant growth form, which would be problematic in linear models.

Our general statistical modeling approach for arthropods, leaf herbivory, bud herbivory, and plant growth included (1) specifying a valid global model, (2) performing AICc model selection on all nested subsets of the global model, (3) checking model diagnostics for the best candidate model, and (4) running likelihood ratio tests of hypotheses. Predictor variables in global models always included additive effects of bird access, plant growth form and study site (Dock or Boa), along with an interactive effect of bird access and plant growth form. In cases where response variables were counts (abundances) but inferences were desired for densities, an offset variable representing plant size (natural log-transformed total number of terminal stems) was added to models as a predictor. We used the package *AICcmodavg* (Mazerolle, 2015) for model selection, the package *MASS* (Venables & Ripley, 2002) for fitting generalized linear models (GLMs) assuming negative binomial error, and the package *nlme* (Pinheiro et al., 2015) for fitting heteroscedastic generalized least squares (HGLS) models.

For analyses of arthropod density, counts of arthropods on experimental plants were modeled using GLMs assuming a Poisson error distribution and including the offset predictor. For analyses of folivory, we used linear models assuming a normal error distribution to model the mean proportion of leaf area consumed on six sampled leaves for each experimental unit. We used logit transformation of the response to satisfy model assumptions (Warton & Hui, 2011). For analyses of bud feeding, counts of bud damage incidents were modeled with GLMs, including the offset term and assuming a negative binomial error distribution. Finally, for analyses of plant growth, we modeled values from PCA axis 1 of growth responses described in *Assessing growth and plant traits*. We used HGLS models that included a variance structure accounting for greater variability in growth rates observed in floc plants compared to dwarf plants.

RESULTS

Comparison of dwarf and floc plant characteristics

Floc was, on average, 5.8 times deeper near floc plants compared to dwarf plants, and this difference was significant (Table 1; Welch's t test: $t = 4.50$, df = 19.17, $p < 0.001$). Though the floc and dwarf experimental units did not significantly differ in their number of terminal shoots at the start of the experiment (Table 1; Welch's t test: $t = 1.37$, df = 32.4, $p = 0.18$), at the end of the

TABLE 1 Summary statistics and Welch's t test p values comparing flocculent detritus accumulation depths, plant traits, and growth rates between mangrove growth forms (dwarf plants vs. floc plants) and between bird access treatments (birds excluded vs. birds allowed) in the experiment

	Dwarf plants		Floc plants		Growth form	Bird access
Variable	**Mean**	**SD**	**Mean**	**SD**	p	p
Floc depth (cm)	1.8	0.57	10.37	8.51	<0.001	0.80
Start terminal shoot number	14.4	3.58	15.7	2.3	0.18	1.00
End terminal shoot number	15.8	3.94	30	9.15	<0.001	0.62
Leaf percent P	0.054	0.008	0.076	0.015	<0.001	0.93
Leaf percent N	0.96	0.12	1.29	0.24	<0.001	0.74
Leaf C:P (molar)	2255.9	299.6	1707.4	304.2	<0.001	0.66
Leaf C:N (molar)	56.7	4.9	45.3	7.6	<0.001	0.44
Leaf toughness (newtons)	8.9	1.39	6.69	1.21	<0.001	0.96
LMA[a] (mg/cm[b])	26.55	3.31	20.94	2.29	<0.001	NA
Stem elongation[b] (mm/month)	1.76	1.62	31.13	22.02	<0.001	0.74
Leaf number change[b] (leaves per month)	0.02	0.14	1.27	0.89	<0.001	0.70

Notes: Means and standard deviations are shown only for plant growth form because values were not different by bird access treatments.

[a] Leaf mass per area (LMA) measured only for a sample of nonexperimental plants at Boa site: dwarf plants $n = 10$, floc plants $n = 10$.

