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Human-mediated impacts on detrital subsides

By

RICARDO DESANTIAGO – AMEZCUA

DISSERTATION

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DOCTOR OF PHILOSOPHY

in

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in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA DAVIS

And

SAN DIEGO STATE UNIVERSITY

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Committee in Charge

2024

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Acknowledgements

This PhD marks the fulfillment of a lifelong dream since I was a kid looking for bugs under rocks and pretending I was a biologist in a dirty pond. A dream born from a love for the natural world gifted to me by my mother and fueled by my family's endless encouragement to always follow my dreams. My family has been my unwavering support, particularly my parents, who emigrated from Mexico and overcame countless obstacles to provide a better life for my sisters and me. Their courage and tireless work ethic have been a constant source of inspiration. I dedicate this dissertation to my family and hope to make them as proud as I am of them. Thank you, Mom and Dad, for everything.

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Abstract

Ecosystems are intricately connected by the exchange of organisms, inorganic materials, energy, and information that traverse ecotones, forming a complex network of interactions. These inputs from donor systems, known as spatial subsidies, can profoundly shape habitats by influencing primary productivity, altering community interactions, impacting resilience, and changing species composition in recipient habitats. However, human activities such as global shipping and urbanization can disrupt these subsidies through increased nutrient flow, species introductions, and climate-mediated range shifts. In this dissertation, I investigate how invasive species in donor systems and human-mediated movement of organic material across habitats impact subsidy-dependent communities.

Chapter 1 explores the impacts of an invasion-mediated shift in seaweed wrack from native kelp, *Macrocystis pyrifera*, to invasive Devilweed, *Sargassum horneri*, on subsidy-dependent communities of rocky shores. The study assesses the species-specific impacts on common detritivores (*Pagurus samuelis* [Blue banded hermit crab], *Pachygrapsus crassipes* [Striped shore crab], and *Tegula funebralis* [Black turban snail]), the historically important but now endangered wrack-consuming giant snail (*Haliotis cracherodii*, [Black abalone]), an assemblage of these grazers, and common native benthic seaweeds (*Centroceras clavulatum*, *Silvetia compressa*, and *Ulva* spp.). Performance impacts are evaluated through long-term feeding assays using common Black turban snails and *Haliotis rufescens* (Red abalone), as a proxy for the rare Black abalone. Food preference was determined through feeding choice assays using individual species of these wrack detritivores, and a "community assay" in which an

assemblage of these grazers fed on three native benthic seaweeds along with either native kelp or invasive Devilweed wrack are conducted.

Performance varied among consumers, with abalone growing better on a kelp diet compared to Devilweed and showing intermediate growth on a mixed diet. Contrary to predictions, Black turban snails grow more on the Devilweed diet over kelp, and those that fed a mixed diet grow similarly to those that ate Devilweed alone. Preference assays reveal that although Black turban snails grow more on Devilweed diets, they prefer kelp, while abalone also display a high preference for kelp. Blue banded hermit crabs prefer Devilweed, and Striped shore crabs show no preference. The assemblage of wrack detritivores shifts consumption away from wrack when kelp is replaced by Devilweed, and increases consumption on *S. compressa*, an already sensitive, canopy-forming rockweed, suggesting Devilweed has the potential to indirectly impact native benthic seaweeds in subsidy-dependent communities.

Chapter 2 aims to understand the spatiotemporal variation in native and invasive wrack deposition on beaches that receive large inputs from adjacent kelp forests, recently invaded by *Sargassum horneri*. We conducted surveys at seven sites on one of the California Channel Islands at four time points across 2022. Our findings reveal spatiotemporal variation in native and invasive wrack inputs to beaches, with Giant kelp, *Macrocystis pyrifera,* dominating wrack inputs throughout the year, and *S. horneri* being relatively rare. Kelp was most abundant on west-northwest facing shores, while *S. horneri* was even more rarely found on west-facing shores. The peak deposition periods for kelp and *S. horneri* differed, with kelp deposition peaking in September and *S. horneri* deposition peaking in March. This chapter highlights the complex spatiotemporal variation in native and invasive wrack inputs, and their potential to shape recipient communities.

In Chapter 3, we delve into the intricate interconnections between ecosystems, focusing on the unique phenomenon of *Sargassum* wrack deposition along coastlines in the Mexican Caribbean. These massive deposits, resulting from seaweed blooms in the Sargasso Sea and the Great Sargassum Belt, present significant ecological and economic challenges. Our study investigates the ecological implications of *Sargassum* deposition, employing manipulative field experiments simulating realistic biomass inputs of several cubic meters in both beach and forest ecosystems. Contrary to expectations based on ecological theory, our findings reveal comparable decomposition rates between beach and forest ecosystems, challenging the notion that naïve ecosystems are incapable of processing novel subsidies. We assess the relative contributions of arthropods and microbes to *Sargassum* decomposition, with microbial communities dominating decomposition in the forest and a combination of microbes and talitrid amphipods driving decomposition on the beach. Furthermore, our study provides insights into the long-term effects of *Sargassum* deposition on nutrient cycling within these two ecosystems. After 12 months, we found that *Sargassum* may serve as a nutrient subsidy to native plants in the forest, albeit with slower utilization rates compared to non-native plants such as Bermuda grass found on beaches in the area. Overall, our results highlight the capacity of forest ecosystems to assimilate and utilize foreign organic matter, challenging traditional ecological paradigms and offering new perspectives on ecosystem functioning.

CHAPTER 1

Consumer- and seaweed-specific impacts of invasion-mediated changes to detrital subsidies on rocky shores *

Ric DeSantiago, Wendi K. White, John R. Hyde, Katherine M. Swiney & Jeremy D. Long

Abstract

Detrital subsidies such as leaf litter, animal carcasses, and marine wrack can profoundly shape recipient habitats by influencing resiliency and productivity. Species introductions and climate-driven range shifts alter the quantity and quality of these subsidies in donor habitats, thereby potentially influencing recipient communities. Such impacts might be particularly important when detrital shifts alter detritivore feeding and performance. Attempts to identify a general theory predicting the consequences of invasive species on detritivores have been challenging, in part because most theories have been based on the study of microbes or consumers of living prey. Further, two recent meta-analyses disagree about the impacts of invasive plants on detritivore populations. Here, we examined the potential impact of a human-mediated shift in macroalgal detrital subsidy from native kelp, *Macrocystis pyrifera,* to invasive Devilweed, *Sargassum horneri,* on recipient rocky shores, with an emphasis on exploring species-specific impacts. We assessed consumer performance on single species diets or on a mixture in no-choice assays, and we assessed feeding preference in choice assays. Additionally, we examined the impacts of this shift on grazing of native benthic seaweeds by an intertidal consumer assemblage. Replacing Kelp with invasive Devilweed had consumer-specific impacts on performance – suppressing growth of Red abalone (*Haliotis rufescens*) but enhancing growth of Black turban snails (*Tegula funebralis*). The effect of mixed diets on consumer growth also

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displayed consumer-specificity. Also, replacing native Kelp with invasive Devilweed increased grazing of native benthic seaweeds by a realistic detritivore assemblage, but only on the habitat-forming brown seaweed, *Silvetia compressa.* Thus, invasion-mediated changes in detrital wrack composition had consumer- and seaweed-specific impacts. Such species-specificity could underlie disagreements about the impact of species invasions on detritivore populations and could impede our ability to identify a general theory about how species invasions will impact recipient communities via detrital pathways.

Introduction

Ecosystems are connected through fluxes of organisms, energy, materials, and information from donor systems that can alter species abundances and interactions in recipient food webs (Polis and Hurd 1996, Nakano et al. 1999, Ostfeld and Keesing 2000, Talley et al. 2006, Gratton et al. 2008, Greig et al. 2012). For example, detrital subsidies can modify key ecological processes (e.g., competition and predation; Yang 2006, Piovia-Scott et al. 2011, Kenny et al. 2017), generate trophic cascades (Polis and Hurd 1996, Polis et al. 1997, Nakano et al. 1999, Jefferies 2000), and stabilize food webs (Takimoto et al. 2002). Changes to these donor communities via species introductions and range shifts are likely to change detrital subsidies and the habitats that rely on them (Zhang et al. 2019).

Detrital food webs may better resist perturbations because of donor control and trophic diversity in recipient habitats (Odum 1969, Neutel et al. 1994, Moore et al. 2004). Changes in community taxa composition of donor habitats arising from species introductions and climate-mediated range shifts may lead to changes in detrital subsidies that could destabilize these recipient ecosystems (Collins and Baxter 2014). For example, species shifts in donor systems may change the quantity and quality of detrital supply leading to consequences on populations of recipient primary consumers (i.e., detritivores), and the species they interact with (Yang 2006). Identifying a general theory about how species invasions affect recipient detritivores and their communities would improve our ability to predict future environmental change (Yang et al. 2010). Unfortunately, there is a lack of consensus about how species invasions will impact detritivores, from both theoretical and meta-analytical perspectives. Clearly, there is a need to better understand how human-mediated changes to donor ecosystems influence recipient detritivores and their communities.

Such human-related impacts are likely to be seen and mediated by detritivores in recipient ecosystems because they are ubiquitous (Ostfeld and Keesing 2000, Yang 2006) and early responders to subsidies (Moore et al. 2004, Levin et al. 2006). These detrital shifts could impact detritivores in at least two ways. First, compositional shifts in donor systems could modify consumer performance. For example, a mixed diet of low- and high-quality detritus can stimulate grazing but reduce lipid content of consumers (Larrañaga et al. 2020). The direction of these impacts will be influenced by the relative quality of the subsidy before and after these shifts. Second, compositional shifts in donor systems could shift feeding to/from resident resources in recipient habitats (Duggins et al. 1989, Bustamante et al. 1995, Parker and Hay 2005). In particular, if novel subsidies are less preferred by recipient consumers, the arrival of novel subsidies may shift consumption onto resident resources/species. Both altered consumer performance and preference could change the strength of interactions between recipient consumers and the species they interact with (Polis and Strong 1996).

Predicting detritivore response to novel resources is challenging given that 1) most theories have focused on predicting responses of native decomposers (i.e., microbes) and consumers to novel resources and 2) these theories disagree with each other. For example, microbial studies generated the Home-Field Advantage Hypothesis (HFA; Bocock et al. 1960, Gholz et al. 2000, Pugnaire et al. 2023) which predicts that microbes will underutilize novel resources, primarily because of a lack of evolutionary history. In contrast, the Prey Naiveté Hypothesis (Cox and Murray 2006, Carthey and Banks 2014, Papacostas and Freestone 2019) predicts that consumers will prefer novel resources because a lack of evolutionary history limits the ability of prey to defend against novel consumers.

Further, two meta-analyses have been unable to resolve these discrepancies. In the first, invasive plants had weakly negative or neutral impacts on detritivore abundance in three ecosystems (wetlands, woodlands, and grasslands; McCary et al. 2016). In contrast, a second meta-analysis found that leaf litter from invasive plants increased detritivore abundance in recipient habitats (Zhang et al. 2019). The uncertainty about invasion impacts on decomposers extends to consumers of seaweed detritus (i.e., detritivores). For example, one meta-analysis found no overall effect of seaweed invasions on density, biomass, and growth of consumer species (Maggi et al. 2015). Another meta-analysis found that arthropods, but not mollusks, had reduced preference for non-native red seaweeds (Swantje et al. 2017).

We tested the impacts of a seaweed invasion on growth and preference of rocky intertidal detritivores in the Southern California Bight. The native wrack in this system is largely composed of California Giant Kelp, *Macrocystis pyrifera* (Hereafter, "Kelp"; Hayes 1974, Dugan et al. 2003, VanBlaricom and Kenner 2020). Kelp is a nutritious, high preference food for various organisms including abalone (*Haliotis cracherodii*) and Black turban snails (*Tegula funebralis*; Leighton and Boolootian 1963). Kelp forests, especially along leeward shores of the Channel Islands, have been invaded by *Sargassum horneri* (Hereafter, "Devilweed"), since 2003 (Marks et al. 2015, Kenner and Tomoleoni 2020). As such, we expect that wrack will increasingly include Devilweed as donor Kelp forests are invaded. Thus, it is important to understand how this novel wrack subsidy will impact recipient detritivores and their communities.

To test how shifts towards Devilweed impact consumer performance, we fed snails (Black abalone, Black turban snails) Kelp, Devilweed, or a mixture of both, and measured soft tissue growth and behavior (self-righting times). To test if Devilweed changed feeding, we

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offered several rocky intertidal wrack consumers a choice between native Kelp and invasive

Devilweed. Lastly, we offered an assemblage of wrack consumers foods made from native

benthic seaweeds and either Kelp or Devilweed to determine if replacement of Kelp with

Devilweed shifts grazing onto native seaweeds.

Methods

Study organisms

Striped shore crabs (*Pachygrapsus crassipes*), Blue banded hermit crabs (*Pagurus samuelis*), Black turban snails (*Tegula funebralis*) Black abalone (*Haliotis cracherodii*) are, or were, abundant seaweed consumers and wrack detritivores along rocky shores of southern California (Morris et al. 1980, Barry and Ehret 1993, Aquilino et al. 2012). For example, Black abalone consume benthic seaweeds and are subsidized by Kelp detritus (VanBlaricom and Kenner 2020). Additionally, Black abalone were historically important seaweed consumers prior to declines related to disease and overharvesting (VanBlaricom 1993, Altstatt et al. 1996, Raimondi et al. 2002). Although Black abalone densities have started to recover on some of the Channel Islands, densities remain at least an order of magnitude below historic levels (Raimondi et al. 2002, Miner et al. 2006). We included all of these species in this study as they represent a typical assemblage of rocky intertidal detritivores in areas receiving detrital inputs of the invasive Devilweed. Furthermore, we included Red abalone (*Haliotis rufescens*) – a local consumer of detrital kelp and kelp detritus in one of the assays (see below).

Devilweed prevalence surveys

To confirm that Devilweed is present and to determine its to wrack, we surveyed large wrack piles deposited on two beaches at two sites on San Nicolas Island in January 2020

(33.27335° N, 119.57629° W, 33.28310° N, 119.53557° W) and measured the proportion of the

wrack pile surface area Devilweed represented. We adopted this qualitative metric of because

our time at these sites was limited and surveying surface area (as opposed to total biomass)

allowed us to quickly survey a large amount of wrack. At each site, we selected the first 20 large

(>1 m) wrack piles encountered along a haphazardly placed 50 m transect. We measured the

longest length and width of the pile each wrack pile and Devilweed individuals on the surface of

the piles. We calculated the area of Devilweed and piles using the equation for an ellipse

($A=\pi ab$), where "a" and "b" are one half the length and width. For each pile, we calculated the

sum area of all Devilweed individuals and divided by the area of the pile to estimate the

proportion of wrack that consisted of Devilweed. Using this method, the relative contribution of

Devilweed to wrack for a large pile could be estimated in minutes as opposed to hours.

Performance Assays

To understand how shifting wrack composition affects the performance of rocky shore

detritivores, we measured the growth of juveniles of two wrack consumer species [Turban snails

and Red abalone (*Haliotis rufescens*)] on diets of Kelp, Devilweed, or an equal mixture of the

two. We used Red abalone as a proxy for Black abalone because of logistical challenges of

conducting research with endangered Black abalone. For example, most captive Black abalone

are mature adults that might not respond to diet changes because of their large size and slow

growth. We justify using a congener as a proxy species because both abalone species 1) consume

brown seaweeds (Leighton and Boolootian 1963, Winter and Estes 1992, Nelson et al. 2002), 2)

have similar growth rates (Ault 2009), and 3) share some overlap in habitat (Díaz et al. 2000,

Neuman et al. 2010). Because Devilweed reduces Kelp abundance in subtidal habitats but does

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not extirpate it across short time scales (Sullaway and Edwards 2020), the mixture treatment is the most ecologically realistic.

We collected Black turban snails (shell length = 6-10 mm) from Sunset Cliffs Natural Park (SCNP, 32.71972° N, -117.25725° W; SC permit #11084). We used lab-reared, juvenile Red abalone from a single cohort (May 2017) provided by NOAA Fisheries Southwest Fisheries Science Center (hereafter, "SFSC"; shell length = 45-60 mm). All organisms were transported to San Diego State University's Coastal and Marine Institute Laboratory (CMIL) and placed in plastic containers (190 x 160 x 110 mm) with mesh (2 mm openings) covers. The performance assay began March 5, 2020. At this time, all containers were completely submerged in tanks with 14°C recirculating, aerated water with a pH of 7.75. Due to facility closures caused by the COVID-19 pandemic, we transported all organisms to a temporary recirculating seawater system setup on March 19, 2020. The experiment continued at this location until the termination on April 17, 2020 (i.e., six weeks after the start). Here, the water temperature was maintained at 15°C. Because artificial seawater was used at this facility, the pH was more basic (range from 8.4-8.7). We monitored ammonia and ammonium daily during this period and used these data to determine dates of partial water replacements (conducted on March 28 and April 1, 2020; 30% and 80% volume replacement, respectively).

Animals were offered one of four diets (Kelp, Devilweed, a ~1:1 mixture of Kelp and Devilweed, or starvation; n=20). Seaweed was offered *ad libitum*. We included the entire thallus (i.e., stipes, blades, and pneumatocysts) to account for tissue-specificity in performance/ preference. We assessed diet-related impacts on performance by calculating the change in dry soft tissue mass of the animals. Final dry tissue mass was calculated by weighing the tissue after dissecting it from the shell, freezing the tissue at -80°C, and freeze-drying it for 24 hours. To

estimate initial dry tissue mass, we subsampled 20 animals from each species at the start of the experiment and calculated a regression of shell length to dry soft tissue mass. Because the relationship between maximum shell length and dry tissue mass was strong and linear for both Turban snails ($R^2 = 0.89$, $F_{(1,18)}=148.20$, $p<0.001$) and Red abalone ($R^2 = 0.89$, $F_{(1,18)}=160.71$, $p<0.001$), we used these regressions to estimate starting soft tissue biomass, non-lethally.

In addition to growth, we assessed how diet impacted abalone self-righting times (n=20). Because abalone are extremely vulnerable to predators when their ventral tissues are exposed, such assays can inform environmental influence on predator-prey interactions (e.g., slow righting time suggests an increased vulnerability to predators; Baldwin et al. 2007, Lachambre et al. 2017). During righting tests, abalone were placed, dorsal side down, in 15°C seawater. We measured the time it took Red abalone to flip over so that the dorsal side of their shell faced up. These tests were conducted until abalone corrected their orientation or 4 minutes passed. We conducted these assays at the start and end of the performance assay.

