



Frozen Green Leaves as Potential Nutrient Subsidies in North American Mangrove Ecosystems

Katelyn Overstreet^{1,4} · Emily M. Dangremond^{1,2} · Ilka C. Feller³

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Abstract

Avicennia germinans, the black mangrove, has shifted its range limit northward, and increased in abundance in the South-eastern United States. In January 2018, a 3-day freeze event caused substantial defoliation of green leaves in *A. germinans* near its northernmost range limit in St. Augustine, FL. During their recovery, plants that lost their leaves grew similarly to plants fertilized with nitrogen, leading to the hypothesis that freeze-killed green leaves (frozen green) may have acted as a fertilizer. To assess the value of frozen green litter as a nutrient subsidy, we performed an experiment in which *A. germinans* seedlings were grown in sand with green, frozen green, senescent, and control leaf litter. We measured growth response in seedlings using the following criteria: total plant height, internode elongation, and plant biomass. All litter treatments stimulated growth in seedlings to a greater extent than that of controls. Seedlings treated with frozen green leaves were at least 5 cm taller and had 0.5 cm longer internodes than those treated with senescent leaves. Seedlings grown in the green leaf treatment were 8 cm taller, on average, and internodes were 0.12 cm longer than the senescent treatment. Biomass was 0.6–0.8 g greater in seedlings treated with green or frozen green litter than in the control treatments. We also conducted a leaching experiment to compare mass loss rates. Frozen and green leaves lost more mass in the leaching experiment than senescent leaves or controls. These results support the hypothesis that green litter that freezes can act as a nutrient source within the ecosystem and spur rapid recovery from freeze damage.

Keywords Disturbance · Freeze · Wetlands · Climate change · Temperate–tropical ecotone

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Highlights

- Seedlings of the mangrove species *Avicennia germinans* were grown with leaf litter from one of four treatments: frozen green, green, senescent, or control.
- Over 6 months, seedlings grown with frozen green and green leaf litter grew taller and had more biomass than seedlings grown with senescent leaf litter or controls.
- Frozen green leaves and non-frozen green leaves leached more mass than senescent leaves.

✉ Katelyn Overstreet
kover005@odu.edu

¹ Roosevelt University, 430 S. Michigan Ave., Chicago, IL 60605, USA

² Wildlife Works, 495 Miller Ave. Suite 100, Mill Valley, CA 94941, USA

³ Smithsonian Environmental Research Center, Edgewater, MD 21037, USA

⁴ Present Address: Old Dominion University, Biological Sciences, 110 Mills Godwin Life Sciences Bldg, Norfolk, VA 23529, USA

Introduction

Coastal ecosystems are among the most highly productive on Earth, with mangrove forests alone contributing an estimated 4.6 kg C ha⁻¹ year⁻¹ and 1.9 kg C ha⁻¹ year⁻¹ in gross and net primary productivity (Alongi 2018). To account for such high productivity rates, coastal wetlands require consistently available nutrients, and thus, largely depend upon nutrient cycling efficiency. Within mangrove ecosystems, such efficacy is primarily achieved through mangrove leaf litter, which upon decomposition yields large quantities of essential nutrients in the form of nitrogen, carbon, and phosphorus (Singh et al. 2005, Alongi 2018).

In mangroves, decomposition of fallen leaves by soil microbiota yields important sources of dissolved inorganic nutrients (Sousa and Dangremond 2011). Leaf litter, which accounts for an estimated 70% of net annual mangrove productivity (NPP) (Kristensen et al. 2017), is the connecting vessel through which macronutrients stored in leaf biomass return to the soil below. Therefore, the source and quality

of leaf litter are of considerable significance to carbon and nitrogen cycles within mangrove ecosystems and in neighboring marine and estuarine ecosystems. In these ecosystems, litter dynamics and consequent nutrient cycling have important consequences for growth in higher plants and phytoplankton (Ray et al. 2015). As mangroves expand into coastal salt marshes, there is evidence that salt marsh food webs are negatively affected (Smith et al. 2019; Goeke and Armitage 2021; Armitage et al. 2021; Goeke et al. 2023). However, because mangrove consumers are also expanding their ranges (Riley et al. 2014), the long-term effects of mangrove leaf litter inputs are unknown.