[b] Measurements from three marked branches averaged per plant.

experiment, terminal shoots were 90% more abundant on floc compared to dwarf *R. mangle* (Table 1; Welch's t test: $t = 6.37$, df $= 25.81$, $p < 0.001$). The positive correlation between the number of terminal shoots and total biomass of branches sampled during the arthropod survey ($r = 0.71$, $t = 6.02$, df $= 36$, $p < 0.001$) indicates that floc plants were more productive in terms of biomass production compared to the dwarf plants. Two other growth measurements besides final terminal stem number were also significantly greater for floc compared to dwarf plants: stem elongation over the duration of the experiment (17.7 times greater, Table 1; Welch's t test: $t = 5.95$, df $= 19.21$, $p < 0.001$), and change in leaf abundance on marked branches (63.5 times greater, Table 1; Welch's t test: $t = 6.23$, df $= 20.0$, $p < 0.001$).

Leaf traits and nutrient composition also differed markedly between floc and dwarf plants. Dwarf trees had 1.3 times denser leaves, as measured by LMA, and 1.3 times tougher leaves, as measured by the force required to penetrate them (Table 1; Welch's t tests; LMA: $t = 4.41$, df $= 16.0$, $p < 0.001$; toughness: $t = 5.36$, df $= 37.33$, $p < 0.001$). Foliar percent N by mass and percent P by mass were significantly greater for floc plants and both C:N and C:P molar ratios were significantly lower for floc plants (Table 1; Welch's t tests; percent N: $t = 5.42$, df $= 26.68$, $p < 0.001$; %P: $t = 5.77$, df $= 28.06$, $p < 0.001$; C:N ratio: $t = 5.54$, df $= 30.4$, $p < 0.001$; C:P ratio: $t = 5.67$, df $= 36.83$, $p < 0.001$). No differences were detected by bird access treatments in the aforementioned ecosystem and plant traits (Table 1).

Evidence of eased nutrient limitation in floc plants due to floc deposits

Floc retrieved from the base of floc plants on pond edges contained 2.5 times more P by mass compared to peat retrieved from dwarf stands in pond interiors (Figure 1a; Welch's t test: $t = 4.63$, df $= 12.29$, $p < 0.001$). Since P-limited dwarf plant are rooted in peat alone, while floc trees are rooted in peat overlain by layers of flocculent detritus, this result supports the hypothesis that plants growing in this zone gain access to P subsidies from the floc.

Floc plants measured in our study were similar in growth and nutrient characteristics compared to dwarf plants that were experimentally stimulated with P additions in a previous experiment at Twin Cays (Feller et al., 2003). Indeed, our floc plants had similar stem elongation rates and foliar percent P compared to dwarf *R. mangle* that had been fertilized with P for 2 years in an experiment by Feller et al. (2003) at Twin Cays (Appendix S1: Table S2).

The SEM (Figure 1b) indicated that the depth of floc deposits beneath *R. mangle* positively impacted P concentrations in leaves, due to direct effects ($r = 0.36$, $p = 0.008$) and to indirect effects mediated by the positive influence of floc depth on plant growth rate ($r = 0.47$, $p < 0.001$) and the positive influence of growth rate on foliar P ($r = 0.53$, $p < 0.001$). The SEM also showed that the faster growth of floc plants compared to dwarf plants is not completely accounted for by floc deposit depth,

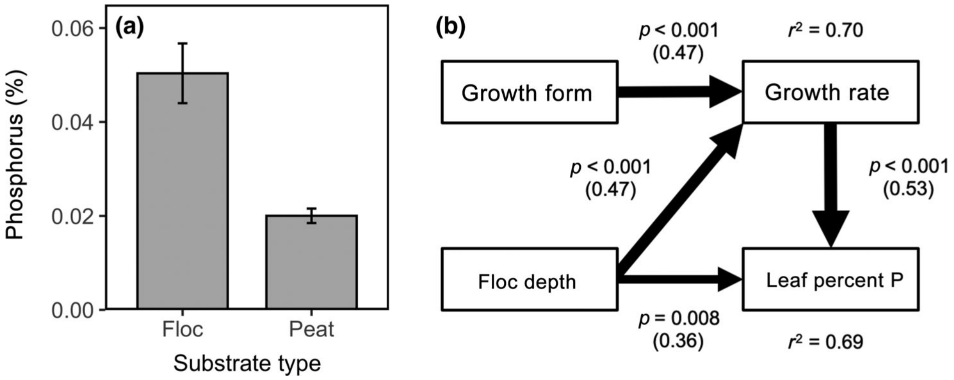

FIGURE 1 (a) Mean percent P by mass (±SE) for flocculent organic material collected from detrital accumulations near floc plants ($n = 12$) and for peat collected near dwarf plants ($n = 12$). (b) Structural equation model of the relationships between plant growth form (floc or dwarf), floc accumulation depth at plant base, plant growth (first PCA axis of three growth indicator variables), and P concentration (%) in leaves for experimental mangroves ($n = 40$). The p values and standardized path coefficients are shown for each hypothesized relationship. The weights of path arrows are proportional to the magnitudes of path coefficients. SE, standard deviation.