Preference Assays

To understand how shifting wrack composition affects feeding preferences, we offered rocky intertidal consumers a choice of Kelp and Devilweed. Kelp was collected as fresh wrack from Ocean Beach (32.75380° N, -117.25284° W) and benthic Devilweed was collected by snorkel from the jetty at Mission Bay in San Diego (32.76158° N, -117.24521° W). Non-abalone animals were collected from SCNP and transported to CMIL and held in flow-through seawater. Adult Black abalone (held under ESA Permit #19571-2R) were held in chilled, flow-through seawater at SFSC. Separate feeding choice assays were conducted with each of the four primary consumer species (Shore crabs, Hermit crabs, Turban snails, and Black abalone). This assay was

conducted with captive Black abalone because choice assays were non-lethal to animals, and we focused on preference rather than growth.

To standardize hunger level and to motivate our animals to feed, all animals were fed *Ulva spp.* for three days and then starved for two days prior to the preference assays. All feeding assays were conducted in June 2019, with the exception of Black abalone (August 2019). We offered 3 Turban snails (n=14), 3 hermit crabs (n=14), or a single shore crab (n=15) a choice of Devilweed and Kelp in plastic containers (190 x 160 x 110 mm). Container walls included six 35mm holes lined with mesh (2 mm openings) to improve water exchange. Black abalone were housed individually in 280 x 230 x 180 mm mesh-lined (5 mm openings), PVC-framed cages with a Plexiglas® floor. We offered animals an equivalent biomass of Kelp and Devilweed that had been anchored with binder clips (mean ± SE: 7.5 ± 0.4 g for Hermit crabs, 7.5 ± 0.3 g for Shore crabs, 6.5 ± 0.3 g for Turban snails, 21 ± 0.4 g for Black abalone). All replicates were paired with no-consumer controls to account for changes in mass unrelated to consumption (Dolecal and Long 2013). Individual replicates were stopped when either ~3/4 of either seaweed was consumed, or six days had passed. All remaining seaweed and seaweed fragments were blotted dry and weighed. We adjusted for autogenic growth using the equation $T_i (C_f /C_i) – T_f$, where T_i and T_f represent the seaweed masses of the experimental treatments and C_f and C_i represent the seaweed masses in control treatments before (i) and after (f) the assay (Sotka and Hay 2002, Dolecal and Long 2013).

Native Benthic Seaweed Assay

To understand if shifts in wrack composition cause intertidal detritivores to change consumption of native benthic seaweeds, we offered an assemblage of intertidal consumers a choice of native benthic seaweeds in the presence of either Kelp or Devilweed. To create realistic

assemblages of wrack consumers, we surveyed the abundance of rocky intertidal detritivorous invertebrates at SCNP in August 2019. We recorded all snails and crabs found within a 0.50 x 0.50 m quadrat that was flipped end over end and parallel to shore (n=10). This procedure was repeated in the low, mid, and high intertidal zones. Although this technique accurately sampled Turban snails and Hermit crabs, it did not sample mobile Shore crabs. To determine a realistic number of animals to add to our experiments, we multiplied field densities by the floor area of the plastic containers used in the assay. This resulted in the addition of three Turban snails and three hermit crabs to each replicate. Because mobile Shore crab densities are difficult to measure, we added a single individual to each replicate. We recognize this approach creates an assemblage with relatively more abundant Shore crabs and therefore might overestimate their role.

We offered animals a choice between three artificial foods (see below) made from native benthic seaweeds (*Ulva spp., Silvetia compressa,* and *Centroceras clavulatum*), and a wrack seaweed (either Devilweed or Kelp). Because we were unable to collect all of our seaweeds at the same time and we were concerned about changes to palatability while maintaining seaweeds in the lab, we fed animals artificial, agar-based foods made from freeze-dried, homogenized seaweeds. We note that this process maintains chemical traits while removing morphological traits that may also impact palatability. Following methods adopted from previous studies (Bolser and Hay 1996, Thornber et al. 2008, Dolecal and Long 2013), we mixed homogenized freeze-dried seaweed (5.6% w:v) into a heated agar solution (2.0% w:v). This mixture was poured into polypropylene petri dishes (50 mm) and allowed to cool for ~30 min. The agar-foods were blotted dry, weighed, and offered to the consumer assemblage.

We secured the petri dishes containing agar-based foods in random order along the length of containers with mesh covered tops (330 x 190 x 108 mm container with 2 mm mesh opening;

n=20 and n=10, for grazing treatments and controls, respectively). Because our previous experiments found negligible autogenic growth in agar-based foods not exposed to consumers, we reduced the number of controls to one control for every two experimental replicates. These assays began simultaneously on November 11, 2019. After ~36 hours, all artificial foods were removed, blotted dry, and reweighed. We calculated changes in mass using the previous formula.

Data analysis

To test the effect of all diet treatments including seaweeds (i.e., all but "starved" treatment) on final dry tissue mass, we used an ANOVA with detritivore species and diets as main effects, and their interaction. We tested the effect of diet treatment on individual species (Red abalone and Black turban snails) using Linear Mixed Effects Models (LMEM) with diet as the main effect and estimated initial dry masses as a random effect to account for differences in starting mass. Starvation treatments were used for reference but were not included in the model. To test the effect of diet on changes in self-righting times of abalone, we used a LMEM with self-righting time difference (before treatment – after treatment) with diet as the main factor and replicate number as a random factor to account for within-subject variability and repeated measures.

For preference assays, we compared changes in seaweed mass, corrected for autogenic growth, using Paired t-tests for each consumer species (Devilweed vs. Kelp). For the native benthic seaweed assay, we compared overall grazing (native benthic seaweeds + wrack) using a paired t-test and tested for interactions using ANOVA. We used a LMEM to investigate the effects of wrack species and native benthic seaweeds on consumption. The model included wrack treatment (native or invasive) and native benthic seaweed species (*Ulva spp., Silvetia compressa,* or *Centroceras clavulatum*) as fixed factors, and their interaction. We also included a

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random factor for replicate number because seaweed choice was not independent within replicates. All statistical analyses and visualizations were conducted using the R Programming Language (R Core Team, 2023). Linear and mixed effect models were conducted using the R base and 'nlme' packages. Necessary assumptions were met for statistical analyses and post-hoc tests were conducted as needed.

Results

Devilweed prevalence survey

Wrack piles on San Nicolas Island were dominated by Giant kelp (*M. pyrifera*), but also included Feather boa kelp (*Egregia menzisii*), Surf grass (*Phyllospadix spp.*), and Devilweed (*S. horneri*). Devilweed was present on 28% of wrack piles (11 of 39 piles), where it constituted $3 \pm 1\%$ of the surface cover of those piles.

Performance

Diet influenced detritivore tissue growth (ANOVA: $F_{3,152}=15.773$, p <0.001). However, detritivore species and diet interacted to influence detritivore tissue growth ($F_{3,152}=15.238$, p<0.001), thus, we analyzed detritivore species separately to understand how each diet impacted growth. After controlling for estimated initial dry tissue mass, Devilweed diet influenced Red abalone and Black turban snail growth, but in opposing directions. Replacing Kelp with Devilweed suppressed Red abalone tissue mass by 25% (E= -0.6144, SE= 0.1903 t=-3.228 p = 0.002), but increased Turban snail tissue mass by 31% (E=0.0064, SE= 0.0028 t=2.314 p = 0.024). Interestingly, the effect of the mixed diet treatment (i.e., offering consumers Kelp and Devilweed in a 1:1 ratio) was also consumer-specific. For Red abalone, a mixed diet had an intermediate effect on tissue mass compared to animals in the no-choice treatments fed one of

the species (i.e., Kelp or Devilweed only diets). In contrast, Turban snails fed mixed diets grew

similar to Devilweed-only treatments and better than Kelp-only treatments (Fig.1). Because no

choice was ever fully consumed, any mixed-diet effect could not be attributed simply to the loss

of a higher quality food. Consistent with Devilweed suppressing Red abalone growth, there was

a trend for Devilweed to increase the amount of time it took Red abalone to right themselves

(Fig. 2). However, after controlling for differences in initial righting time, this effect was not

statistically significant ($F_{2,57} = 2.091$, p=0.133).

Preference

Detritivores displayed species-specific feeding preferences for wrack seaweeds. Black

abalone and Turban snails consumed 111% and 158% more Kelp than Devilweed (Fig. 3a and

3b: t=4.5053, p<0.001 and t= 5.7152, p<0.001, respectively). Although these two detritivores

preferred Kelp, both species consumed some Devilweed (One sample t-test, t=4.782, p<0.001

and t=2.105, p=0.055, for Black abalone and Turban snails, respectively). Shore crabs fed

similarly on the two wrack species (Fig. 3c, t=0.0739, p=0.9422). In contrast, Hermit crabs

preferred Devilweed (Fig. 3d, t=-3.7593, p=0.002). This apparent preference was driven, at least

in part, by a complete avoidance of Kelp (One sample t-test, t=0.147, p=0.89).

Native Benthic Seaweed Assay

In the presence of foods made from native benthic seaweeds, replacing native wrack

species (Devilweed for native Kelp) reduced grazing on wrack by 134% (t=7.5289, p<0.001).

This reduction was not associated with a change in overall grazing rates (i.e., the sum of grazing

on wrack and native benthic seaweeds; 5.97 ± 0.22 g and 5.22 ± 0.20 g for native and invasive

wrack type, respectively; t-test, t = -1.261 p = 0.215), suggesting consumers shifted grazing onto

native benthic seaweeds in the presence of Devilweed wrack. This suggestion was confirmed by the discovery that feeding on artificial foods made from native benthic seaweeds depended on wrack type (interaction: ANOVA, $F_{3,152}$=17.116, p<0.001). Including Devilweed wrack increased grazing on *Silvetia* (M=0.75, SE=0.28, p=0.0265), but did not affect feeding on the two other benthic native seaweed (p>0.05; Fig. 4).

Discussion

Invasion mediated changes in wrack composition had both consumer- and seaweed-specific impacts. Replacing Kelp with invasive Devilweed had species-specific performance impacts that suppressed Red abalone growth but enhanced Black turban snail growth. This is consistent with recent findings that suggest a diet of Devilweed negatively affects growth and survival of Red abalone (Bauer et al. 2023). The effect of mixed diets on consumer growth also displayed consumer-specificity (Red abalone displayed intermediate growth on mixed diets whereas Turban snail growth on mixed diets was high and indistinguishable from Devilweed). Also, replacing Kelp with Devilweed increased grazing of native benthic seaweeds by a realistic detritivore assemblage, but only on the brown seaweed, *Silvetia compressa*.

Detritivore-specific performance impacts of an invasive seaweed on different intertidal snails are consistent with detritivore-specific population-level impacts of invasive plants. Such specificity has been observed within several taxonomic levels including Phylum and Superorder. For example, leaf litter detritus from plots invaded by an annual invasive *Impatiens glandulifera* had higher densities of leaf litter dwelling Acari (Phylum Arthropoda, Subphylum Chelicerata) but did not show differences in springtail densities (Phylum Arthropoda, Subphylum Hexapoda) relative to leaf litter from uninvaded plots (Rusterholz et al. 2014). Similarly, vegetated plots containing invasive giant knotweed (*Reynoutria* spp.) had reduced densities of detritivorous

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isopods (Superorder Peracarida, Order Isopoda) but similar densities of detritivorous amphipods (Superorder Peracarida, Order Amphipoda), relative to uninvaded plots (Kappes et al. 2007). The detritivore-specific impacts on growth we observed indicates that we observed variation at a more specific taxonomic level (i.e., within the Subclass Vetigrastropoda).

Detritus from invasive plants could have within-Subclass, detritivore-specific impacts in the presence of native detritus via several pathways. First, detritivores may differ in their attraction to or preference for detritus from invasive plants (Mews et al. 2006). However, because both Black abalone and Turban snails strongly preferred Kelp in choice assays, the differing impact of a mixed diet of detrital Kelp and Devilweed on their performance was likely unrelated to behavioral differences that resulted in consumption of proportionally different amounts of invasive seaweed. Second, detritivores may be differentially impacted by how detritus from invasive plants modifies abiotic conditions (Rodil et al. 2008). For example, invasive seaweeds may release allelopathic chemicals into seawater or may modify abiotic factors like pH or oxygen (Lapointe et al. 2018, Bauer et al. 2023). However, this shouldn't lead to detritivore specificity as they would likely have a general impact on both species. Finally, detritivores may differ in post-ingestive processes that influence their ability to assimilate or detoxify detritus from invasive plants (Frost et al. 2005). This appears likely in our system because Devilweed-only diets suppressed Red abalone but enhanced Turban snail growth. Interestingly, because both species preferred Kelp, this apparent post-ingestion impact in mixed diet treatments was associated with a relatively small amount of Devilweed. This suggests that a) Devilweed positively impacted Turban snails (e.g., it provided a key limiting nutrient for Turban snails), b) Devilweed negatively impacted Red abalone (e.g., it was toxic to Red abalone), or both.

In addition to direct effects on detritivore performance, shifts in detrital subsidies may shape recipient primary producer communities indirectly (David et al. 2017). For example, replacing detritus from Kelp to Devilweed increased feeding on foods made from native seaweeds in intertidal habitats, but only on the most preferred seaweed (i.e., *Silvetia compressa*). We hypothesize that when detrital shifts involve a reduction in detritus palatability like this, consumers in recipient habitats will increase consumption of more palatable living, native plants/seaweeds. Because the relative palatability of non-native and native seaweeds is variable, for example, arthropods feeding on red seaweeds display a preference for native species, but mollusks do not (Swantje et al. 2017), it may continue to be challenging to predict the impacts of detrital shifts on recipient communities. Further, because these plants or seaweeds also differ in their palatability, detrital shifts may have plant or seaweed-specific impacts.

Such impacts may be particularly common for rocky shore consumers that directly and indirectly affect community dynamics and structure by influencing seaweed abundance, diversity, and productivity (Sousa 1984, Aquilino and Stachowicz 2012, Rhoades et al. 2018). Therefore, changing wrack that shifts consumption onto habitat-forming species like *S. compressa* (Sapper and Murray 2003, Whitaker et al. 2010, Graham et al. 2018), may have additional community level impacts. For example, *S. compressa* understories inhabited by diverse algae, sessile and mobile invertebrate communities that are protected from desiccation during tidal emersion will suffer from *Silvetia* reductions (Sapper and Murray 2003, Truong et al. in press).

Although our native benthic seaweed assay including consumers with a preference for Kelp (Turban snails), a preference for Devilweed (Hermit crabs), or a lack of a preference for these two wrack species (Striped shore crabs), replacing Kelp with Devilweed reduced grazing

on wrack and shifted grazing *Silvetia compressa* for this consumer assemblage. This shift could be explained simply by Turban snails shifting onto native benthic seaweeds when they were offered a less preferred wrack species. Additionally, interactions with heterospecific consumers may have modified consumption in this assay. The complexity of these interactions will likely make it difficult to predict the impacts of Devilweed and other non-native species, on invaded, naïve ecosystems and the communities they subsidize.

Kelp forests are in decline in many regions globally, being replaced by non-native species that may not serve the same ecological roles (Layton et al. 2020). For example, Australian kelp forests with the habitat-building kelp, *Ecklonia radiata*, have been replaced by turf algae, changing habitat complexity, reducing productivity, and detritus (Layton et al. 2020). Even if Devilweed does not completely replace Kelp, it is expected to continue to invade Kelp forests, and declines in kelp cover may facilitate this invasion (Cruz-Trejo et al. 2015, Marks et al. 2020). Moreover, it has been suggested that although Devilweed in California has a reduced thermal tolerance compared to populations in its native habitat (the Seto Inland Sea of Japan), current and future ocean temperatures are not likely to stop its northward and southward invasion success (Small and Edwards 2021). Subsequently, Devilweed will continue to change wrack species composition on the coast. In addition to encountering Devilweed as detritus, intertidal consumers are increasingly co-occurring with living, benthic Devilweed. For instance, Devilweed has been found in lower intertidal zones in Todos Santos Bay, Baja California, Mexico (Cruz-Trejo et al. 2015) and more recently in high to low intertidal pools in San Clemente and San Nicolas Islands (Pollard et al., in prep). This is of special concern in areas inhabited by recovering Black abalone populations such as San Nicolas Island.

Considerable progress has been made in the study of resource subsidies and consumer interactions; however, the diversity and extraordinary nature of species introductions and climate-mediated range shifts continue to pose a challenge to identifying and understanding general patterns (Yang et al. 2010). Consumer-specific impacts may prevent the identification of a single, unifying theory about how plant invasions influence detritivores and may suggest limited usefulness of HFA and Prey Naiveté. Such specificity could lead to contrasting results within and between studies. For example, two meta-analyses were unable to agree about the impact of invasive plants on detritivores, with one study finding positive and one study finding negative effects. Our results did not find strong evidence to support either side, rather, we highlight the importance of species-specific responses to novel subsidies and potential indirect effects on recipient communities.

Acknowledgements

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Figure captions

Figure 1

Final dry tissue mass of Red abalone (A) and Black turban snails (B) starved or fed Kelp, Devilweed, or mixed diets for 42 days. The dotted line separates the starved treatment that was not included in the analysis. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier ranges. Lower case letters above boxes denote significance. The black dots are outliers. Illustrations by R. DeSantiago.

Figure 2

Initial and final righting times (sec) for Red abalone starved, or fed Kelp, Devilweed or mixed diets. The dotted line separates the starved treatment as it was not included in the analysis. Bars represent the mean righting time for individuals in that treatment and lines represent standard error.