Mangroves occur globally throughout tropical and subtropical coastlines, and trends in climate change will likely alter current species distributions. In North America, mangrove range limits have historically been restricted to subtropical coastlines, due to species sensitivity to cold (Stuart et al. 2007; Cavanaugh et al. 2014) such that freeze events are associated with mangrove dieback. The intensity and scale of freeze-induced mangrove dieback are dictated, in part, by minimum temperature and freeze duration (Cavanaugh et al. 2019). A freeze event in which temperatures reach less than -7°C causes lethal damage to *A. germinans*. Temperatures less than -4°C can cause leaf damage but are considered sub-lethal (Kaalstad et al. 2023; Osland et al. 2019). In North America, the extent to which climate change will alter the frequency, intensity, and duration of freeze events may vary by region (Bardou et al. 2021; Cavanaugh et al. 2014; Cohen et al. 2024). However, along the Southeastern Atlantic coast, climate change is projected to result in a trend of decreased freeze event frequency, allowing for regions adjacent to and beyond range limits to maintain mangrove populations (Cavanaugh et al. 2019). Thus, as northern regions in the Southeastern United States warm, mangrove forest range limits are projected to shift poleward.

Non-lethal freezing events on the Southeastern Atlantic coast, though infrequent, may play a significant role in coastal nutrient cycling, as greenfall produced during such events should possess a higher nutritional quality than that of senescent leaves. Mangrove leaf litter can be derived from various sources. The bulk of leaf litter annually produced in a mangrove ecosystem consists of senescent leaves that fall naturally as a result of the tree's life cycle. Senescent leaves in mangroves do not fall seasonally, but gradually throughout the year. During leaf senescence, nutritional content is reallocated back to the tree itself. Because of this, senescent leaves retain essential nutrients such as nitrogen, phosphorus, and potassium (Lin and Wang 2001) to a much lesser extent than do green leaves (litter from tropical storms and cyclones), or frozen green leaves (litter resulting from freeze events) (Fonte and Schowalter 2004). Thus, green leaves produced during a tropical storm or freeze should provide a

surplus of nutrients compared to the senescent litter typically produced — potentially leading to nutrient enrichment and elevated plant growth, which can help plants recover from damage caused by disturbance.

In January 2018, a 3-day freeze event caused substantial defoliation of green leaves in a fertilization experiment of *A. germinans* near its northernmost range limit in St. Augustine, FL (see Dangremond et al. 2020 for description of the experiment), except in N-fertilized plants. Trees that were defoliated experienced complete recovery within 1.5 years of the freeze, and their interim growth mirrored the growth of N-fertilized trees (Feller et al. 2023). Thus, we predicted that frozen green leaves can serve as a source of nutrients for mangrove growth. Here, we tested the hypothesis that *A. germinans* seedlings fertilized using either frozen green or green leaves would experience higher growth rates than those fertilized with senescent leaves. We used a laboratory experiment with leaves collected from the field to assess seedling growth responses to four leaf litter treatments: green, frozen green, senescent, and control.

Methods

Study System *Avicennia germinans*, the black mangrove, is a neotropical halophyte. It occurs in Western Africa and along the Atlantic and Pacific coastlines of the Americas (Dodd and Afzal Rafii 2002). Though over 80 species of mangroves are found globally (Sandilyan and Kathiresan 2012), *A. germinans*, *Rhizophora mangle* (the red mangrove) and *Laguncularia racemosa* (the white mangrove) comprise the only three species native to the United States — likely due to restricting factors such as aridity and dispersal limitation (Bardou et al. 2021). *Avicennia germinans* is considered the most freeze-tolerant of the three naturally occurring North American species (Cook-Patton et al. 2015) and is the most abundant mangrove species in northern Florida. Due to its freeze tolerance, *A. germinans* is also the most likely of the three North American species to migrate northward past currently defined range margins.