since a direct pathway between plant growth form and growth rate was significant and equal in strength ($r = 0.47$, $p < 0.001$) to the path between floc depth and growth. The estimated covariance matrix of the SEM did not differ from the observed covariance matrix ($\chi^2 = 2.364$, df = 1, $p = 0.12$), indicating that the fit of the SEM was adequate.

Impacts of birds and plant growth forms on arthropods, herbivory, and growth rate

We collected 110 arthropods belonging to 11 orders from experimental units at the end of the experiment. Araneae (spiders) were the most abundant taxonomic group (23%) followed by Hymenoptera (19%, mostly ants), Hemiptera (13%), Psocoptera (9%), and Lepidoptera (8%). Blattodea, Orthoptera, Thysanoptera, Coleoptera, Diptera, and Decapoda each represented <4% of the sampled arthropods. Arthropod counts were significantly positively correlated with the number of terminal shoots on experimental trees ($r = 0.54$, df = 36, $p < 0.001$). After model selection, bird access was the only informative predictor of arthropod densities on *R. mangle* (Appendix S1: Table S3; McFadden's pseudo $R^2_{\text{McFadden}} = 0.1$). Excluding birds from mangroves significantly increased arthropod densities over 2.6 times compared to mangroves with birds (LRT: $\chi^2 = 14.27$, df = 1, $p < 0.001$, Figure 2a). Neither site nor growth form (dwarf or floc) affected arthropod densities (LRTs; site: $\chi^2 = 1.78$, df = 1, $p = 0.18$; growth form: $\chi^2 = 1.07$, df = 1, $p = 0.30$). These results were consistent with repeated measures analyses of abundance over time (Appendix S1: Table S1) and with plant-feeding arthropods alone at the study's conclusion, which were fivefold higher in the absence of birds (Appendix S1: Section S2, Table S4).

Rates of leaf damage on trees varied from 0% to 32% leaf area removed, with a mean of 3.4% (Figure 2b). Bird access and growth form were informative predictors of feeding damage on leaves: the top two models identified from model selection, additive and interaction models with birds and growth form, accounted for AICc weight of 0.70 (Appendix S1: Table S5; $R^2_{\text{McFadden}} = 0.09$). Excluding birds from mangroves significantly increased leaf damage 1.8-fold (LRT: $\chi^2 = 24.76$, df = 1, $p < 0.001$), and leaf damage was 2 times greater on floc plants (LRT: $\chi^2 = 11.9$, df = 1, $p = 0.02$). The interaction effect showed a strong trend toward more similar herbivory levels without birds than with them (LRT: $\chi^2 = 6.86$, df = 1, $p = 0.07$). Leaf damage did not vary among sites (LRT: $\chi^2 = 0.43$, df = 1, $p = 0.67$).

Bird access, growth form, and site were all informative predictors of rates of herbivory on buds, according to the best model from model selection (Appendix S1: Table S6, $R^2_{\text{McFadden}} = 0.37$). The rate of bud damage (number of bud attacks per number of terminal shoots; Figure 2c) doubled when birds were excluded (LRT: $\chi^2 = 4.58$, df = 1, $p = 0.03$), and was four times greater on floc plants (LRT: $\chi^2 = 15.78$, df = 1, $p < 0.001$). Bud damage was 2.3 times greater at the Dock site (LRT: $\chi^2 = 7.26$, df = 1, $p = 0.007$). Bird access and growth form did not have interactive effects (LRT: $\chi^2 = 0.17$, df = 1, $p = 0.68$).