Figure 3

Total detrital seaweed biomass consumed by Black abalone (A), Black turban snails (B), Striped shore crabs (C), and Blue banded hermit crabs (D) in choice feeding experiments. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier values. The black dots are outliers, and the asterisks denote statistical significance (p<0.05). Illustrations by R. DeSantiago

Figure 4

Total mass of artificial foods made from detritus (either Kelp or Devilweed) and *C. clavulatum, Ulva spp.,* and *S. compressa* consumed by assemblage of consumers in native (gray) and

invasive (white) wrack treatments. The lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non outlier values. The black dots are outliers.
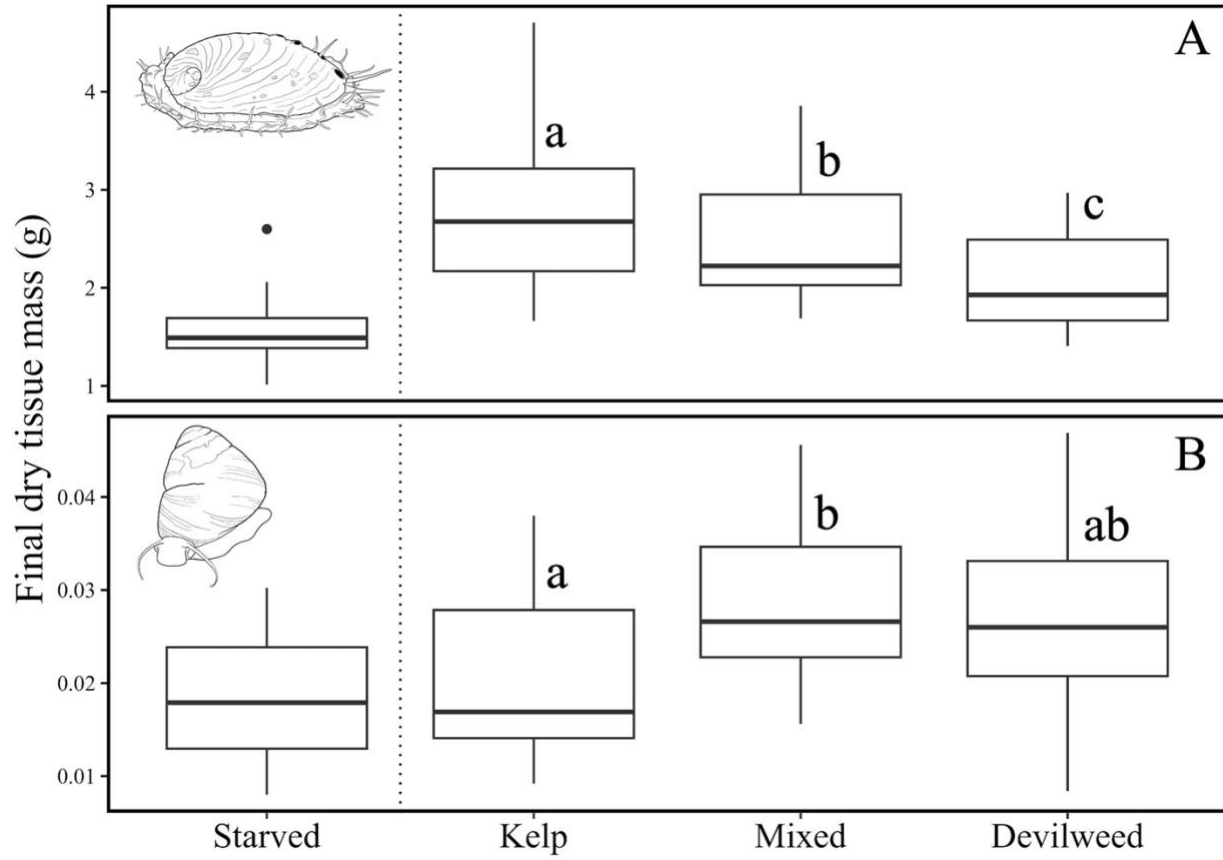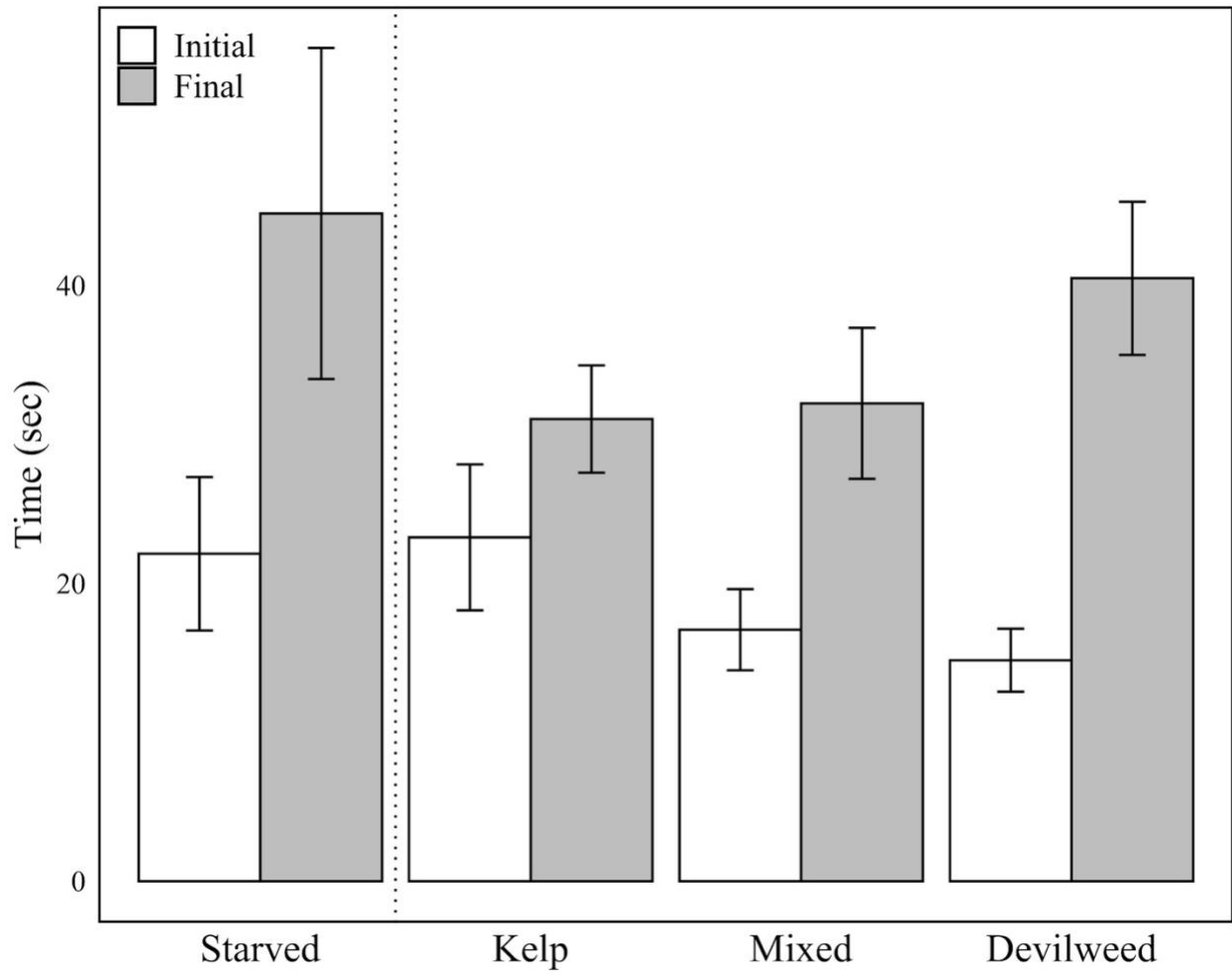
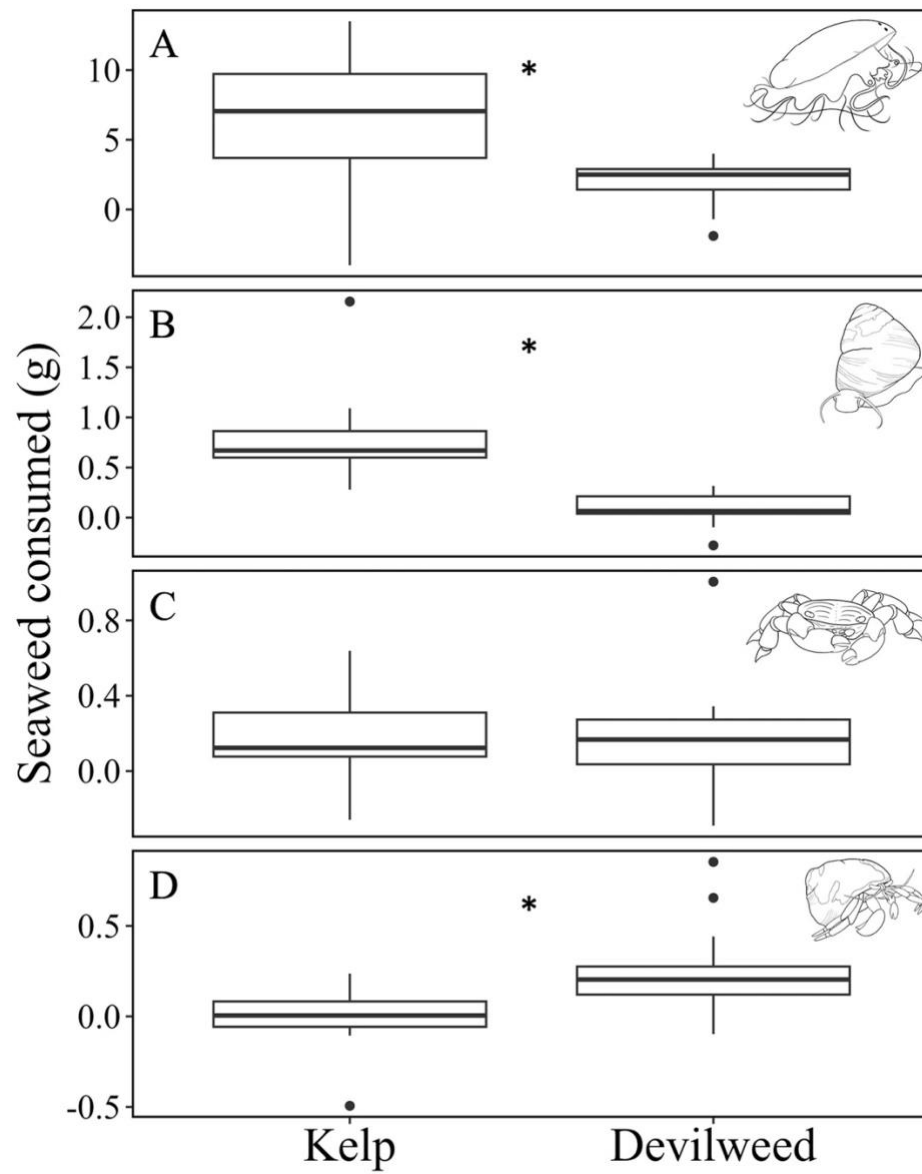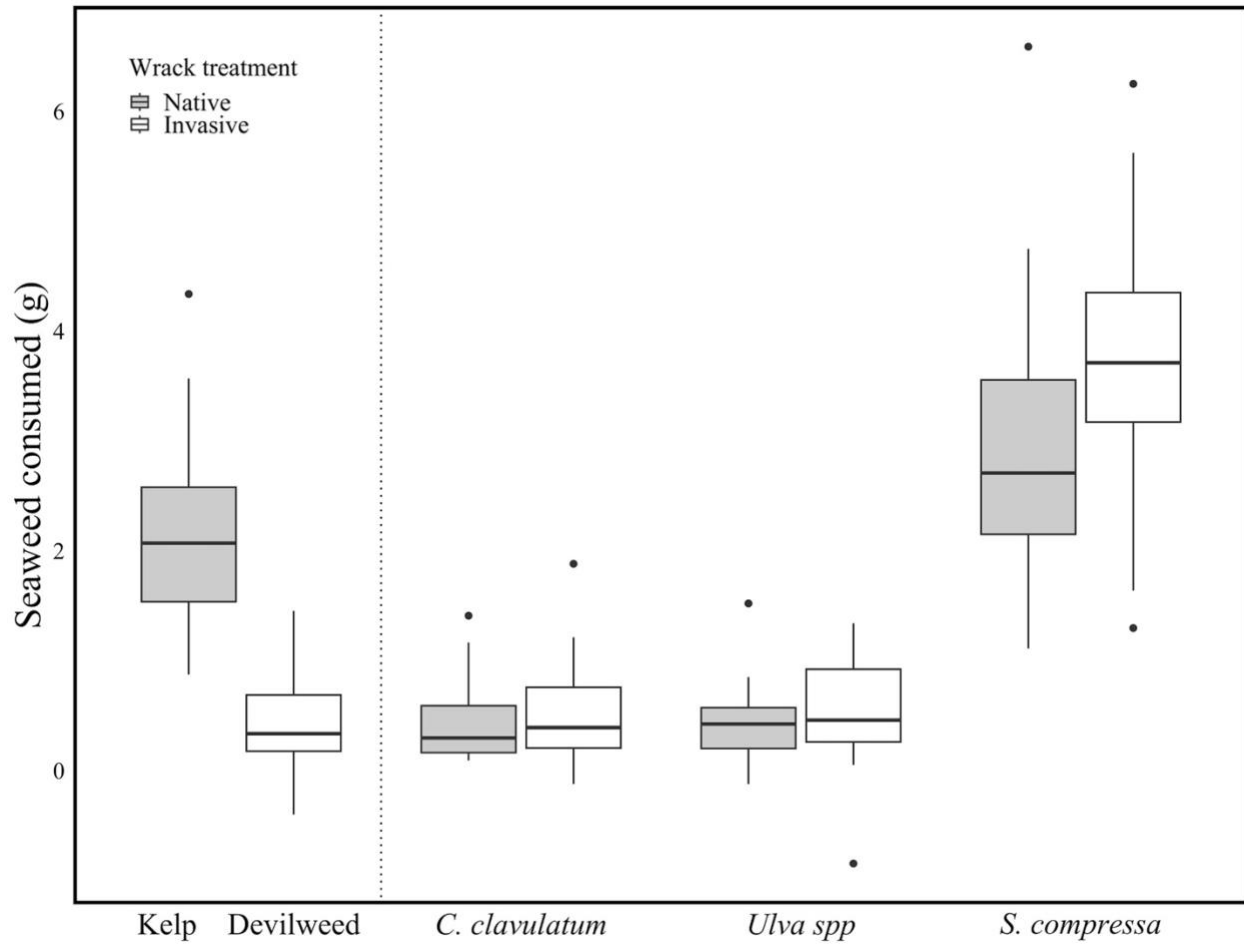**Figures**

Figure 1

Figure 2

Figure 3

Figure 4

CHAPTER 2

Spatial and temporal variability of wrack and the contribution of an invasive macroalga,
Sargassum horneri

Ric DeSantiago and Jeremy D. Long

Abstract

Habitat subsidies can strongly shape the structure and function of recipient ecosystems. Human-mediated changes to donor ecosystems via species invasions and climate change could influence the impact of these subsidies. However, the spatiotemporal variation in native and invasive wrack deposition is largely unknown. With respect to spatial variation, the distribution of native and invasive species in donor systems may differ. With respect to temporal variation, native and invasive species may subsidize adjacent systems at different times of the year. Such variation could essentially extend the season during which subsidies influence recipient systems. We surveyed seaweed wrack on beaches that receive large inputs from adjacent kelp forests but that have recently been invaded by the seaweed *Sargassum horneri*. We conducted surveys at seven sites on one of the California Channel Islands at four time points across 2022. We observed spatiotemporal variation in native and invasive wrack inputs to beaches. Kelp dominated wrack inputs throughout the year and *S. horneri* was relatively rare (never exceeding 3% of all wrack found). Kelp was most abundant on west-northwest facing shores, but *S. horneri* was even more rarely found on west-facing shores. The peak period of deposition for these two species also differed, with kelp deposition peaking in September and *S. horneri* deposition peaking in March. These findings highlight the complex spatiotemporal variation in native and invasive wrack inputs, highlighting the complex interplay between these species and their potential to shape recipient communities.

Introduction

Habitat subsidies can strongly shape the structure and function of recipient ecosystems (Polis and Hurd 1996, Menge et al. 1997, 2003, Nakano et al. 1999, Jefferies 2000, Palumbi 2003, Spiller et al. 2010). Changes in community structure in donor systems mediated by species invasions and climate change can influence recipient systems (Yang et al. 2008). However, our understanding of how biological invasions in donor communities influence the supply and timing of subsidies to recipient habitats remains limited. Given the strong influence of subsidies on recipient systems, it is important to assess how invasive species affect subsidy exports to fully comprehend the impact of biological invasions.

Marine phytodetritus, dislodged seagrasses, and seaweeds washed ashore (collectively termed "wrack") critically shape coastal ecosystems (Duggins et al. 1989, Bustamante et al. 1995, Orr et al. 2005). Thus, invasions in subtidal communities may impact the timing and magnitude of wrack subsidies from these donor systems to recipient coastal communities. However, the impact of invasive macroalgae on detrital subsidies to shorelines remains difficult to predict. For instance, invasive species can present a lower quality resource for detritivores in recipient systems. Conversely, non-native primary producers can also diversify detrital food webs by providing an additional food resource to detritivores and decomposers (Rodriguez 2006). For example, a non-native red macroalga *Agarophyton vermiculophyllum*, provides a complementary source of labile organic matter relative to native *Spartina alterniflora* in intertidal salt marshes and mudflats of the southeastern USA (Haram et al. 2020). Similarly, beach-cast tissues of the invasive subtidal macroalga, *Undaria pinnatifida,* provide an alternative food source to native kelps consumed by talitrid amphipods on beaches in southern New Zealand (Suárez-Jiménez et al. 2017).

An example of an invasive seaweed whose impacts on wrack and recipient communities are difficult to predict is *Sargassum horneri*. Because this seaweed can reduce kelp abundance in the California Bight (Marks et al. 2015, Caselle et al. 2018, Sullaway and Edwards 2020) and *S. horneri* is a lower preference food to gastropod detritivores, this invasion may reduce the quantity and quality of wrack (DeSantiago et al., in review). However, the different phenology between *S. horneri* and native seaweeds suggest that this invasion could positively impact recipient habitats. *S. horneri* is most abundant in the subtidal in the winter and spring (Marks et al. 2018) while most dominant native macroalgae in the region, including giant kelp, *Macrocystis pyrifera,* is most abundant in the summer and fall (Reed et al. 2009, Harrer et al. 2013, Marks 2018). Consequently, although *S. horneri* may be a lower quality food than kelp to some consumers, it may extend the amount of time that wrack is available to intertidal detritivores.

Here, we surveyed wrack at seven sites on one of the California Channel Islands (San Nicolas Island, hereafter SNI) at four time points across one year (March, May, September, and December 2022). At each survey, we measured the proportion of *S. horneri* on the surface of large wrack piles, quantified *S. horneri* and *M. pyrifera* fragments on sandy beaches, and conducted timed searches for *S. horneri* at each survey. Because subtidal kelp and *S. horneri* abundance is non-randomly distributed around the island, we selected four sites on the windward side and three sites on the leeward side of SNI.

Methods

We surveyed wrack on seven sites on San Nicolas Island, California (Fig. 1 Bachelor, Cosign, Red Eye, and Tender on windward, Tranquility, Cissy, Artist on leeward). To determine the relative contribution of *S. horneri* to wrack, we measured the proportion of the surface area of large kelp wrack piles (length > 1m) represented by *S. horneri*. This qualitative metric of *S.*

horneri prevalence allowed us to quickly and non-destructively sample wrack piles at various sites along the coast. Along a 50 m transect, we measured all large wrack piles, identified the dominant seaweed species, and calculated the pile and *S. horneri* surface area. We estimated the three-dimensional surface area of wrack piles using the formula for a hemi ellipsoid A $\approx 2\pi *$ ($((a*b)^{1.6}+(a*c)^{1.6}+(b*c)^{1.6})/3$)$^{1/1.6}+\pi * b * c$, where "a" is the depth, "b" and "c" are the semi major axis lengths of the pile. For each *S. horneri* individual encountered on the surface of the pile, we measured its longest length and width to calculate the area using the equation for an ellipse (A=πab), where "a" and "b" are the semi major axis lengths. For a single pile, we calculated the sum area of all *S. horneri* individuals and divided it by the surface area of the pile to estimate the proportion of wrack that consisted of *S. horneri*. Using this method, the relative contribution of *S. horneri* to wrack for a large pile could be estimated in minutes as opposed to hours (DeSantiago et al. *in review*).