On the Atlantic coast of North America, northernmost mangrove range limits occur near St. Augustine and Jacksonville, FL, at roughly 30°N (Williams et al. 2014; Cavanaugh et al. 2015, personal observation). Along the Florida coastline, winters are typically mild and experience average temperatures ranging from 8.2 to 9.5°C (Stuart et al. 2007). However, occasional frosts as severe as -10°C occur in Florida, taking place on average once every 8 years over the past century (Stuart et al. 2007). Climate change has been associated with the poleward expansion of mangroves into temperate regions, by virtue

of fewer lethal freezes in recent decades. The most recent lethal freeze in the mangrove-saltmarsh ecotone of Florida was in December 1989, when the air temperature reached -8°C at the St. Augustine lighthouse weather station (NCEI 2018). In January 2018, 3 days was below freezing, and the minimum temperature was -4°C (see Feller et al. 2023 for details). Prior to 2018, the most recent sub-lethal freeze was in 2014, when temperatures reached -3.3°C on 1 day. Historically, mangrove abundance in the mangrove-saltmarsh ecotone has fluctuated, but projected climate trends may favor a persistent state of mangrove dominance (Cavanaugh et al. 2019).

Experimental Design *Avicennia germinans* propagules were collected from Ft. George (30.4194° N, 81.4389° W) and Amelia Island, FL (30.6266° N, 81.4609° W), near where *A. germinans* reaches its northernmost range limit, in December 2020. Propagules traveled in plastic ziplock bags to the laboratory at Roosevelt University, Schaumburg, IL, via postal mail. Propagules were soaked in water for a minimum of 7 days or until their cotyledons opened, and then were placed into their growing medium.

Sand was used as a growing medium so that media-based nutrients would be minimal (Chapman and Feller 2011). Propagules were potted directly into the sand and assigned experimental treatments (January 2021–July 2021). Once potted into their growing medium, plants were watered using deionized water once a week. Approximately 2 g of leaf litter was added to each pot. The light source was fluorescent grow lights on 12-h timers. Seedlings were assigned to one of four litter treatments: green, frozen green, senescent, and control, with 12 replicates in each litter treatment for the experiment. Each seedling received 2 g of shredded dried leaves as its litter treatment. Controls received 2 g of shredded brown packing paper.

Litter treatments came from *A. germinans* leaves collected at the same sites as propagules, near the northernmost range limit of North American mangroves (Cavanaugh et al. 2019). Green and senescent leaves were collected in December 2020. The frozen green leaves spent 3 days at -4°C in a laboratory freezer. Nutrient content of the litter treatments was analyzed using a complete ICP analysis that incorporated total nitrogen plus acid digestion by the agricultural analytical services lab at Pennsylvania State University. This tested the percentage of the following elements: N, P, K, Ca, Mg, Mn, Fe, Cu, B, Al, Zn, Na, S.

Mangrove growth was assessed in seedlings, according to the following three criteria: (1) total plant height, (2) elongation of the first 5 internodes, and (3) dried plant biomass. A leaching experiment was performed to track biomass loss from leaf litter. Seedlings were potted in January, and measurements were taken after hypocotyl elongation, from March through July 2021.

Plant Height and Internode Elongation Plant height and elongation rate of the first internode were measured weekly. Plant height was measured from the edge of the pot to the apical-most leaf pair. Before seedlings developed true leaves, height was measured to the cotyledons. Internode elongation was measured as the distance between the topmost leaf pairs.

Biomass Following the completion of all experiments, plants were harvested, and roots and shoots were separated. Roots and shoots were placed into individual paper bags and oven-dried at 60°C for 3 days. At the end of the 3-day period, dried roots and shoots were separately weighed and their masses recorded, though total biomass is reported in the “Results” section. Cotyledons were excluded from the biomass.

Leaching Experiment A leaching experiment was conducted to compare mass loss over time among the different types of litter. Approximately 2 g of each leaf type was added to glass beakers and treated with DI water over the course of a 6-week period. Each treatment had four replicates. Mass (g) of the leaf material was recorded twice — once at the beginning of the experiment and once following the 6-week period. Mass loss was calculated by subtracting the final mass from the initial mass.

Statistical Analysis In the seedling growth experiment, the independent variables were litter types. Dependent variables were height, internode elongation, and biomass. One-way analysis of variance (ANOVA) was used to compare differences in growth metrics across litter treatments. When an ANOVA found significant effects, Tukey’s HSD test was used to compare treatment groups. In the leaching experiment, the mass loss through the leaching experiment was analyzed with a one-way ANOVA. ANOVA assumptions were tested with the Bartlett test.