Growth form was the only informative predictor of our PCA-based measurement of overall plant growth (Figure 2d), according to the best model identified by model selection (Appendix S1: Table S7, $R^2_{\text{McFadden}} = 0.26$). Floc plants grew 7.6-fold faster than dwarf plants (LRT: $\chi^2 = 25.03$, df = 1, $p < 0.001$), while neither bird access nor site affected mangrove growth (LRTs; birds: $\chi^2 = 0.07$, df = 1, $p = 0.79$; site: LRT: $\chi^2 = 0.02$, df = 1,

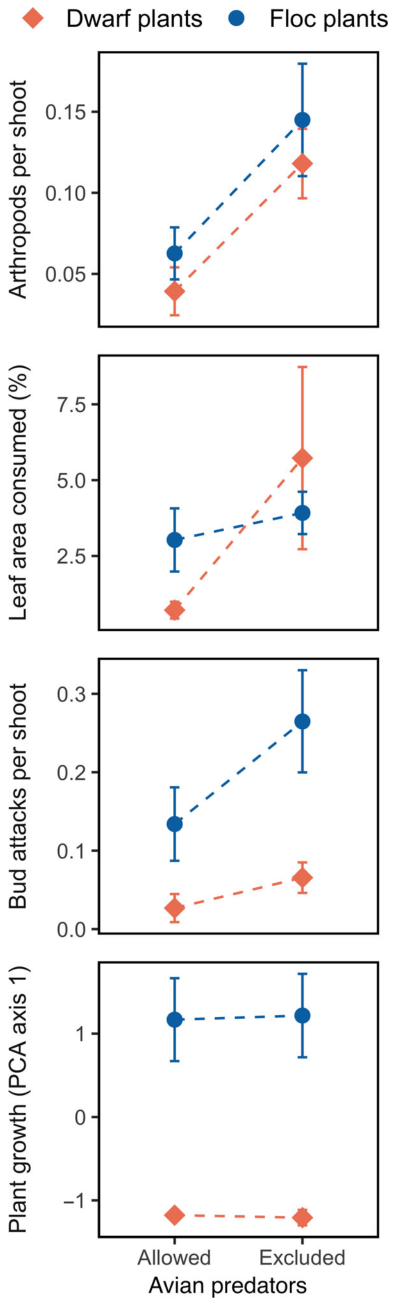

FIGURE 2 For floc and dwarf plants crossed factorially with bird access treatments, (a) mean arthropods per terminal shoot (±SE), (b) mean percent of leaf area removed by herbivores (±SE), (c) mean number of "bud attacks," i.e., damaged buds plus leaf pairs with symmetrical damage per terminal shoot (±SE), and (d) mean plant growth (±SE) as measured by the first axis of a PCA of shoot elongation, change in leaf abundance, and change in shoot abundance over 13 months. SE, standard deviation.

$p = 0.90$). Qualitatively, these results for PCA1 were identical (with smaller effect sizes) to analyses of the individual plant growth metrics (Appendix S1: Section S3).

DISCUSSION

Our study demonstrated strong forcing from both the bottom-up via detrital subsidies that increased plant vigor and growth in mangrove ponds, and experimentally from the top down as avian insectivores suppressed arthropod abundances. *Rhizophora mangle* plants subsidized by flocculent detritus were enriched in foliar nutrient content, had reduced leaf toughness and LMA, and grew at 6- to 60-fold higher rates (Table 1 and Figure 2d; Appendix S1: Section S3). Bird predation also cascaded to reduce invertebrate damage to leaves and buds by factors of two- to fourfold, but reduced herbivory did not influence mangrove growth. Thus, after 13 months of experimental manipulation, we did not find evidence that these positive indirect effects of birds translated to higher plant growth in this mangrove ecosystem.

Effects of nutrient subsidies

Microbial mats and associated organic detritus produce floating flocculent aggregates in shallow mangrove inlets and ponds (Faust & Gulledge, 1996). These ponds, occupied by slow-growing, P-limited dwarf mangroves, are surrounded by wind-blown floc deposits that accumulate to stimulate vigorous mangrove growth on pond margins (Feller, 1995; Feller et al., 2003; Rodriguez & Feller, 2004). Indeed, floc contained 150% higher P by mass than peat sampled 10 m away, and vigorous plants rooted in floc zones had similar growth rates and foliar P when compared to experimentally P-fertilized, fast-growing dwarf mangroves (Appendix S1: Table S2). Furthermore, increasing floc depth corresponded with greater positive effects on mangrove growth and elevated foliar P concentration (Figure 1b). Taken together, these results provide strong evidence that flocculent microbial biomass provides localized resource subsidies that alleviate P-limitation and increase productivity of red mangrove stands.