To survey wrack not associated with large piles, we also quantified the presence of *M. pyrifera* and *S. horneri* fragments at five of our sites (Artist, Cissy, Red Eye, Tender, Tranquility). To do this, we haphazardly placed a 50m transect parallel with the water on the highest end of each beach, adjacent to the transects in the survey described above. From this transect, we used a measuring wheel starting from three randomly selected points on the transect and moved towards the waterline. Along this "vertical" transect, we counted and measured every fragment of seaweed that was touched by the wheel.

To quantify any *S. horneri* that was not captured by the foregoing methods, we exhaustively searched for *S. horneri* at all sites for 30 minutes by one person or 15 minutes with two people. We conducted these surveys in areas adjacent to the surveys described above to avoid overlap. The length of all *S. horneri* stipes and fragments were measured and recorded.

Data Analysis

To compare the total surface area of wrack piles over time, we used a Kruskal-Wallis non-parametric test due to the non-normal distribution of data. We conducted a Dunn's post-hoc pairwise comparisons test with a Bonferroni adjustment to further investigate the contributions of sites to the variability of wrack area over time. Because *S. horneri* was low in abundance on wrack piles, we did not conduct a formal statistical analysis.

We used the same series of analyses as above to test for differences in seaweed fragments and fragment length per length of beach over time and among sites and conducted Dunn's post-hoc pairwise tests where appropriate. Since sitewide *S. horneri* occurrence surveys resulted in very few *S. horneri* individual counts, no formal statistics were conducted. All statistical analyses and map visualization were conducted using the R Programming Language (R Core Team, 2023) and ArcGIS® software by Esri.

Results

Total wrack abundance displayed spatial variation between sites on San Nicolas Island, with more wrack generally being deposited along sites facing the west to northwest (Bachelor Beach, Cosign, Red Eye, Tender) than sites facing the north to northeast (Tranquility, Cissy, Artist; Fig. 2-4). Three observations about the area of large wrack piles supported this pattern (Fig. 2). First, in March, wrack area was higher at Bachelor, Red Eye, and Tender ($p>0.05$). Second, in May, wrack area was higher in Tender than Cissy ($p<0.005$). In September, Bachelor and Cosign had more wrack area than Tranquility ($p=0.01$ and $p<0.001$, respectively). Large wrack piles were always dominated by *M. pyrifera*.

Our fragment density surveys revealed a similar spatial pattern whether we considered number of fragments or length of fragments per unit length (Fig. 3, Kruskal-Wallis: $X^2 = 16.283$, df = 4, p =0.002 and Fig. 4, Kruskal-Wallis: $X^2 = 16.374$, df = 4, p =0.003) but not over time (p= 0.09; Fig. 3). The density of seaweed fragments was higher at Tender (a northwest facing beach) than all sites (p<0.05) except Red Eye (also a northwest facing beach, p=0.19). Tranquility was excluded from this analysis because the site was not accessible during March and May. In these fragment density surveys, *S. horneri* was found rarely and only at the northwest/north facing shorelines [one fragment at Cissy (March and May) and Artist (September), 6 fragments at Red Eye, and 25 fragments at Tender (September)]. Similarly, when fragment length was considered, *S. horneri* was most prevalent at Red Eye and Tender (Fig. 4).

Total wrack abundance of large piles (as determined by calculating the sum of the large pile surface area) displayed temporal variation (Kruskal-Wallis: $X^2 = 38.336$, df = 3, p <0.001) (Fig. 2-4). These large wrack piles were dominated by *M. pyrifera* throughout the year (Fig. 2). For any given site, *M. pyrifera* was most abundant in May or September. Although total area of large wrack piles did not differ between May and September (p=0.08), large piles were only found at three out of the seven sites in May suggesting September was the peak period (Fig. 2C, E, F). *Sargassum horneri* was rare on pile surfaces, and was only seen in March (2.5 ± 1.7 % of pile surface area at Cissy and Red Eye) and May (0.3 ± 0.2 % of pile surface area at Cissy and Tender).

Sargassum horneri was most prevalent in our March timed searches whether we considered number of sites where it was found, number of thalli found at a site, or length of thalli found (Table 1). Unlike *M. pyrifera* which was common in September, we found no *S. horneri* in our September timed searches. All *S. horneri* individuals found in March and December were

partial or complete sections of adult plants, and those found in May were complete, reproductive adults.

Discussion

Wrack piles on San Nicolas Island were dominated by *M. pyrifera* throughout time. In a few instances, there were no piles larger than 1m to conduct this survey (Artist and Bachelor in May; Cissy and Tranquility in December). We did not have access to Tranquility and Cosign in March and May. Wrack cover by pile surface area was highest in May and September, however, most of the wrack cover in May was due to the large piles on Tender (Fig. 2F). *S. horneri* was present during March and May but only accounted for a small percent of the surface area (2.5 ± 1.7 % in March and 0.3 ± 0.2 % in May). There was no strong temporal pattern of seaweed fragment frequency per length of beach but there were more fragments at Tender and Red Eye. Similarly, fragments were generally longer at Tender and Red Eye. *Sargassum horneri* fragments were rare but identified in March, May, and September. Surprisingly, exhaustive searches did not reveal any *S. horneri* in September but were found at every other sampling period (March, May, and December).

While there were no strong temporal patterns, wrack subsidies may reflect the *S. horneri* invasion of nearby kelp forests. For example, kelp forests around SNI are dominated by canopy-forming Giant kelp *M. pyrifera*, which in turn dominated the wrack. Moreover, wrack piles at Artist and Cissy were dominated by *Stephanocystis* in March, a dominant fucoid in a nearby kelp forest monitoring site (Nav Fac 100; Kenner and Tomoleoni 2021). Furthermore, Nav Fac 100 has been invaded by *S. horneri* since it was first observed in 2015 and has occurred on every subsequent monitoring trip (Kenner and Tomoleoni 2021). Although sources of macrophyte drift

on coasts is dependent on currents, wind, wave action, morphological features and exposure of recipient habitats, it is likely that this invaded kelp forest exported *S. horneri* to nearby sites.

The pattern of the *S. horneri* invasion on San Nicolas Island kelp forests remains unclear. For example, *S. horneri* densities at Nav Fac 100 are low during the spring and increase several-fold in the fall (Kenner and Tomoleoni 2021), in concurrence with its reproductive lifecycle. However, *S. horneri* densities have decreased every spring since it was initially recorded. While our year-long monitoring effort allowed us to see differences in seasonal and spatial variability of *S. horneri*, a longer monitoring effort may better estimate the impact of this kelp forest invasion. Furthermore, *S. horneri* has not been recorded at any other kelp forest monitoring site (sites within Kenner and Tomoleoni 2021), yet our study found that *S. horneri* was also in the wrack at Bachelor (SNI west end, windward side), Red Eye and Tender (SNI northwest, windward side), Artist and Cissy (SNI north, leeward side), in at least one of three surveys. It should be noted that although we were unable to access Cosign (September and December), *S. horneri* has previously been quantified in the wrack on this site (DeSantiago et al. *in review*). Moreover *S. horneri* has been observed attached intertidally at Cosign (S. Graham, *unpublished data*, 2020, cited within Kenner and Tomoleoni 2021; DeSantiago *pers. ob.* 2020).

The distribution of *S. horneri* on SNI suggests that the invasion has spread beyond kelp monitoring sites. Moreover, our exhaustive surveys found that *S. horneri* plants found in March were reproductive adults at all sites, suggesting that although densities may be low in Nav Fac 100, reproductive *S. horneri* may be propagating on other sites at SNI. Despite *S. horneri's* local recruitment, its ability to self-fertilize, and pneumatocysts that allow it to float, make it a highly successful gamete propagator (Marks et al. 2015). Additionally, *M. pyrifera* detached by wave

action could also detach *S. horneri*, evidenced by our wrack pile surveys that reveal *S. horneri* intertangled with *M. pyrifera*.

Our results suggest that *S. horneri* can be found in the wrack throughout the year. This was surprising due to *S. horneri*'s known reproductive cycle in which biomass is low during winter when *S. horneri* are small tufts of seaweed, yet we found mature adults in the wrack in December. While it is known that *S. horneri* has the features to be a highly successful invader, it is unknown to us if the genotype of this species found on SNI and other Channel Islands has adapted to a differing reproductive cycle to that of its native range. For example, *S. horneri* adults have been established in at least two intertidal sites on San Clemente Island throughout the year (Pollard et al., *unpublished data;* DeSantiago *pers. ob.* 2021). Our study suggests there is a complexity to *S. horneri* that is not easily captured by a single survey type. We highlight the importance of using various methods when monitoring invasive species to properly assess spatial and temporal distribution.

Although we did not find strong evidence to support complementary timing of *S. horneri* compared to native wrack species, *S. horneri* may provide an additional food source for some species while reducing fitness of others. For example, sandy beaches and the macrofauna that inhabit them are almost entirely supported by allochthonous subsidies (Dugan et al. 2003). Recent studies revealed that native amphipods, *Megalorchestia benedicti*, exhibited lower preference for *S. horneri* and lower performance on diets of *S. horneri* compared to *M. pyrifera* in the lab, and smaller *M. benedicti* were associated with *S. horneri* in the field. Moreover, abalone fed *S. horneri* and a mixed diet that included *S. horneri*, grew less than those fed *M. pyrifera* alone (DeSantiago et al. *in review*). In a separate study, abalone who were fed *S. horneri* diets displayed lower performance and higher mortality than those fed *M. pyrifera* and an

invasive alga, *Undaria pinnatifida* (Bauer et al. 2023). Conversely, although black turban snails, *Tegula funebralis*, did not show a preference for *S. horneri,* they grew more on diets that included it (DeSantiago et al. *in review*). Understanding the distribution of invasive *S. horneri* in the wrack is critical in assessing its potential impacts on subsidy-dependent communities in both rocky and sandy beaches, as it has the potential to impact detritivores and consumers at both.

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Figure and table captions

Figure 1

Map of San Nicolas Island field sites.

Figure 2

Total surface area of large wrack piles (m^2) over sampling period (March, May, September, December) by site Artist (A), Bachelor (B), Cissy (C), Cosign (D), Red Eye (E), Tender (F), Tranquility (G). Colors represent dominant wrack species. * Denotes sites we were unable to access, and zeroes (0) denote there was no wrack piles found on that site.

Figure 3

Mean seaweed fragment frequency per meter of sandy beach by site in March (A), May (B), September (C) and December (D). Colors represent seaweed species. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier ranges.* Denotes sites we were unable to access.

Figure 4

Mean seaweed fragment length per meter of sandy beach by site in March (A), May (B), September (C) and December (D). Colors represent seaweed species. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier ranges.* Denotes sites we were unable to access.

Table 1

Results of total *Sargassum horneri* thalli found in exhaustive timed searches by sampling period and site. Mean length of total *S. horneri* found on each site during that sampling period and standard error are reported in each column.

Figures and tables

Figure 1
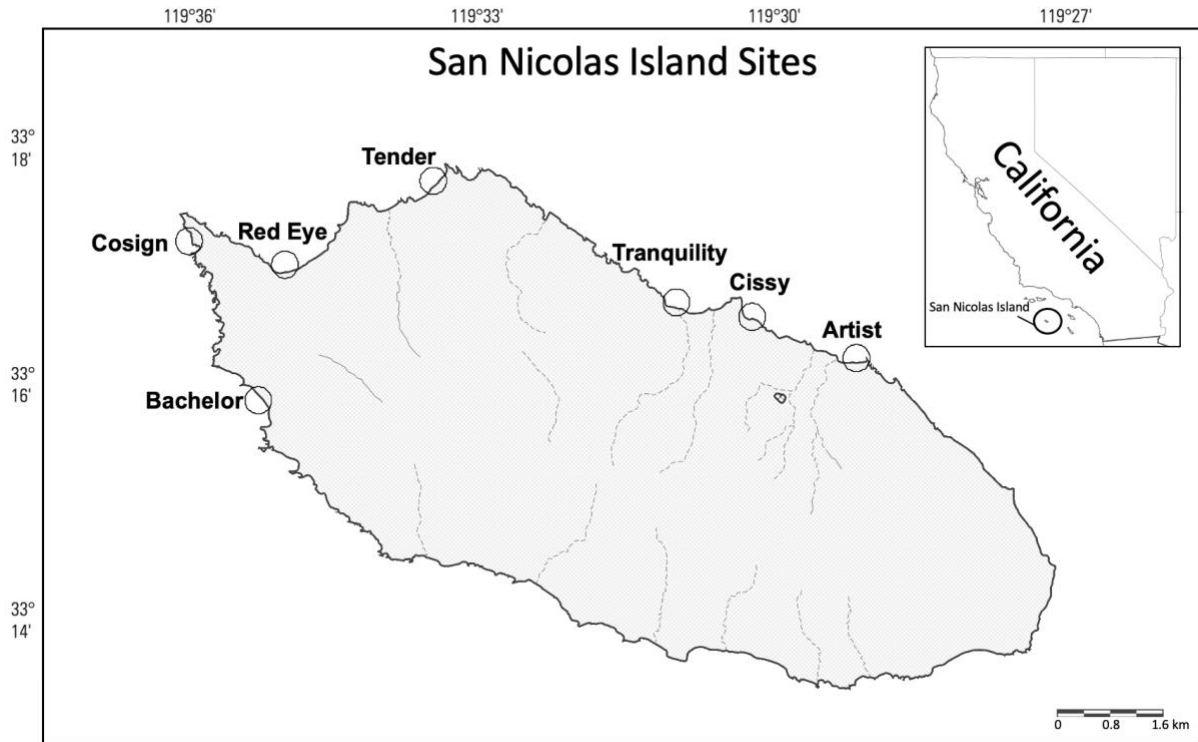
San Nicolas Island Sites
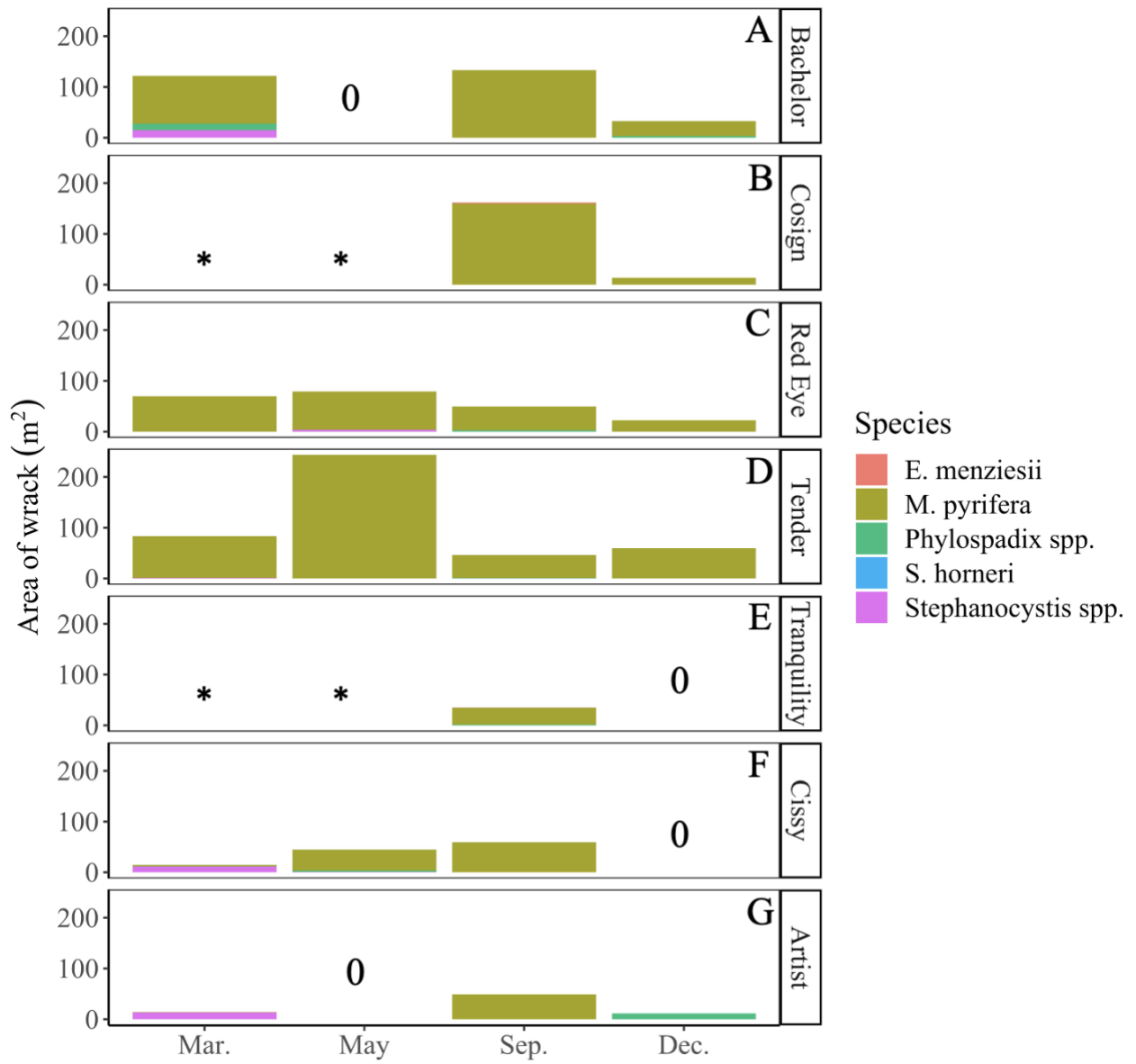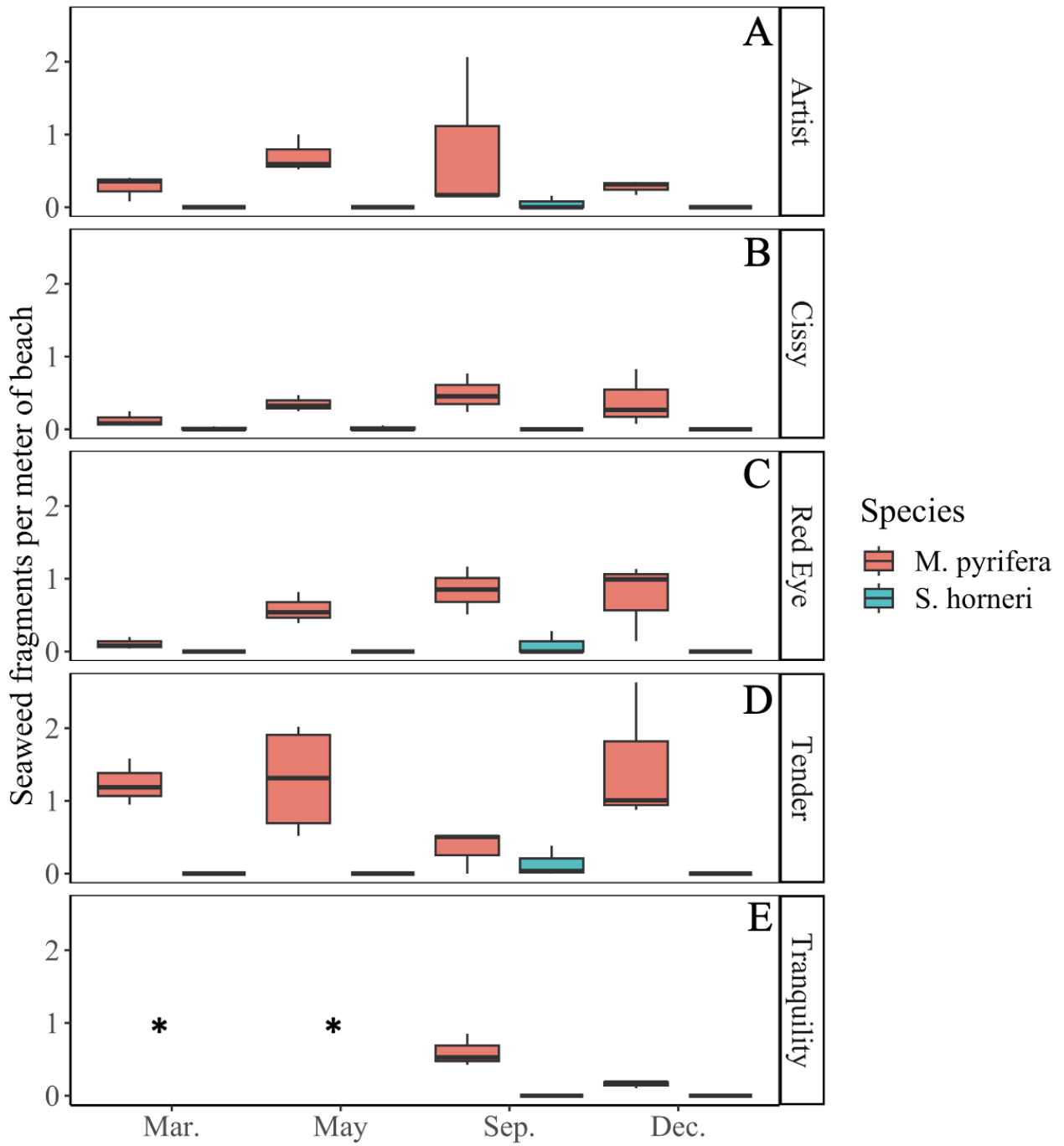
Figure 2