Results

Leaf Litter Nutrient Content

Green and frozen green leaves were higher in N and P than the senescent leaf litter treatment (Table 1).

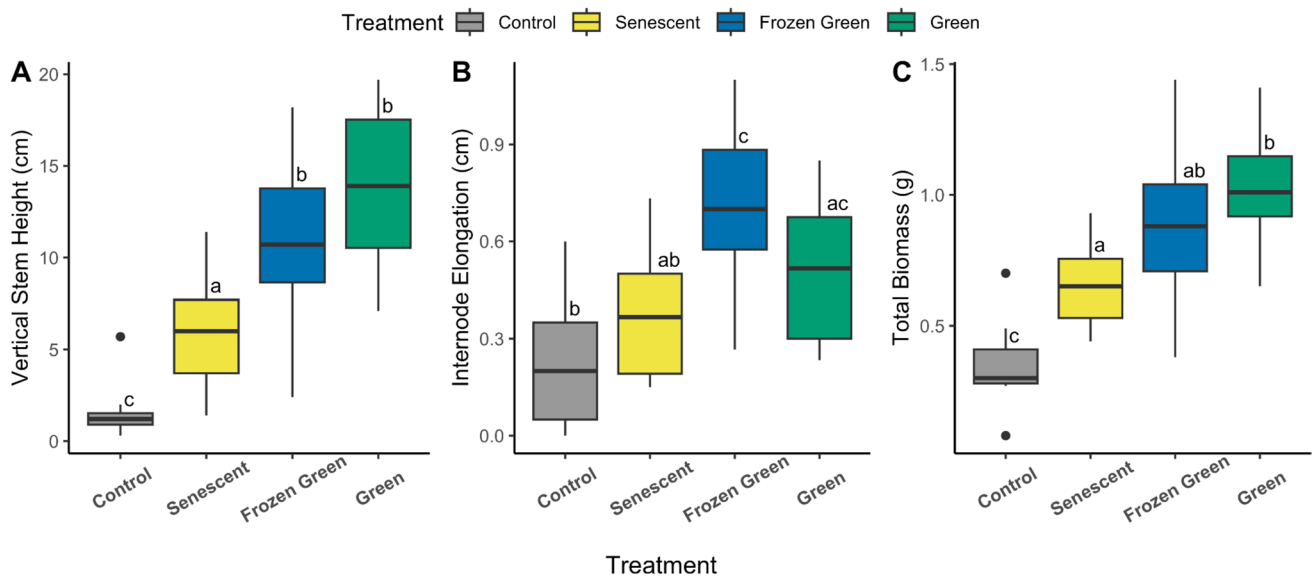
Plant Height

Seedlings grew twice as tall in the frozen green (mean height $\pm$ SE was $11.2\text{ cm} \pm 1.3$) and green litter treatments ($14.0\text{ cm} \pm 1.14$) than in senescent ($6\text{ cm} \pm 0.9$) treatments and approximately five times greater than in controls ($1.55\text{ cm} \pm 0.4$) (one-way ANOVA, $F_{3,43} = 37.47$, $p < 0.001$, Fig. 1A).

Table 1 A nutrient ICP analysis from Pennsylvania State of collected leaf litter samples, including senescent, green, frozen green, and control

		N	P	K	Ca	Mg	S	Mn	Fe	Cu	B	Al	Zn	Na
Lab ID	Sample ID	%	%	%	%	%	%	mg/kg	mg/kg	mg/kg	mg/kg	mg/kg	mg/kg	mg/kg
P24-03195	SL01	0.495	0.06	0.93	0.46	1.2	1.23	190	185	2	46	32	35	25,958
P24-03196	GL02	1.669	0.13	0.74	0.33	0.77	0.85	69	116	4	40	30	21	28,084
P24-03197	FL03	1.779	0.14	0.72	0.33	0.73	0.8	56	90	4	33	20	14	28,959
P24-03198	CL04	0.467	0.01	0.01	0.43	0.02	0.05	46	41	1	2	194	3	926