Resource subsidies provided by floc accumulations did not increase arthropod densities, but did alter plant–herbivore interactions by increasing rates of damage to both leaves and buds, both results consistent with synthetic analyses across terrestrial and aquatic manipulations of nutrients and predators (Borer et al., 2006). Since arthropod densities did not differ between resource zones, resources may have altered arthropod community composition, or the per capita rate of damage inflicted by herbivores, resulting in higher herbivory. Compared to dwarf plants growing without such subsidies, mangroves growing in resource-rich floc deposits provided greater quantity and quality of plant resources. Consistent with general results from fertilized plant communities (e.g., Gruner et al., 2005; Lind et al., 2017), plant growth and standing biomass were higher, leaves were thinner and less tough, and N and P concentrations increased by 35% to 40%. A comparison of red mangrove insect communities and herbivory rates with and without seabirds showed that heavy N supplementation by seabirds increased plant growth and nutritive value of vegetation, producing fourfold greater losses to herbivory on buds and leaves (Onuf et al., 1977). Such changes in plant traits reliably improve palatability and increase herbivory rates (Carmona et al., 2011). Our results are consistent with the hypothesis that floc-associated P-enrichment altered levels of herbivory via changes in mangrove leaf traits producing more palatable tissues.

Cascading effects of top predators

Avian top predators consistently decreased the density of arthropods and plant-feeding arthropods in particular (Appendix S1: Section S2), both in areas of high resource availability where tall, vigorous detritus-subsidized *R. mangle* occur, and in areas of low resource availability where low-stature, slow-growing dwarf plants predominate. Repeated arthropod surveys showed persistently lower densities on plants exposed to birds throughout the press experiment (Appendix S1: Section S1). Birds also indirectly decreased two important forms of herbivore damage: feeding on leaves and buds, which is consistent with meta-analyses showing positive indirect effects of vertebrate insectivores on herbivory but no significant trend for woody plant growth (Mäntylä et al., 2011; Mooney et al., 2010).

Herbivore damage on mangrove leaves at our sites is caused predominantly by the mangrove tree crab *Aratus pisonii* (Erickson et al., 2004), which is fed upon by birds (Olmos et al., 2001), and will drop or leap from trees into water to escape avian attacks, thereby becoming vulnerable to predation by fish (Yeager et al., 2016). *Aratus pisonii* are highly visual and secretive, rapidly changing their behavior when they perceive a threat (Beever et al., 1979). Thus, the effects of birds on leaf damage may be due to both lethal effects on crab abundances and sublethal effects on crab behavior. Bud damage, on the other hand, is largely attributable to a specialist, endophytic moth caterpillar (Tortricidae: *Ecdytolopha* spp.). Effects of birds on bud feeding damage therefore is more likely due to consumptive effects rather than behaviorally mediated. While *Ecdytolopha* larvae primarily feed within unopened buds, their presence is often visually apparent due to an accumulation of ejected frass (A. J. Forde, *personal observation*). In other systems, leaf damage provides visual or olfactory cues to birds that enhances their localized predation pressure (Gunnarsson et al., 2018; Mäntylä et al., 2020). Although our visual surveys likely underestimated arthropod numbers relative to destructive sampling methods, densities are often quite low in mangrove forests due to their spatiotemporal patchiness in a physiologically stressful, saline environment (e.g., Adeduntan & Olusola, 2013).