Figure 3

Figure 4
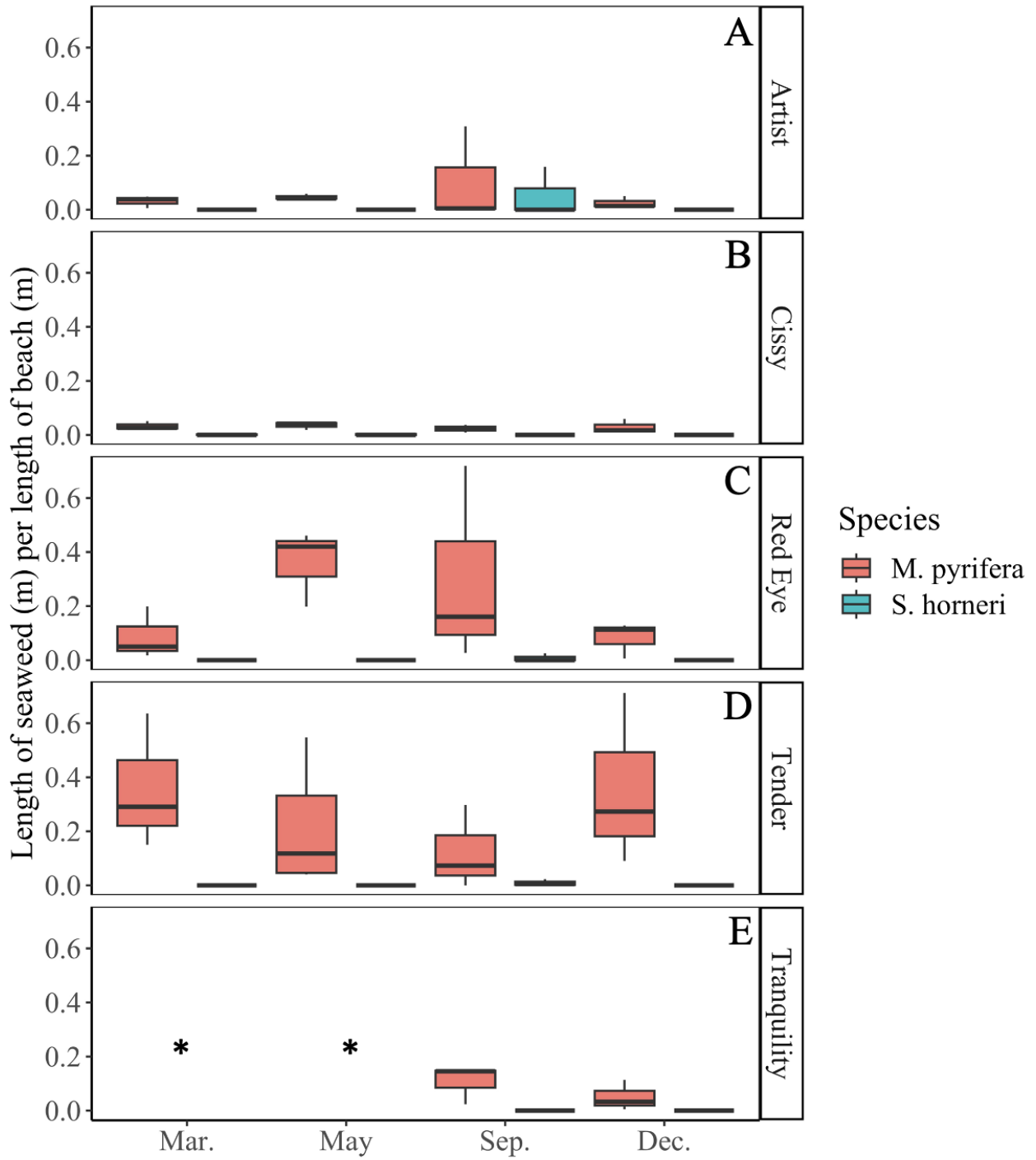
Table 1

Trip	Site	# of thali	Mean length (m)	Length SE
March	Bachelor	3	0.74	0.18
	Cosign	NA	NA	NA
	Red Eye	5	0.48	0.10
	Tender	2	0.75	0.13
	Tranquility	NA	NA	NA
	Cissy	8	0.72	0.14
	Artist	2	0.83	0.01
May	Bachelor	NA	NA	NA
	Cosign	NA	NA	NA
	Red Eye	2	0.36	0.07
	Tender	2	0.08	0.01
	Tranquility	NA	NA	NA
	Cissy	3	0.38	0.18
	Artist	NA	NA	NA
September	Bachelor	NA	NA	NA
	Cosign	NA	NA	NA
	Red Eye	NA	NA	NA
	Tender	NA	NA	NA
	Tranquility	NA	NA	NA
	Cissy	NA	NA	NA
	Artist	NA	NA	NA
December	Bachelor	NA	NA	NA
	Cosign	NA	NA	NA
	Red Eye	NA	NA	NA
	Tender	3	0.37	0.63
	Tranquility	NA	NA	NA
	Cissy	NA	NA	NA
	Artist	1	0.52	0

CHAPTER 3

The ecological impacts of *Sargassum* deposition in beach and forest ecosystems

Ric DeSantiago and Jeremy D. Long

Abstract

Anthropogenic activities and urbanization have increased the frequency and scale of seaweed strandings (pelagic *Sargassum*) along Caribbean and West African shores. Such strandings present significant ecological and economic challenges. To mitigate these impacts, people remove substantial amounts of *Sargassum* biomass from coastlines and dump it into nearby ecosystems. We investigated the ecological implications of *Sargassum* deposition using manipulative field experiments whereby realistic amounts of *Sargassum* (several cubic meters) were added to beach and forest ecosystems. Contrary to expectations based on ecological theory (i.e., the Home Field Advantage hypothesis), our findings reveal comparable decomposition rates between beach and forest ecosystems. Additionally, a "litter bag" experiment revealed that decomposition processes differed between ecosystems - microbes dominated decomposition in the forest and a combination of microbes and talitrid amphipods drove decomposition on the beach. *Sargassum* additions increased nitrate levels to agricultural levels in both habitats, though these levels peaked later in the beach than the forest. This influx stimulated plant growth in the beach but not the forest. Although the beach initially contained low plant cover (5%), *Sargassum* additions dramatically increased cover of invasive Bermuda grass, *Cynodon dactylon*, to >75%. This effect on Bermuda grass spilled over to adjacent areas of the beach beyond the initial plot footprints. Thus, the bottom-up effect of *Sargassum* addition to plant fertilization overwhelmed toxicity effects of additional salts or chemicals associated with

seaweeds. *Sargassum* additions more strongly impacted beach arthropods, with an increase in talitrid amphipods, spiders, ants, and flies. Crawling arthropods in pitfall traps consisted of arachnids and hymenopterans, mainly spiders and ants at both sites, and talitrid amphipods at the beach. Our findings challenge the notion that naïve ecosystems are incapable of processing novel subsidies. These habitat-specific impacts should be considered when making decisions about where and how to dump massive amounts of *Sargassum* into adjacent terrestrial habitats.

Introduction

Human population growth and urbanization deliver high levels of nutrients into coastal waters that stimulate algal blooms (Teichberg et al. 2010, Kang et al. 2021). Such blooms present economic and ecological challenges to impacted countries (Lapointe 1997, Teichberg et al. 2010, Smetacek and Zingone 2013, Rodríguez-Martínez et al. 2023). Seasonal or periodic landings of macroalgae typically confer benefits to beaches by serving as a foundation for and contributing to the fertilization of coastal dunes and serve as a resource subsidy to food webs (Polis et al. 1997, Huxel and McCann 1998, Anderson and Polis 1998, Marczak et al. 2007, Yang et al. 2010, Spiller et al. 2010, Williams and Feagin 2010, Wright et al. 2013, Piovia-Scott et al. 2013). However, massive blooms disrupt ecological processes and can be a nuisance to coastal communities. For example, macroalgal blooms can clog fishing nets, impede the passage of boats, and release unpleasant or harmful chemicals (Teichberg et al. 2010, Smetacek and Zingone 2013, Resiere et al. 2021, Rodríguez-Martínez et al. 2023). Also, beach-cast macroalgal blooms can create anoxic conditions and shade benthic taxa (Hauxwell et al. 2001, Teichberg et al. 2010, Van Tussenbroek et al. 2017, Rodríguez-Martínez et al. 2019). Because seaweed blooms negatively impact coastal economies and environments, it is common for this biomass to be removed from shorelines and dumped into adjacent habitats. However, the impacts of dumping massive quantities in adjacent habitats remain unknown. There is a need for manipulative experiments to understand how such anthropogenic activities subsidize and influence communities in recipient habitats.

Currently, residual biomass from hydrocolloid extractions (e.g., agar, alginate, and carrageenan) and removal of seaweed blooms contributes a significant amount of waste that is discarded in landfills and natural terrestrial habitats (Dang et al. 2023). There is only a nascent

understanding of the impacts of seaweed dumping on these terrestrial habitats. However, such impacts could be likely for at least two reasons. First, macroalgae added to terrestrial habitats are known to improve soil fertility (Pereira et al. 2019). Indeed, the direct application of macroalgae as an agricultural fertilizer is a traditional practice in places like the Patagonia region in Argentina, that receive large amounts of seaweed wrack (Eyras et al. 2008, Gibilisco et al. 2020, Madejón et al. 2022). Second, seaweeds may negatively impact recipient terrestrial habitats because of the addition of salts, toxins (e.g., heavy metals), and material that otherwise could be difficult to decompose. Further, the lack of co-evolution of terrestrial organisms in recipient habitats with seaweed impairs our ability to predict the impacts of seaweed dumping on land.

An important bloom-forming seaweed that increasingly impacts coastal economies and ecology and habitats where it is dumped is the pelagic seaweed *Sargassum* that consists of a mixture of *S. fluitans* and *S. natans* (Gower et al. 2013, Rodríguez-Martínez et al. 2020, Chávez et al. 2020). Although floating *Sargassum* patches have been observed in the tropical and subtropical Atlantic Ocean since the 1800s (Brooks et al. 2018, Uribe-Martínez et al. 2022), massive strandings of *Sargassum* are a relatively new phenomenon. For example, since 2011, the shores of Caribbean countries, West Africa, and the Gulf of Mexico are often smothered in *Sargassum* deposits that are regularly over 1m deep (Doyle et al. 2015) and can cover the entire length and breadth of beaches (as pictured in Chávez et al. 2020). The extent of beached *Sargassum* can be impressive - the northern sector of the Mexican Caribbean is now estimated to receive volumes ranging from 10,000 - 40,000 m³ of *Sargassum* per kilometer of beach per year with most landings happening between April and September (Rodríguez-Martínez et al., 2023). Furthermore, *Sargassum* bloom intensity and frequency is predicted to continue to increase (Smetacek and Zingone 2013, Rodríguez-Martínez et al. 2023).

This recent influx of *Sargassum* deposition on beaches negatively impacts coastal economies and ecologies. *Sargassum* degrades pristine white sand beaches and turquoise waters that attract tourists to the Caribbean. Such tourism provides the basis for the majority of the Gross Domestic Product for many of these countries. For example, the Mexican state of Quintana Roo attracted nearly 15 million tourists and generated an income of approximately US$10.8 billion in 2021 even with high *Sargassum* deposition (Rodríguez-Martínez et al., 2023). As a result, increasing *Sargassum* deposition presents a significant obstacle for the entire region. In addition to the economic impacts, there are negative ecological consequences of leaving *Sargassum* on beaches. Without removal of *Sargassum*, leachates and organic matter reduce oxygen and pH levels, and increase turbidity, sulfur, and ammonia concentrations (Van Tussenbroek et al. 2017, Chávez et al. 2020, Rodríguez-Martínez et al. 2023). For instance, a significant *Sargassum* beaching event in 2018 was associated with a coastal fish and invertebrate mortality event, where hypoxic conditions led to the demise of 78 species of neritic fish, crustaceans, echinoderms, mollusks, and polychaetes (Van Tussenbroek et al. 2017, Rodríguez-Martínez et al. 2019).

To minimize the negative impacts of beached *Sargassum*, humans deploy barriers offshore to catch *Sargassum* with various success and remove *Sargassum* from beaches. All strategies require that the collected biomass be moved into adjacent habitats including beach dunes, forests, quarries, farms, and garbage dumps (R. DeSantiago, R. Rodriguez-Martinez, J. Long, pers. obs.) Unfortunately, the impacts of this large-scale "experiment" are largely uncertain for at least two reasons. First, the capacity of local communities that have historically received smaller amounts of *Sargassum* (e.g., beach dune communities) to keep pace, decompose and incorporate this material is unlikely given the sheer volume of material needing processing.

Second, *Sargassum* is being dumped into some habitats that are completely naïve to seaweed subsidies and might lack the capacity to decompose and utilize this material (e.g., forests).

Ecological theory suggests that local adaptation through coevolution would result in faster decomposition of litter by familiar or experienced soil communities, termed '*the home field advantage*' (Bocock et al. 1960, Gholz et al. 2000, Pugnaire et al. 2023). Thus, beach-cast *Sargassum* should decompose more quickly over sand dunes than forest soil. Furthermore, terrestrial predator foraging in beach-cast macroalgae is a common feature in coastal ecosystems (Kirkman and Kendrick 1997, Rose and Polis 1998, Dugan et al. 2003, Colombini and Chelazzi 2003, Kenny et al. 2017), but less is known about the responses of terrestrial insects that are likely some of the first responders to such detrital inputs. Moreover, previous work with *Sargassum* biomass showed a fertilization effect on plants on shorelines Bahamian islands (Piovia-Scott et al. 2013) and there have been efforts to use *Sargassum* as a fertilizer for vascular plants. Yet, the fertilization effect of *Sargassum* in forest has not been tested.

Here, we used manipulative experiments to examine the ecological consequences of dumping large amounts (i.e., several cubic meters) of *Sargassum* in habitats currently used as *Sargassum* dumps (i.e., beaches and forests). At both habitats, we created realistic piles of *Sargassum* with paired, unmanipulated controls, and surveyed plots quarterly for one year. We estimated pile decomposition by estimating pile volume and by measuring mass change of smaller amounts of *Sargassum* in mesh bags with different accessibility to microbes and arthropods. We surveyed soil respiration and soil ammonium, nitrate, and dissolved organic carbon. To study *Sargassum* impacts on the plant community, we surveyed vegetation on plots and adjacent to plots. To measure the impact of *Sargassum* on the arthropod community, we used pitfall traps and sticky traps to survey crawling and flying arthropods, respectively.

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Methods

Between July 23, 2022, and August 3, 2022 (hereafter, August 2022), we created

Sargassum (~4 m^3) piles in a beach and forest habitat in Puerto Morelos, Quintana Roo, Mexico.

These habitats are commonly targeted as dumping sites and this region has been greatly impacted

by increased deposition of *Sargassum* onto beaches since 2011. All experiments were permitted

by the Mexican government (CNANP-00-007) and the local property managers (Moon Palace

Resort and Dr. Alfredo Barrera Marín Botanical Garden, for the beach and forest habitat,

respectively). Both sites provide limited access to the public and therefore, should be minimally

impacted by human disturbance. This region experiences a "hot subhumid climate with rainfall

during the summer", "a mean annual temperature of 27°C", and "a mean annual precipitation of

1,105 mm" (Garcia 1973, Sánchez Sánchez and Islebe 1999).