Italicized values at this sample mass, analyte is below the displayed reporting limit

**Fig. 1** Vertical growth (height) (A), internode elongation (B), and biomass (C) of *Avicennia germinans* seedlings. Results varied by leaf litter type. Treatments that share a letter are not statistically different from each other according to a Tukey post hoc analysis

Internode Elongation

Internode length varied by treatment type (ANOVA, $F_{3,43} = 9.53$, $p < 0.001$). The mean internode length for seedlings in the frozen green treatment was $0.71 \text{ cm} \pm 0.06$ and was approximately two times greater than seedlings grown in the senescent treatment (mean internode = $0.38 \text{ cm} \pm 0.06$) and three times greater than that of control treatments ($0.23 \text{ cm} \pm 0.06$) but was not significantly different than green litter treatments ($0.50 \text{ cm} \pm 0.06$) (Fig. 1B).

Biomass

There was a significant effect of treatment on seedling biomass (ANOVA, $F_{3,43} = 21.31$, $p < 0.001$). Seedling biomass was significantly greater in the green ($1.02 \text{ g} \pm 0.06$) and frozen green ($0.88 \text{ g} \pm 0.09$) treatments than in controls ($0.35 \text{ g} \pm 0.05$). The green litter treatment resulted in seedlings with a mean biomass 1.5 times greater than the senescent ($0.66 \text{ g} \pm 0.05$) treatment, but biomass in the frozen

and senescent treatments was not significantly different (Fig. 1C).

Leaching Experiment

Over the course of 6 weeks, frozen leaves lost $15.2\% \pm 0.69$ of their mass, which was statistically different than the percentage lost from senescent leaves ($6.99\% \pm 0.35$) and controls ($2.63\% \pm 1.30$), but not different than green leaves ($11.1\% \pm 1.52$) (ANOVA, $F_{3,12} = 25.4$, $p < 0.001$; Fig. 2).

Discussion

We predicted that frozen green leaves would act as a fertilizer for *A. germinans* seedlings. We found support for this hypothesis from height and biomass data, as seedlings growing with frozen green and non-frozen green leaves grew taller, had longer internodes, and had higher biomass than controls. In the leaching experiment, frozen green leaves and