We could not detect the indirect impacts of birds on growth of *R. mangle* over the 13-month duration of the experiment, notwithstanding their strong reduction in the amount of leaf and bud herbivory on mangroves. We hypothesize that mangroves are well-adapted to tolerating these small to moderate levels of herbivory via induced physiological responses that partially, fully, or overcompensate for damage (Strauss & Agrawal, 1999), perhaps through mobilization of belowground carbon reserves. *Rhizophora mangle* is sclerophyllic, which Feller (1995) argues is an adaptive mechanism related to nutrient conservation in an oligotrophic ecosystem rather than an adaptation to herbivory. Demographic growth analyses of *R. mangle* in this ecosystem demonstrated that plant growth, despite attack from insect folivores and isopods consuming roots, was limited by water depth, sedimentation rates, seasonal variation in solar insolation, and nutrients, primarily P (Ellison & Farnsworth, 1996; Feller, 1995). Slow-growing dwarf plants also accumulate higher concentrations of foliar secondary metabolites, such as phenolics, gallotannins, and condensed tannins (McKee, 1995), which can approach 25% of dry mass in *R. mangle* (Kandil et al., 2004). These compounds may defend plants from herbivory or serve other functions, such as the absorption of ultraviolet radiation (Lovelock et al., 1992).

Top-down and bottom-up interactions

Despite striking differences in productivity and structure among dwarf and floc plants across the two site locations, and evidence of strong top-down and bottom-up forcing, the effects of birds on arthropod suppression did not differ among productivity zones. Theory predicts, with some empirical support, that detrital subsidies, higher productivity, and improved plant quality should increase secondary production to support larger predator populations and stronger top-down control (Cross et al., 2006; Hall et al., 2007; Leroux & Loreau, 2008; Lind et al., 2017; Oksanen et al., 1981). Multiple features of the study system may explain our lack of support for these predictions. First, productivity gradients in this system are steep and fine grained, yet mobile predators such as insectivorous birds forage over large spatial scales and may perceive resources as more coarse grained (McCann et al., 2005). Although mobile generalists can respond functionally to gradients of prey abundance (Eveleigh et al., 2007), and outbreaks are known to occur in this system (Ellison & Farnsworth, 1996), no such outbreaks occurred during this study and arthropod densities did not vary with plant growth forms. Second, *R. mangle* in floc-subsidized areas were larger and had more physical connections with other neighboring plants, by contrast with isolated dwarf plants in ponds (Appendix S1: Figure S2). This increased connectivity may have facilitated faster recolonization of experimental units by arboreal arthropods, thus obscuring greater predation rates in these zones (Maguire et al., 2015). Although a longer study duration may have allowed opportunities for insect irruptions, we believe it unlikely that the strong and consistent effects we observed over time would produce new, qualitatively distinct effects if allowed additional years to develop.

The great discrepancy in size between dwarf and floc plants represented a challenge in our design; given that we standardized the size of experimental units and the initial biomass within units, we could not manipulate bird access on entire floc plants. While nutrient enrichment impacts the leaf traits and growth of whole plants, disturbances and top-down impacts can be more localized and heterogeneous. Phytochrome receptors and other leaf traits are distributed according to the light environment, and plants may induce physical and chemical changes in response to touch or feeding at the leaf and branch levels (Karban, 2021). The resulting modular, chemical mosaic can influence variation in herbivory and predation (Volf et al., 2022), although this hypothesis needs investigation in mangrove ecosystems.

CONCLUSIONS

Increased nutrient availability due to localized accumulations of flocculent detritus altered a suite of *R. mangle* foliar traits and resulted in greater levels of herbivory, particularly in the absence of birds. Avian top predators consistently decreased arthropod densities and herbivory across adjacent zones of higher and lower nutrient availability, but did not indirectly increase plant growth. Because we did not detect top-down effects on plant growth, our results suggest that bird predation has relatively weak indirect effects on mangrove productivity, a finding common to other forested ecosystems (Harris et al., 2020; Mäntylä et al., 2011; Mooney et al., 2010). Future studies should focus on the factors that mediate the strength of tri-trophic interactions in forests, including productivity-mediated changes to herbivory rates and tolerance to herbivory, but also the long-term effects of these interactions on mangrove structure and function. Such studies will help us more precisely determine when and where bird predation alters forest productivity, population dynamics, and stand structure.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and metadata (Forde et al, 2022a) are available from Dryad at https://doi.org/10.5061/dryad.m37pvmd34. R software code (Forde et al., 2022b) is available from Zenodo at https://doi.org/10.5281/zenodo.5528080.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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