Because people dump *Sargassum* high on beaches and in beach dunes, our beach

manipulation was deployed at the transition from the beach dune to the beach (20.99343° N, -

86.82442° W). The beaches in this region are formed from calcareous sand derived from coral

reefs and shells, as well as limestone from the Yucatan Peninsula (Castillo and Moreno-Casasola

1996, Mendoza-González et al. 2016). This coast is inhabited by >200 plant species that are

mostly salt-tolerant, low, non-woody plants (<30 cm high) belonging to cosmopolitan families

(e.g., *Poacea*, *Astracea*, and *Leguiminosae*). Additionally, woody species occur at higher

elevations (Islebe et al. 2015). *Ambrosia hispida, Tournefortia gnaphalodes, Suriana maritima,*

Tribulus cistoides, Ipomoea pes-caprae, Sesuvium portulacastrum, Sporobolus virginicus,

Canavalia rosea, Okenia hypogea, Croton punctatus Tribulus cistoides, Ernodea littoralis,

Scaevola plumierii, Coccoloba uvifera Pithecellobium keyense, *Cakile lanceolata, Erithalis*

fruticosa, and *Ernodea litteralis,* are widely distributed in this area (Castillo and Moreno-

Casasola 1996, Mendoza-González et al. 2016). Further, we identified African Bermuda grass (*Cynodon nlemfuensis,* hereafter "grass") throughout the site.

Because people dump *Sargassum* in forest clearings that allow access for large dump trucks, our forest manipulation was deployed on the perimeter of a forest clearing in a botanical garden (Jardín Botánico ECOSUR "Dr. Alfredo Barrera Marín"; 20.84400° N, 86.90278° W). This forest is 4.2 km away from known forest *Sargassum* dumps. The dry forests in this region are considered tropical semi-evergreen forests (Miranda and Hernández-X. 1963) that reach canopy heights of 15-20 m (Sánchez Sánchez and Islebe 1999). Characteristic trees in the forest include *Brosimum alicastrum*, *Talisia olivaeformis*, *Manilkara zapota*, *Myrcianthes fragrans*, and *Dideroxylon gaumeriq*. Characteristic understory species include *Drypetes lateriflora*, *Coccoloba diversifolio*, *Gymnanthes lucida*, *Thrinax radiata*, and *Coccothrinax readii* (Sánchez Sánchez and Islebe 1999). The forest soil type is Lithosol-Rendzina and thus has a well-developed topsoil, no subsoil, and is shallow (<30cm) over limestone (Islebe et al. 2015).

Our manipulation crossed Habitat (Beach, Forest) with *Sargassum* (Addition, Control). At each site, we haphazardly selected locations for paired plots (separated by 9 m between pile centers) and then randomly assigned one plot of each pair to either *Sargassum* addition or unmanipulated control (n=5). For *Sargassum a*ddition plots, we created large piles of *Sargassum* (~1.88 m radius) with a backhoe or wheelbarrows (for the beach and forest habitat, respectively). *Sargassum* piles were initially larger at the beach than the forest (5.25 ± 0.03 and 3.31 ± 0.09 m³, beach and forest, respectively; two-sample t test, t = 5.3058, df = 4.5363, p-value < 0.05). These pile sizes are within the range that humans currently dump in beaches and forests in this region (pers. obs.). All *Sargassum* used in this experiment was collected from drift *Sargassum* accumulated in the ocean at the offshore barriers installed by Moon Palace Environmental

Services. As a result, terrestrial organisms (e.g., talitrid amphipods) should have initially been absent from the experimental *Sargassum*. Beach plots were placed parallel to the water line.

To consider seasonal variation and successional patterns in the impacts of *Sargassum* dumping, we surveyed plots at deployment (August 2022 and three additional dates: November 2022, March 2023, and August 2023). During each sampling period, we assessed pile decomposition and the impact of these manipulations on edaphic conditions, soil respiration, plants, and arthropods. To sample the same locations within plots across sampling dates, we marked the plot center with a flag, and we placed a rope circle around this flag whose radius was the mean radius of *Sargassum* addition plots at the initial deployment date (radius = 1.88m). We confirmed the position of the center flag using multiple photographs of each plot before placing the rope circle.

To estimate decomposition of entire *Sargassum* piles, we measured pile volume at each time point. Pile volume was determined with the equation of an elliptic cone ($V=1/3\ \pi abh$), where a=length of the semi-major axis of the pile footprint, b=the length of the semi-minor axis perpendicular to a, and h=pile height. Because pile volume is confounded by water loss and we wanted to understand the relative contribution of microbes and macrofauna to decomposition, we also measured decomposition of smaller amounts of *Sargassum* (wet mass = 235 ± 0.4g) deployed in each habitat inside bags with small and large mesh openings (0.18 mm and 10 mm; 350 x 250 mm bags, n=10). Decomposition in small mesh bags should have been driven by microbes since these bags excluded larger arthropods, whereas decomposition in large mesh bags was the result of both microbes and mesodetritivores smaller than 10mm.

Mesh bags deployed in the beach habitat were placed adjacent to the large pile manipulation above the substrate. Mesh bags deployed in the forest habitat were placed in a

nearby forested location (20.8636° N, -86.9138° W) from August-November 2022, because this mesh bag experiment was started prior to identification of a forest site for deployment of the large pile manipulation. However, all forest mesh bags were moved to the botanical garden adjacent to the large pile manipulation in November 2022. At each sampling date (i.e., November 2022 and March 2023), we measured *Sargassum* wet mass. At the final sampling in March 2023, we also dried *Sargassum* to directly measure final dry biomass. We estimated starting dry biomass by calculating a dry:wet mass ratio and multiplying starting wet biomass by this ratio. These measurements were then used to calculate decomposition as a percentage of the initial dry biomass. In addition to the mesh bags providing a more accurate assessment of decomposition, the large mesh bags also provided the opportunity to quantify the invertebrates attracted to *Sargassum*. After initial deployment of mesh bags in August 2022, we collected them after 7 days, removed all arthropods, and weighed and returned the *Sargassum* biomass into the mesh bags before returning them to the sites. After 4 months, we collected all bags and repeated these steps. Arthropods found in large mesh bags were identified to family or order and counted. Unfortunately, due to vandalism, we were unable to recover the large mesh bags from the beach habitat in March 2023. Thus, at this point we obtained final wet and dry mass and concluded the mesh bag experiment.

To understand if *Sargassum* additions increased soil nutrients, we collected 50 mL sediment cores from all plots. To minimize disturbance to the *Sargassum* piles, sediment cores were collected ~30 cm towards the plot center from plot edges. We cleared overlaying *Sargassum* and leaf litter before collecting soil. Samples from August 2022, March and August 2023 were dried using the lowest setting of a conventional oven (3 hrs, 190ºC) then kept at -80ºC until transported to San Diego State University (SDSU) in August 2023 where they were kept

at -20ºC until analysis. Because we did not have access to an oven in November 2022, these samples were dried at SDSU in a 65ºC oven for 6 hr before the analysis in December 2023. To assess the accumulation of ammonium and nitrate in sediment, we conducted a Spectrophotometric Nitrate assay using the methods outlined in Pérez Castro et al. (2020) adapted to our sample sizes (10 g). We assessed the dissolved organic carbon content of sediment samples using the method outlined in Bartlett and Ross (1988).

To determine the impact of *Sargassum* additions on soil respiration, we used two separate techniques. First, we collected gas samples that were later analyzed for CO_2 levels with Mass Spectroscopy. Gas samples were collected from inverted containers (1.87 L) placed ~30 cm towards the plot center from plot edges for 1 hr. Prior to pushing these containers into the sediment, we removed overlying detritus. Gas was collected from containers with vacutainers immediately after deployment and then one hour later. The samples were analyzed by gas chromatography with flame ionization at San Diego State University.

Plant Community Impacts

To assess the effect of *Sargassum* on plant cover directly on plots (i.e., plot interior), we surveyed percent cover using 0.5 x 0.5 m quadrats with a 100-point grid. In August and November 2022, we haphazardly tossed a marker over the shoulder onto the interior and placed a quadrat where the marker landed (n=3). In March and August 2023, we switched to random sampling (by randomly selected cardinal directions and distances from the plot center). For all plant surveys, we only recorded the top "canopy" layer of plants beneath the 100 points (identified to genus and species when possible, supplementary Fig. 3, 4).

Plot perimeter survey

To assess the effect of *Sargassum* on plant cover beyond piles, we surveyed percent cover adjacent to the edge of the initial plot footprint of all treatments in August 2022 and 2023. We placed a quadrat at the edge of *Sargassum* plots and an equivalent location on control plots (i.e., 1.88m from the plot center), at four opposing poles or points of tangency. We measured percent cover using the methods described in the section above. For two of these poles, we also surveyed plant cover at two additional distances extending away from the pile edge [D_1 and D_2 = 0.75 and 1.5 m at both sites (August 2022); 0.52 and 1.27m at beach and 0.62 and 1.37m at forest (November 2022); 0.32 and 1.07m at beach and 0.43 and 1.18m at forest (March 2023); Appendix Fig. S2]. Distances varied between dates and habitats because quadrats were placed 0.75 and 1.5m from the edge of the *Sargassum* piles and then an equivalent distance was used for control plots. After the fact, we corrected these two distances at each date and habitat because we were interested in understanding how far away from the initial plot footprint any *Sargassum* effect would appear.

We recognize this approach limits our ability to rigorously compare across habitats. In March 2023, we did not see variation between sampling distances and decided to drop this portion of the survey in the interest of sampling efforts and time (see results section). Additionally, because in March 2023 Bermuda grass was so prevalent at the beach sites and there were no obvious patterns observed in forest grasses or with other specific plant taxa in either habitat, we collapsed all plants other than Bermuda grass into one category in the Forest, and both sites in August 2023. Thus, we present "grass" and "other plants" for all sampling periods in the figures.

Arthropod Community Impacts

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To assess the effect of *Sargassum* on the crawling arthropod community, we placed yellow plastic cups (210 ml) at two opposing poles of each plot for 24 hours. Pitfall traps were buried flush with the substrate and filled approximately halfway with water and ~5 drops of dish soap to break the surface tension and prevent arthropods from escaping. Because we wanted to assess arthropod abundance at the same time for each habitat to reduce variability from deployment dates, we waited until all *Sargassum* piles were completed at the beach before installing pitfall and sticky traps. At the point of installation, two *Sargassum* piles had been complete for two days, two had been completed for one day, and the traps were deployed after the final pile was made. All *Sargassum* piles were completed in one day in the forest and arthropod traps were deployed on the same day. After 24 hours, we collected the entire contents of each trap, and then counted and identified arthropods to family or order.

To assess the effect of *Sargassum* on the flying arthropod community, we placed two double-sided sticky cards (127mm x 76mm, Catchmaster ®), attached to wire rods, on each plot. The sticky traps were placed ~130mm above the substrate or *Sargassum* piles, ~1m from the center of the plot. After 24 hours, we photographed all sticky traps *in-situ* to process at a later time. Arthropods were counted on both sides of sticky traps and identified to order. We note that such traps could also catch non-flying amphipods (e.g., talitrid amphipods that often move via jumping).

Statistical Analyses

To test decomposition of *Sargassum* piles, we analyzed pile volume as a percent of starting volume using a Linear Mixed Effects Model (LMEM), with site and sampling trip as the main effects and their interaction. We included *Sargassum* pile number in the model as a random factor to account for differences in starting volume. To test if decomposition of *Sargassum*

differed in mesh bags with and without arthropod access, we used a LMEM with treatment, habitat, sampling trip as the main effects and their interactions, and bag identification number as a random factor to account for repeated measures. To test if arthropod abundance in large mesh bags differed between sites over time, we used a Linear Model with arthropod order, habitat, and sampling trip as main effects with their interactions. To test the effects of *Sargassum* addition on edaphic conditions we conducted three linear models with ammonium, nitrate, or DOC as a response variable with treatment as the main effect, habitat and sampling trip as interacting factors.

To test the effect of *Sargassum* additions on plant cover on the interior and the perimeter of plots, we directly compared percent cover of grass and "other plants," in *Sargassum* addition plots to paired controls by habitat at each sampling period. We used *Cohen's d*, which quantifies the difference in means between two groups (i.e., control vs. addition), divided by the weighted average of the standard deviations between both groups to determine the effect size. Using this standardized effect size allows for comparisons of magnitude of the effect between groups on a common scale (i.e., small d≈0.2, medium d≈0.5, and large d≈0.8 effect sizes). We analyzed the effect sizes of *Sargassum* addition on crawling and flying arthropod abundances using the same method.

All statistical analyses and visualizations were conducted using the R Programming Language (R Core Team, 2023). Linear models and LMEM were conducted using the R base and 'nlme' packages. Necessary assumptions were met for statistical analyses and post-hoc tests were conducted as needed.

Results

Dumped *Sargassum* decomposed in both habitats, as measured both via change in pile volume (Appendix Fig. S1) and biomass loss in the mesh-bag experiment (Fig. 1). The majority of decomposition occurred during the first four months. After one year, pile volume decreased by >85%. Pile volume as a percent of starting volume differed between habitats in November 2022 (LMEM: Estimate = 2.020, Std. Error = 4.857, t-value 3.918, p <0.001), but this effect was not observed in later sampling periods (p=0.65).

In November 2022, habitat interacted with mesh size to influence decomposition of *Sargassum* in mesh bags (LMEM: Estimate = 21.05, Std. Error = 5.973, t-value 3.525, p <0.001). At this time point, decomposition in the forest was similar for large and small mesh bags suggesting that microbes drove decomposition in the forest. In contrast, decomposition in the small mesh bags at the beach was only 51% of the decomposition in the large mesh bags, suggesting that detritivores between 0.18-10mm played a much more significant role at the beach. Decomposition in large mesh bags between habitats did not differ suggesting similar total decomposition in both habitats (Estimate = 8.78, Std. Error = 4.18, p = 0.43). Consistent with the pile volume temporal pattern, most decomposition occurred in the first four months of the mesh-bag experiment (LMEM: Estimate -17.805, Std. Error = 6.352, t-value = -2.803, p < 0.005). Unfortunately, we lost the large mesh bags at the beach in March.

In August 2022, habitat interacted with sampling trip to influence total count of arthropods in large mesh bags (LM: Estimate = 27.68, Std. Error = 8.63, t-value = 3.198, p = 0.001). Fewer arthropods were attracted to these large mesh bags in the forest (Estimate = -28.50, Std. Error = 6.12, t-value = -4.66, p < 0.001), likely due to high abundances of talitrid

amphipods caught at the beach. In contrast, no amphipods were found in the mesh bags during November sampling at either habitat.

Soil nutrients

Ammonium levels were consistently higher in forest soils where they peaked in August and November 2022 (Fig. 3A, B). Although there was no treatment effect on ammonium levels from *Sargassum* addition in either habitat (LM: Estimate =0.738, Std. Error = 3.889, t-value = 0.19, p=0.85), there was a trend for *Sargassum* additions to suppress ammonium in forest soils in November 2022. *Sargassum* addition increased nitrate levels in both habitats (LM: Estimate =55.887, Std. Error =12.61, t-value = 4.432, p < 0.001). Nitrate levels peaked later in the beach than in the forest (March 2023 and November 2022, respectively; Fig. 3C, D). *Sargassum* addition significantly increased DOC at both locations (LM: Estimate =199.32, Std. Error = 56.93, t-value = 3.501, p < 0.001; Fig. 3E, F).

Soil respiration

Sargassum addition tended to increase carbon dioxide production in November 2022 (Fig. 4). However, neither the treatment effect, site effect, or their interaction were statistically significant (ANOVA: $F_{(1,12)}$=1.679, p=0.219; $F_{(1,12)}$==0.953, p=0.348, and $F_{(1,12)}$==0.025, p=0.878; respectively).

Plant community impacts

Although the beach initially contained low plant cover (5%, Appendix Fig. S3, S5), *Sargassum* additions dramatically increased grass cover to >75% (Fig. 5A, C; 2 sample t-test: -9.861, df = 18.057, p<0.001). This effect began to appear in November 2022 but was most apparent in March and August 2023. In contrast, grass cover remained low in control plots

throughout the year (<10%; Fig. 5A). Non-grass plants only displayed weak responses to *Sargassum* additions. Although the effect was weaker than directly in the plots, the effect of *Sargassum* additions at the beach spilled over to increase grass cover 3.8x just beyond the plot perimeters (after one year d=1.02, Fig. 6A, C). There was no effect beyond perimeter in November 2022 or March 2023, so we did not continue to survey at distances beyond the perimeter (November 2022 and March 2023, d=0). This spillover effect was taxon-specific as *Sargassum* additions at the beach did not strongly impact non-grass plants outside of the plots in November 2022, March 2023, or August 2023 (d=0.45, 0.2, 0.16, respectively).

Similar to the beach, the forest floor contained low plant cover at deployment (4%; Appendix Fig. S4, S6). Unlike the beach, *Sargassum* additions in the forest did not increase plant cover for any taxon within plots (Fig. 5B, D). There was a slight increase in effect size in "other plants" in the forest habitat in March 2023 (d=0.09, Fig. 5D), but this was the result of a plot that was covered by a *Cucumis* plant that was not rooted within the *Sargassum* pile. After removing this plot from the analysis, the effect size was large and negative, indicating percent cover of "other plants" was much higher in control plots compared to *Sargassum* pile interior (d=-1.18). Although there was not a direct effect of *Sargassum* additions on forest plots, there was a spillover effect – *Sargassum* additions increased non-grass plants at plot perimeters (d=0.56 Fig. 6B, D).

Arthropod community impacts

Crawling arthropods in pitfall traps consisted of arachnids and hymenopterans, mainly spiders and ants at both sites, and talitrid amphipods at the beach (Fig. 7). Adding *Sargassum* at the beach immediately increased amphipod abundance 42x in August 2022 (Fig. 7A, C, E). After the initial sampling of plots in August 2022, amphipods were rare [only 1 amphipod was found

75

in a control plot in November 2022 and 1 in a *Sargassum* plot in March 2023 (Fig. 7C,E)].

Additionally, *Sargassum* additions at the beach initially increased arachnids and hymenopterans

(August 2022). This effect remained for hymenopterans during later sampling events but not

arachnids (Fig. 7A, C, E). In the forest, *Sargassum* addition only weakly affected crawling

arthropods (Fig. 7B, D, F). Importantly, no amphipods were found in forest pitfall traps during

any of the sampling periods (Fig. 7 B, D).

Flying arthropods sampled on sticky traps at the beach consisted of dipterans and

hymenopterans, mostly flies and wasps (Fig. 8). On the initial deployment of the experiment,

amphipods (21 ± 7) were also captured on sticky traps, presumably because they move via

jumping. Beach *Sargassum* additions initially increased dipterans 23x more than controls–

however, this effect diminished over time (Fig. 8A, C, E). *Sargassum* additions also increased

hymenopteran abundance – but this effect was not apparent until November and March. Similar

to the beach, *Sargassum* additions to the forest increased both dipterans and hymenopterans (Fig.