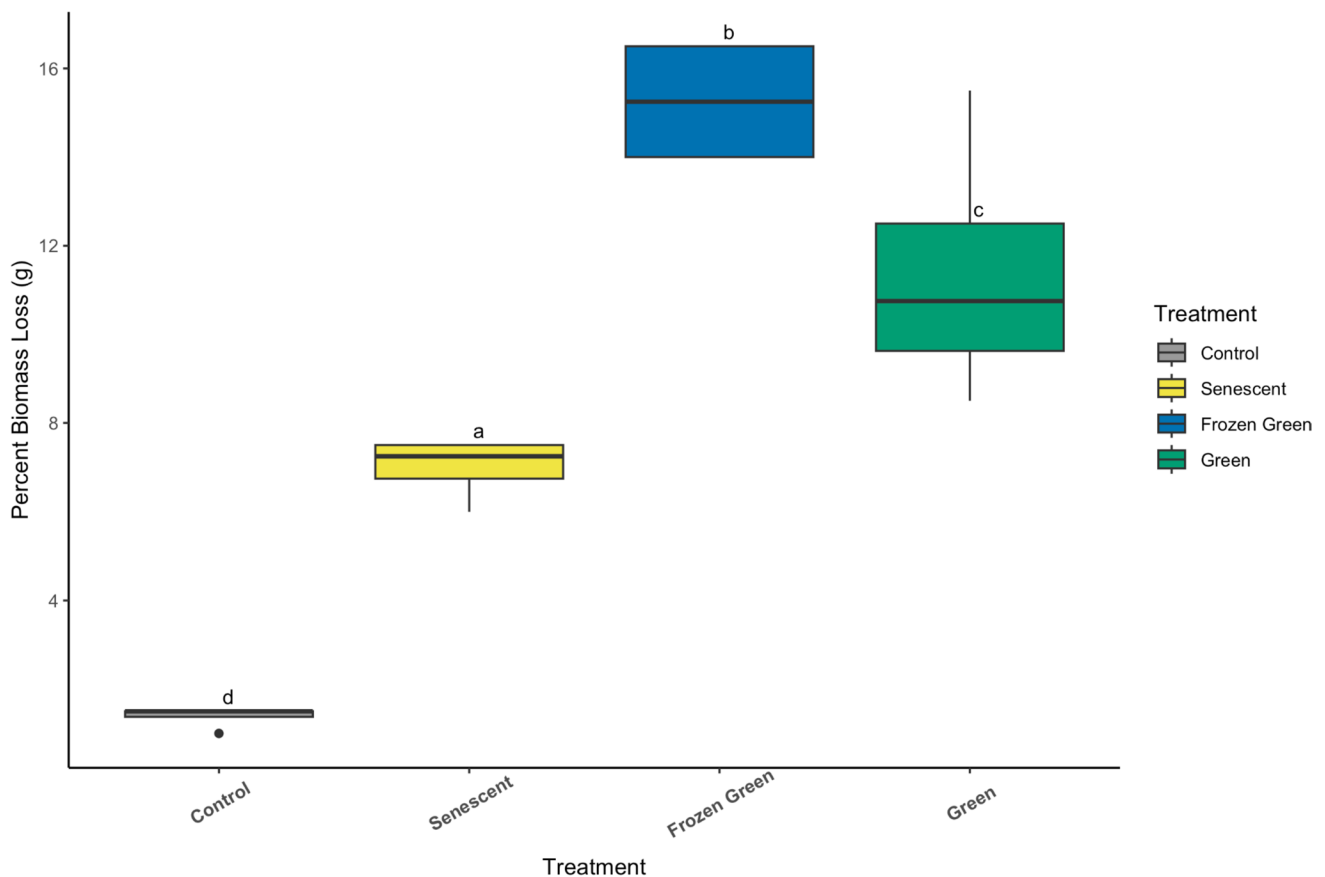


Fig. 2 Total biomass loss from *Avicennia germinans* leaves by litter type in a leaching experiment. Treatments that share a letter are not statistically different from each other according to a Tukey post hoc analysis

non-frozen green leaves lost more biomass than senescent leaves or controls.

Green and frozen green leaves had higher N and P content than senescent leaves. Our results showed growth variation between litter treatment types over the course of this experiment, and most notably, that green and frozen green leaf litter stimulated growth in sand-grown seedlings to a higher extent than that of senescent or control treatments.

In natural settings, senescent leaves fall occasionally and not all at once. This experiment had a one-time high input scenario, which simulates a disturbance event but not the gradual input of leaf litter that occurs in field conditions without a major disturbance. Therefore, the effect of the senescent litter treatment might be inflated compared to the natural scenario, and the difference between a one-time greenfall and gradual senescent leaf drop might be even greater than we show here.

This study shows support for the idea that green leaf litter, like that falling after a disturbance, can aid plant growth. Multiple freeze/thaw events would likely result in leaf nutrient content being more readily available. However, growth responses seen in the 1.5 years after the 2018 freeze (Feller

et al. 2023) could also be due to other sources of nutrients that increased after the freeze. Kominoski et al. (2020) found that TN and TP increased following cold events, likely because freeze-induced mortality of plants or animals causes increased detritus. The extent of freeze damage to other parts of the coastal landscape in January 2018 is not well described, but it is possible that other nutrient sources entered the ecosystem after the freeze.

Our results agree with other studies that show that not all leaf litter is nutritionally equal. Our results showed that green and frozen green leaves were higher in N and P than the other treatments. This is similar to previously published studies showing N and P content in *A. germinans* leaves in the mangrove-saltmarsh ecotone (Dangremond et al. 2020) and from another site in Florida (Feller et al. 2003), and that senescent leaf nutrient content is lower compared to green leaves in other species of mangroves (Lin and Wang 2001). Green leaves removed from trees during a tropical storm retain a higher amount of nutrients than senescent leaves, but frozen leaves, in particular, have been found to be richer in nitrogen and carbon with lower C:N ratios than other litter sources (Ellis et al. 2006). Freezing may act to break up the

leaf structure in a way that aids decomposition. Taylor and Parkinson (1988) found that the amount of mass leached doubled after repeated freeze and thaw cycles, compared to litter frozen only once. In this experiment, leaves were frozen only once. However, in a real-world freeze such as the one that occurred in St. Augustine, FL, in January 2018, ambient temperatures often drop below freezing, then rise during the day and then drop below freezing again at night, thus exposing leaves to multiple freezes and thaws.