8B, D, F). However, the dipteran effect in the forest was stronger and delayed.

Discussion

Realistic amounts of *Sargassum* (i.e., several cubic meter piles) dumped into adjacent

terrestrial habitats commonly used as dumping grounds (e.g., beach dunes and forests)

decomposed at similar rates. Most decomposition of *Sargassum* occurred within the first four

months (August 2022 - November 2022). Interestingly, the drivers of decomposition differed

between habitats - microbes predominantly drove decomposition in the forest, while talitrid

amphipods played an equivalent role as microbes on the beach. Decomposing *Sargassum* also

increased soil nitrates and dissolved organic carbon, with nitrates entering the soil several

months earlier in the forest. Additionally, there was a trend for *Sargassum* dumps to increase soil

respiration beneath the piles. While *Sargassum* dumping modified edaphic conditions in both habitats, the aboveground plant and arthropod communities were more strongly impacted at the beach. *Sargassum* additions at the beach dramatically increased the cover of the invasive Bermuda grass to over 85% total coverage, and attracted talitrid amphipods, flies, wasps, and ants. Conversely, in the forest, *Sargassum* additions had a weaker or neutral effect on plants and arthropods.

Although *Sargassum* decomposed at similar rates in the two habitats, the roles of microbes and mesodetritivores were habitat-specific in at least two ways. First, decomposition by microbes was twice as fast in the forest. This finding contrasts with the Home Field Advantage hypothesis that predicts that microbial use of subsidies should be faster in the experienced habitat (i.e., the beach). Despite the naivete of forest microbes to seaweed detritus, the more favorable abiotic conditions (e.g., increased humidity and reduced temperature) and ambient microbial communities may have overwhelmed the evolutionary co-occurrence of forest microbes and seaweed detritus. Second, mesodetritivores contributed to approximately half of overall decomposition in the beach but were relatively unimportant in the forest. Beach mesodetritivores were dominated by talitrid amphipods, a detritivore that specializes in seaweed wrack that colonized our *Sargassum* piles within days (Wildish et al. 2016).

Habitat-specific roles of microbes and mesodetritivores could influence how *Sargassum* subsidies move through food webs and habitats where it is dumped. When *Sargassum* is dumped into forests, the dominance of microbes as decomposers suggests that this material will be incorporated into subterranean food webs in soils directly beneath the piles and perhaps diluted into local water tables. In contrast, the material from *Sargassum* dumped into beaches will more quickly enter aboveground food webs, including those away from the piles because talitrid

amphipods that feed on this material are mobile and are consumed by a variety of terrestrial

predators including birds and lizards (Dugan et al. 2003, Wright et al. 2020).

Although *Sargassum* dumping increased soil nitrate levels in both habitats, it only

stimulated plant production in the beach habitat. *Sargassum* plots at the beach were quickly

colonized by the invasive Bermuda grass within eight months. This colonization was associated

with an increase in total vegetation cover from 5 to 85%. The lack of a fertilization effect in the

forest could be related to at least four factors. First, forest soils may not have been nutrient

limited at the start of the experiment. In support of this hypothesis, we observed higher

ammonium, nitrate, and dissolved organic carbon in forest soils than beach sediments. Second,

another abiotic factor may have limited productivity in the forest. For example, forest plots

beneath the tree canopy may have been primarily limited by light. Third, the timing of the

nutrient pulse may have differed from the phenology of forest plants relative to beach plants.

Fourth, forest plants may have been dispersal-limited. In this regard, it was interesting that the

only forest *Sargassum* plot to stimulate plant productivity was colonized by cucumber with vine

growth.

The positive impact on plants suggests that any potential toxic or negative effects from

the addition of *Sargassum* seaweeds were outweighed by the fertilization effect. This strong

fertilization potential by *Sargassum* has been seen in previous studies (Piovia-Scott et al. 2013,

Adderley et al. 2023). Local farmers and entrepreneurial companies interested in converting

Sargassum biomass to marketable fertilizers have long recognized the potential for *Sargassum* to

fertilize terrestrial habitats. We found that nitrate levels following the addition of *Sargassum*

were comparable to agricultural levels and similar to those in pot experiments using *Sargassum*

as a biofertilizer (i.e., >100 mg Nitrate per kg soil; Adderley et al. 2023), indicating an increase

in soil fertility. Additionally, our unpublished data revealed that arsenic levels after one year were orders of magnitude lower than the concentration necessary to be toxic to Bermuda grass (Weaver et al. 1984). While these findings are promising, it is important to acknowledge certain caveats. Our study did not rigorously assess the contents of arsenic in plant tissues or if leachates from *Sargassum* decomposition enter belowground waterways. Thus, understanding the accumulation of arsenic up the food web is crucial in order to fully assess potential negative impacts on consumers.

The arthropod response to *Sargassum* was habitat-specific and appeared to be a direct response to *Sargassum* and not Bermuda grass. On the beach, amphipods, flies, and ants initially showed a strong response, which was likely due to the moist environment and scent of fresh wrack. This effect, however, diminished over time. Because the location of the piles at the beach were above the high tide line, it was interesting that amphipods traversed the entire length of the beach to access the freshly deposited *Sargassum*. The lack of amphipods on subsequent trips was perhaps related to the lower palatability of dried *Sargassum* or alternately, easier access to fresh wrack deposits on the shoreline. Conversely, ants continued to utilize the wrack piles throughout the experiment, possibly due to the physical structure of *Sargassum* piles providing shelter from the environment. Spiders also responded initially, possibly due to their predatory nature and a response to amphipod densities, but this effect diminished in later sampling periods. Wasps showed a delayed but strong response after four months in both habitats, suggesting that this response was not due to an attraction to plants. However, it remains unclear if the numerical response of wasps was a predatory reaction to increased flies, especially in the forest habitat.

Decisions about dumping *Sargassum* will depend on management priorities. For example, if the goals are to minimize impact on aboveground communities including invasive

grasses or to minimize impact on beach tourism, our study would suggest continuing to prioritize dumping in forests. However, it is important to note that although arsenic was not found to be toxic to Bermuda grass, it did leach from the *Sargassum* into the soil. This raises concerns about the possibility of arsenic entering groundwater, particularly in areas like the Yucatan Peninsula where the water table is shallow and underneath karst, which could have implications for human health (Rodríguez-Martínez et al. 2020, Vázquez-Delfín et al. 2021). Beaches are unlikely to process massive amounts of *Sargassum* and leaving that biomass on the beach could fuel invasions by opportunistic species such as Bermuda grass, ultimately reducing tourism and having negative economic impacts. Furthermore, there is strong evidence that accumulation of *Sargassum* in coastal waters has detrimental impacts on fish, invertebrates, seagrass beds, and coral reefs (Lapointe 1997, Van Tussenbroek et al. 2017, Rodríguez-Martínez et al. 2019, Chávez et al. 2020). It is also important to note the potential negative effects of current uses of *Sargassum*, such as fertilizer for livestock feed, which could have implications for human consumption. However, it remains unknown to us if the bioaccumulation and biomagnification arsenic in plants fertilized by *Sargassum* reach levels that are toxic for human consumption.

Our results challenge the notion that ecosystems can't process novel subsidies effectively. Specifically, the decomposition rates of *Sargassum* seaweed were similar in both the forest and beach habitats, and naïve microbes appeared to play a more prominent role in the forest. Additionally, nutrients mobilized faster in the forest environment, which may be attributed to the leachates from *Sargassum* providing resources, such as nitrates and dissolved organic carbon, usable by generalist decomposers. This contradicts the Home Field Advantage hypothesis, which predicts that microbial use of subsidies should be faster in the experienced habitat (Vivanco and Austin 2008). The fact that the familiar system decomposed *Sargassum* at a similar rate to the

naïve system suggests that the idea that familiar systems process subsidies better needs to be reconsidered.

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Figure captions

Figure 1

Percent decomposition of initial dry mass of large (gray bars) and small (white bars) mesh bags at Beach (left column) and the Forest (right column) in November 2022 (A) and March 2023 (B). Error bars represent mean ± SE. Note that no values are reported for large mesh bags at the beach in March 2022, the lack of a bar does not indicate zero decomposition.

Figure 2

Mean arthropod abundance in large (10 mm) mesh bags over sampling period (August and November 2022) in the Beach (left column, panels A, C) and the Forest (right column, panels B, D). Error bars represent mean ± SE.

Figure 3

Ammonium (A,B), Nitrate (C,D), and Dissolved Organic Carbon (E,F) content (mg) per kg of sediment over sampling periods (August and November 2022, March and August 2023) by site (Beach A,C,E and Forest B,D,F). Light gray bars represent Control treatments and dark gray bars represent *Sargassum* treatments. Error bars represent mean ± SE. Note that no samples were collected at the Beach site in August 2022.

Figure 4

Grams of CO_2 per m^2 over an hour in Control and *Sargassum* plots at the Beach (A) and Forest (B). Error bars represent mean ± SE.

Figure 5

Mean percent cover of plot interiors over sampling period (August and November 2022, March and August 2023) at the Beach (A) and Forest (B). Shapes represent grass (●) and other plants (▲) and colors represent Control plots (gray) and *Sargassum* plots (black). Error bars represent mean ± SE. Lower panels show the effect sizes by sampling period associated with the panel above (i.e., panel C effect sizes associated with panel A, and panel D effect sizes are associated panel B). Effect sizes were calculated using Cohen's d (*Sargassum* vs. Control) for grass and other plants.

Figure 6

Mean percent cover of plot perimeter over sampling period (August 2022 and August 2023) at the Beach (A) and Forest (B). Shapes represent grass (●) and other plants (▲) and colors represent Control plots (gray) and *Sargassum* plots (black). Error bars represent mean ± SE. Lower panels show the effect sizes by sampling period associated with the panel above (i.e., panel C effect sizes are associated with panel A, and panel D effect sizes are associated panel B). Effect sizes were calculated using Cohen's d (*Sargassum* vs. Control) for grass (●) and other plants (▲).

Figure 7

Mean crawling arthropod abundance in pitfall traps over sampling period (August and November 2022, and March 2023) in the Beach (top row, panels A, B) and the Forest (middle row, panels C,D). Arthropod abundances are separated by Controls (left column, panels A, C) and *Sargassum* (right column, panels B, D). Effect size plots are associated with plots above (i.e., panel E effect sizes are associated with panels A and B, panel F effect sizes are associated with panels C and D). Effect sizes were calculated using Cohen's d (*Sargassum* vs. Control). Shapes

represent Amphipoda (●), Arachnida (▲), and Hymenoptera (■) and error bars represent mean ±

SE.

Figure 8

Mean flying arthropod abundance in pitfall traps over sampling period (August and November

2022, and March 2023) in the Beach (top row, panels A, B) and the Forest (middle row, panels

C,D). Arthropod abundances are separated by Controls (left column, panels A, C) and

Sargassum (right column, panels B, D). Effect size plots are associated with plots above (i.e.,

panel E effect sizes are associated with panels A and B, panel F effect sizes are associated with

panels C and D). Effect sizes were calculated using Cohen's d (*Sargassum* vs. Control). Shapes

represent Amphipoda (●), Diptera (▲), and Hymenoptera (■) and error bars represent mean ±

SE.

Appendix figure captions

Figure S1

Sargasso pile volume loss over sampling periods (August and November 2022, March and August 2023) as a percent (%) of original volume calculated for sargasso treatments in August 2022. Individual dots represent replicates at the Beach (black) and the Forest (white).

Figure S2

Percent cover of grass (top four panels) and other plants (bottom four panels) over sampling periods (August 2022, November 2022, and March 2023). Control treatments (light gray) and *Sargassum* addition treatments (dark gray) are shown at Distance 1 (closest to plot perimeter) and Distance 2 (furthest from plot perimeter). Error bars represent mean ± SE.

Figure S3

Proportion of cover categories in plot interiors over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the Beach site. Columns designate treatment type (left is Control and right is *Sargassum*) and rows represent treatment block.
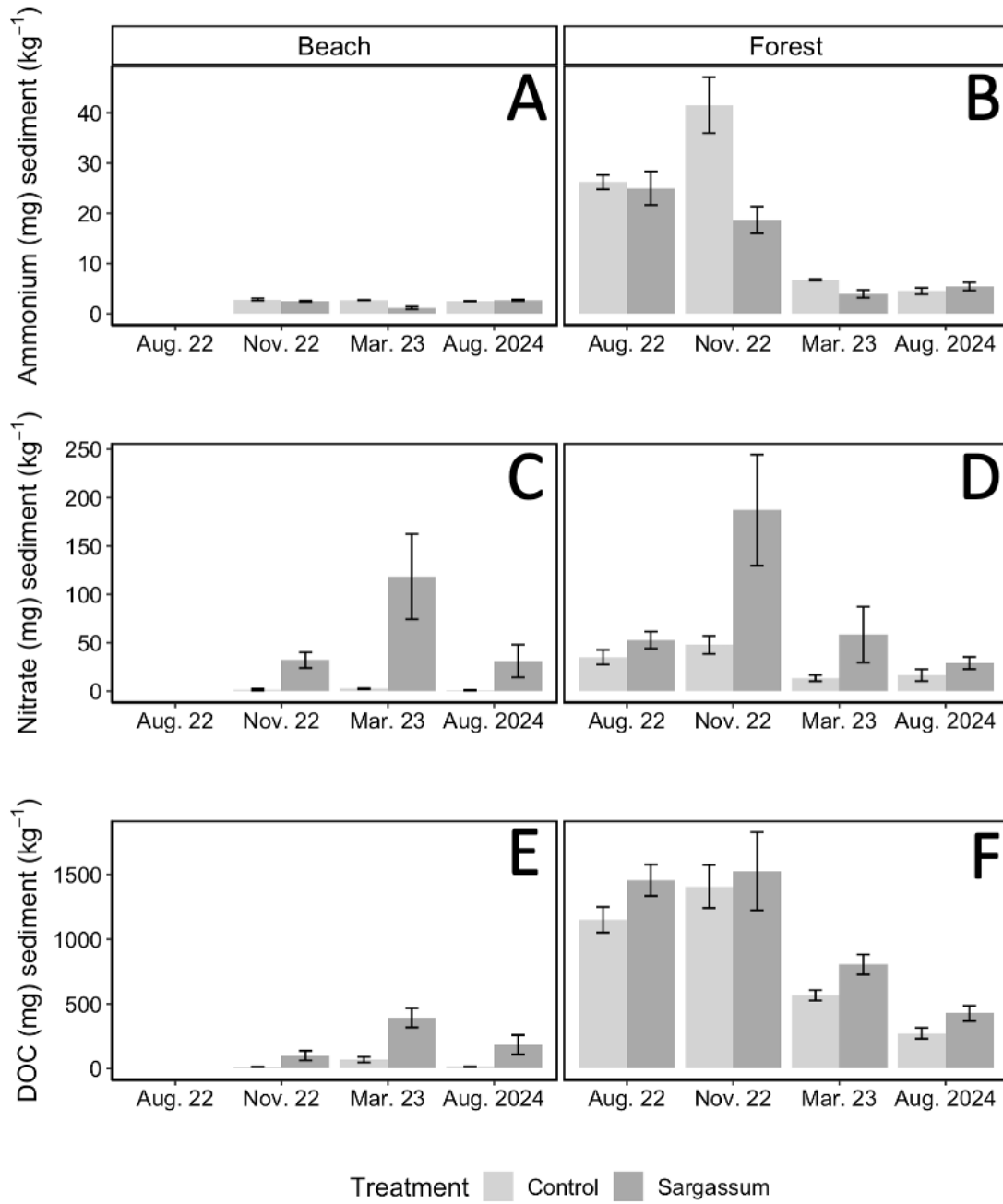
Figure S4

Proportion of cover categories in plot interiors over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the Forest site. Columns designate treatment type (left is Control and right is *Sargassum*) and rows represent treatment block.

Figure S5

Proportion of cover categories in plot perimeter over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the Beach site. Columns designate treatment type (left is Control and right is *Sargassum*) and rows represent treatment block.

Figure S6

Proportion of cover categories in plot perimeter over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the Forest site. Columns designate treatment type (left is Control and right is *Sargassum*) and rows represent treatment block.