The nutrient inputs and growth we describe here affect the recovery of mangroves to freeze events. As detailed in Feller et al. (2023), mangroves that experienced sub-lethal freeze damage experienced rapid growth and fully recovered over the 1.5 years following the freeze. This type of greenfall that occurs after a freeze, or a hurricane, is a valuable nutrient subsidy that increases recovery after disturbance, though damage and recovery processes vary considerably between freezes and hurricanes. Hurricanes have been shown to deliver P-rich sediments to mangroves (Castañeda-Moya et al. 2020), and freeze-killed leaf fall is an additional example of nutrient inputs from a disturbance in mangroves. Mangroves also lose leaves as greenfall as a result of wood-boring herbivores (Feller and Mathis 1997), but to our knowledge the effect of that greenfall as a potential fertilizer has not been evaluated.

Avicennia germinans is the most abundant and freeze-tolerant species at the northern edge of the mangrove-salt-marsh ecotone, but *Rhizophora mangle* and *Laguncularia racemosa* are also present. While the nutrient subsidy from other species may not be equivalent, it would likely be similar, as freeze-killed *Laguncularia* leaves were shown to have higher N content than green or senescent leaves (Ellis et al. 2006). Chapman and Feller (2011) found that mixed litter from *A. germinans* and *L. racemosa* provided a larger fertilizer effect than *A. germinans* litter on its own. *Rhizophora mangle* has slower decomposition rates than *L. racemosa* and *A. schaueriana* (Lima and Colpo 2014) so *R. mangle* might not have as large of a subsidy effect. However, the temperature threshold for lethal freeze damage varies by species (Cook-Patton et al. 2015), which means that for any given freeze event, each species may respond and recover differently.

In this experiment, all seedlings were grown in a lab, using an artificial growing medium (sand). Using sand, a nutrient-deprived soil medium, in addition to only distilled water in a laboratory setting, helped to distinguish effects of litter type. However, this was not representative of soil microbes in a natural mangrove ecosystem. In natural mangrove systems, microbial activity has shown to be influenced by estuarine gradients resulting from seasonal changes (Fernandes et al. 2014; Wang et al. 2022) — with a number of studies suggesting that microbial richness and diversity may increase with warmer summer temperatures and decrease

with colder winter temperatures (Lin and Das Peddada 2020; Wang et al. 2022). However, there is a lack of understanding regarding the mechanisms through which changes in temperature shape microbial communities. Understanding differences between decomposition rates in leaf litter types and the effects could be a direction for future studies.

Few studies have addressed the impacts of climate change on mangrove nutrient cycling, and even fewer, the implications of freeze event declination, as it pertains to projected mangrove encroachment.

Mangroves are expected to increase in abundance in regions formerly too cold for long-term survival (Cavanaugh et al. 2019). These regions, though warmer than typical conditions over the last century, will still likely encounter freeze events due to their northern geography compared to coastal regions historically associated with mangroves. These freezing events have the potential to cause great damage to mangroves by causing top kill and loss of leaves (Cavanaugh et al. 2019; Kaalstad et al. 2023). Our results are one line of evidence demonstrating the resilience of mangrove ecosystems to extreme cold temperatures, a knowledge gap identified by Osland et al. (2021). This study adds to growing literature showing that *A. germinans* recovers quickly from freezes (Feller et al. 2023), faster than recovery from hurricanes (Cohen et al. 2024), and that they may be more resilient to freezes than previously thought. The nutrient dynamics we address may act as yet another positive feedback mechanism increasing mangroves' ability to encroach into saltmarsh (Weaver and Armitage 2018; Macy et al. 2019). We suggest that land managers interested in monitoring and/or managing mangrove encroachment consider the potential fertilization effects of both hurricanes and freezes, so that recovery from disturbance is considered in monitoring and management plans.

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Data Availability All data are available upon request.

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