Figures

Figure 1
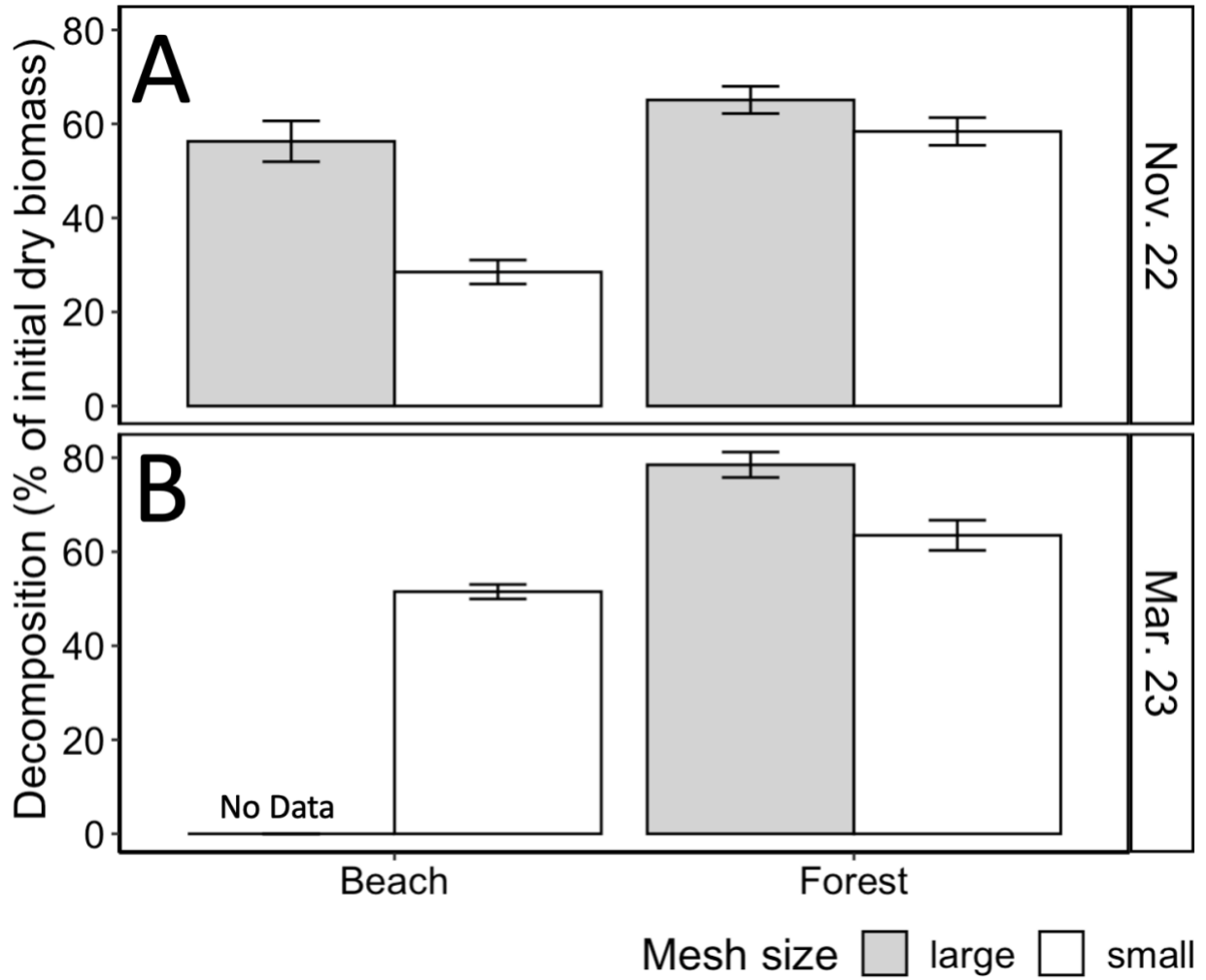
Figure 2
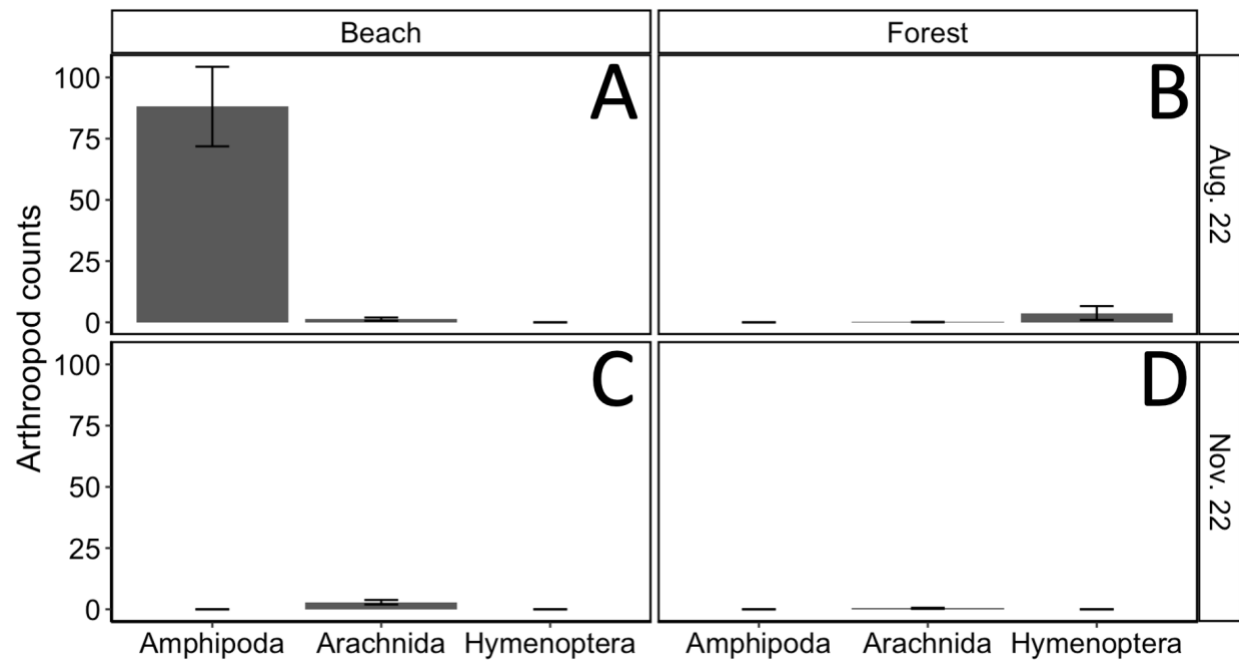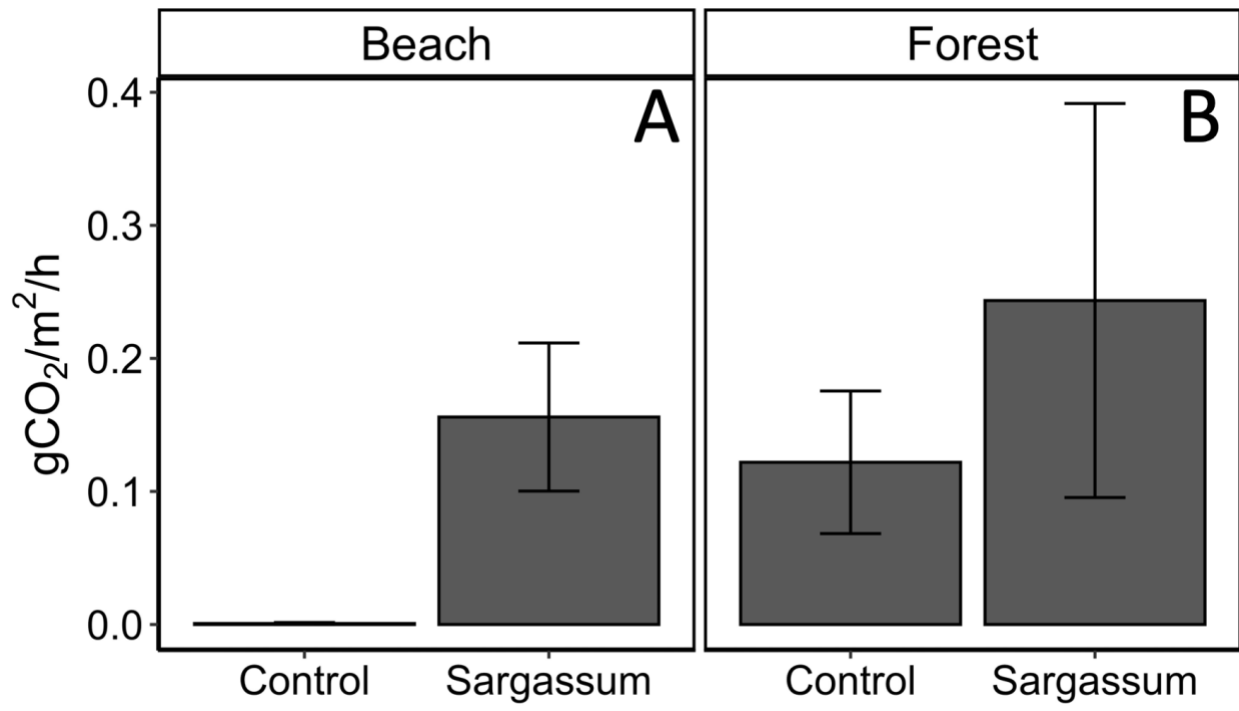
Figure 3

Figure 4

Figure 5
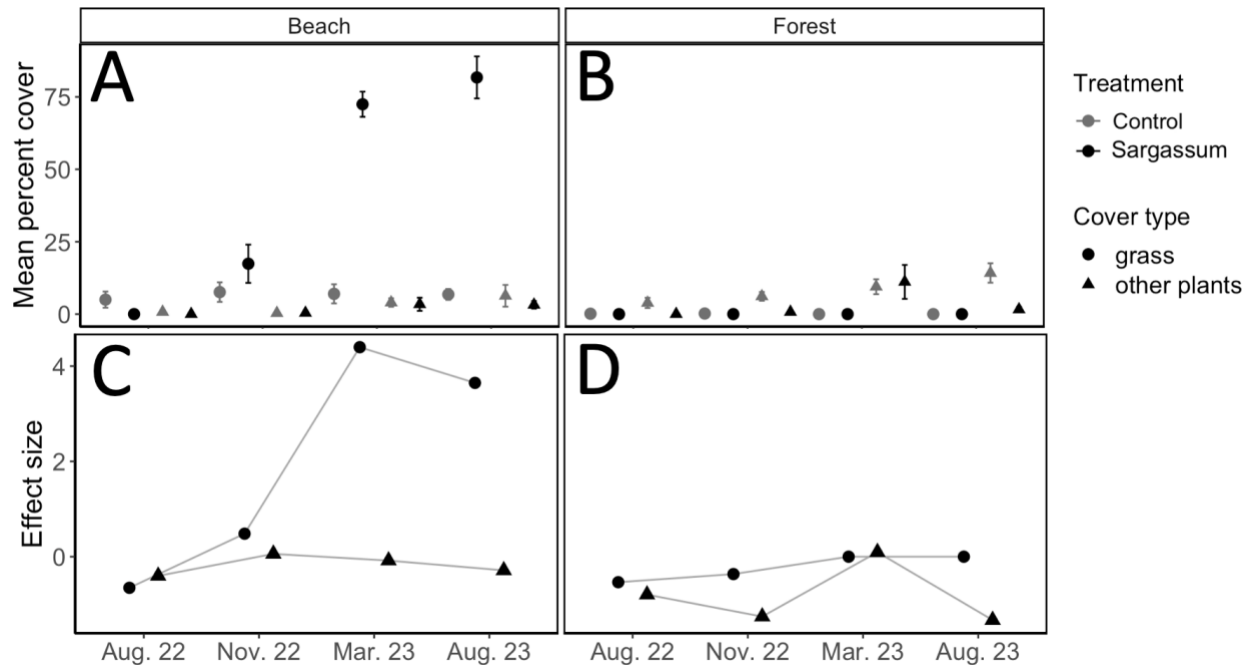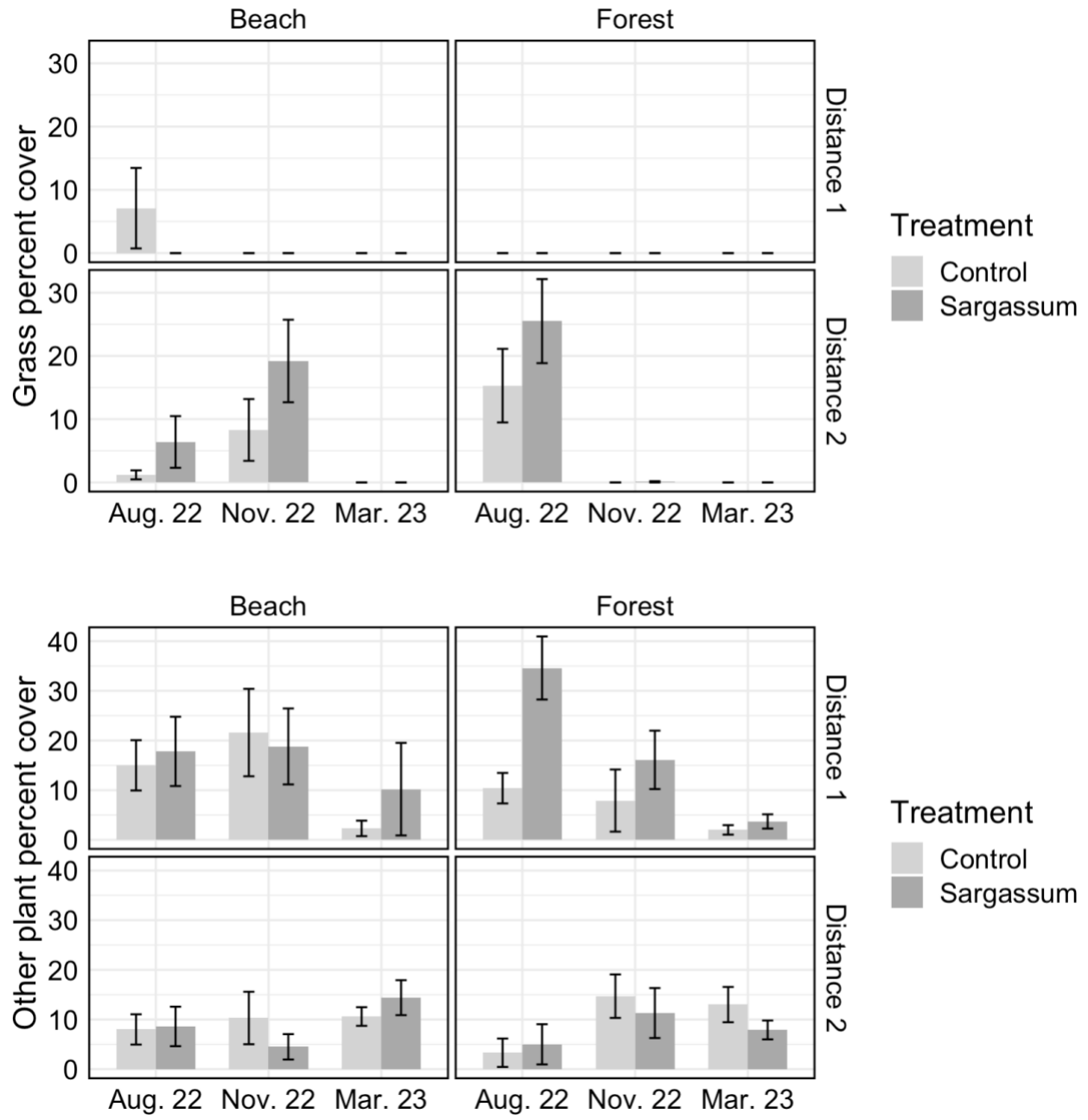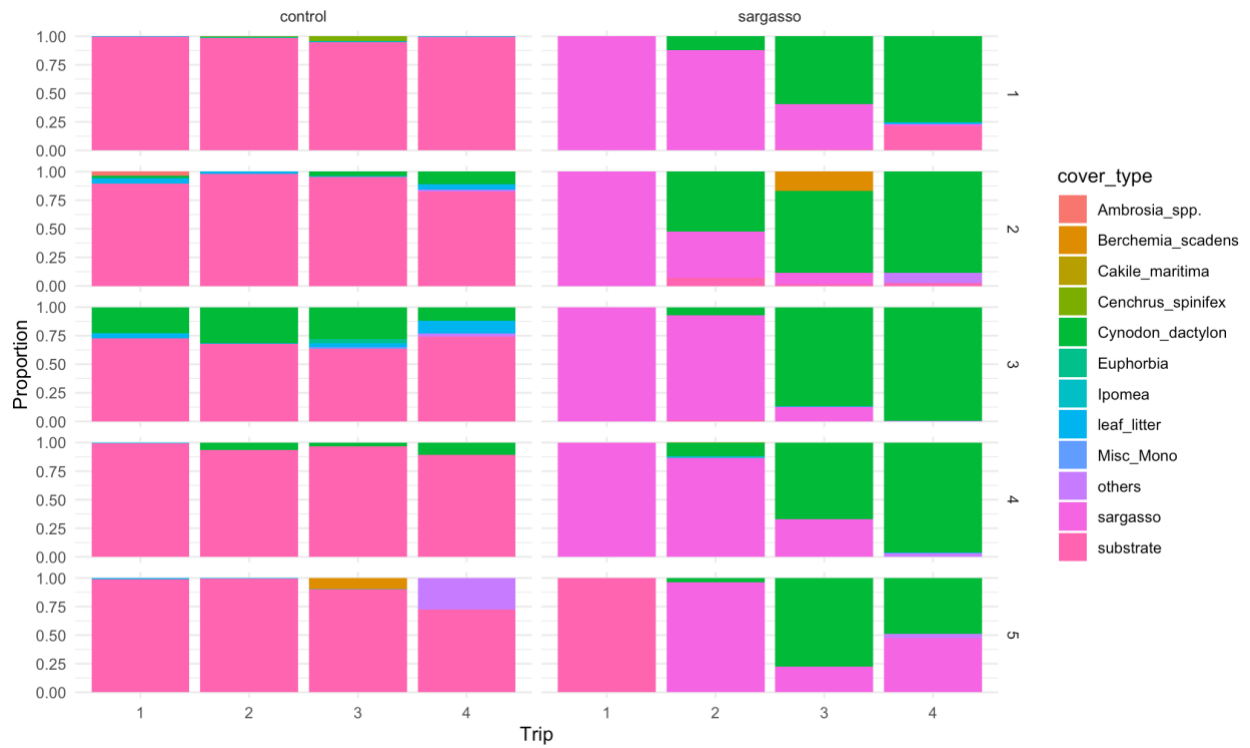
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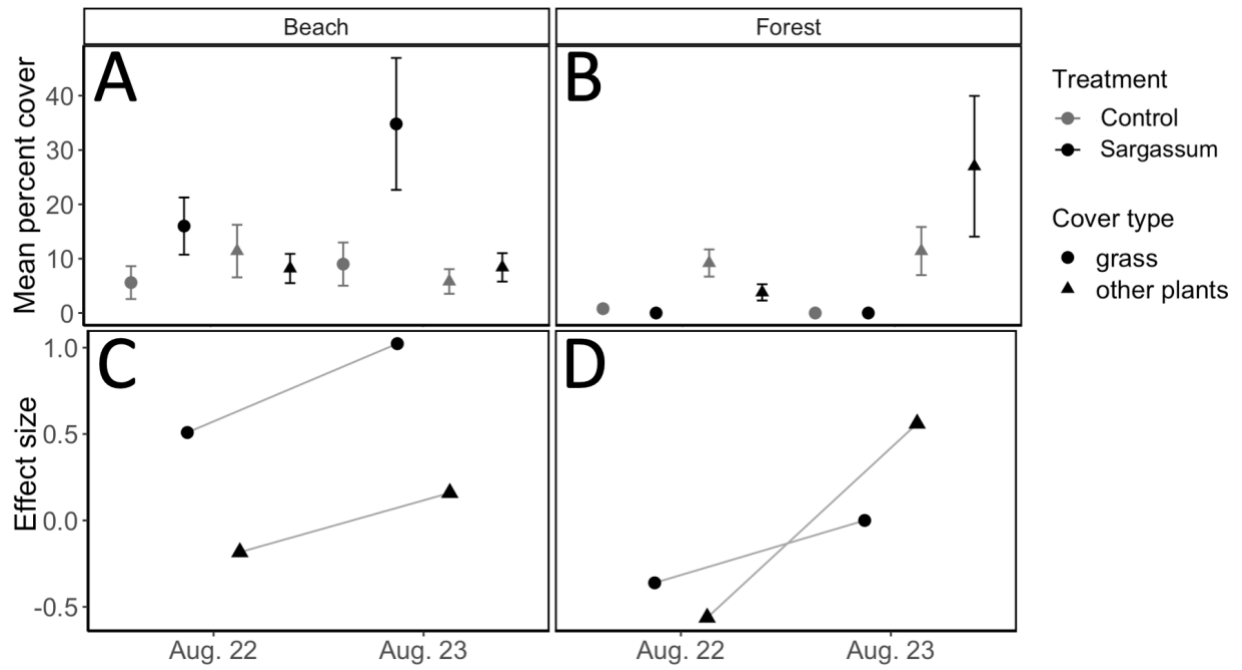
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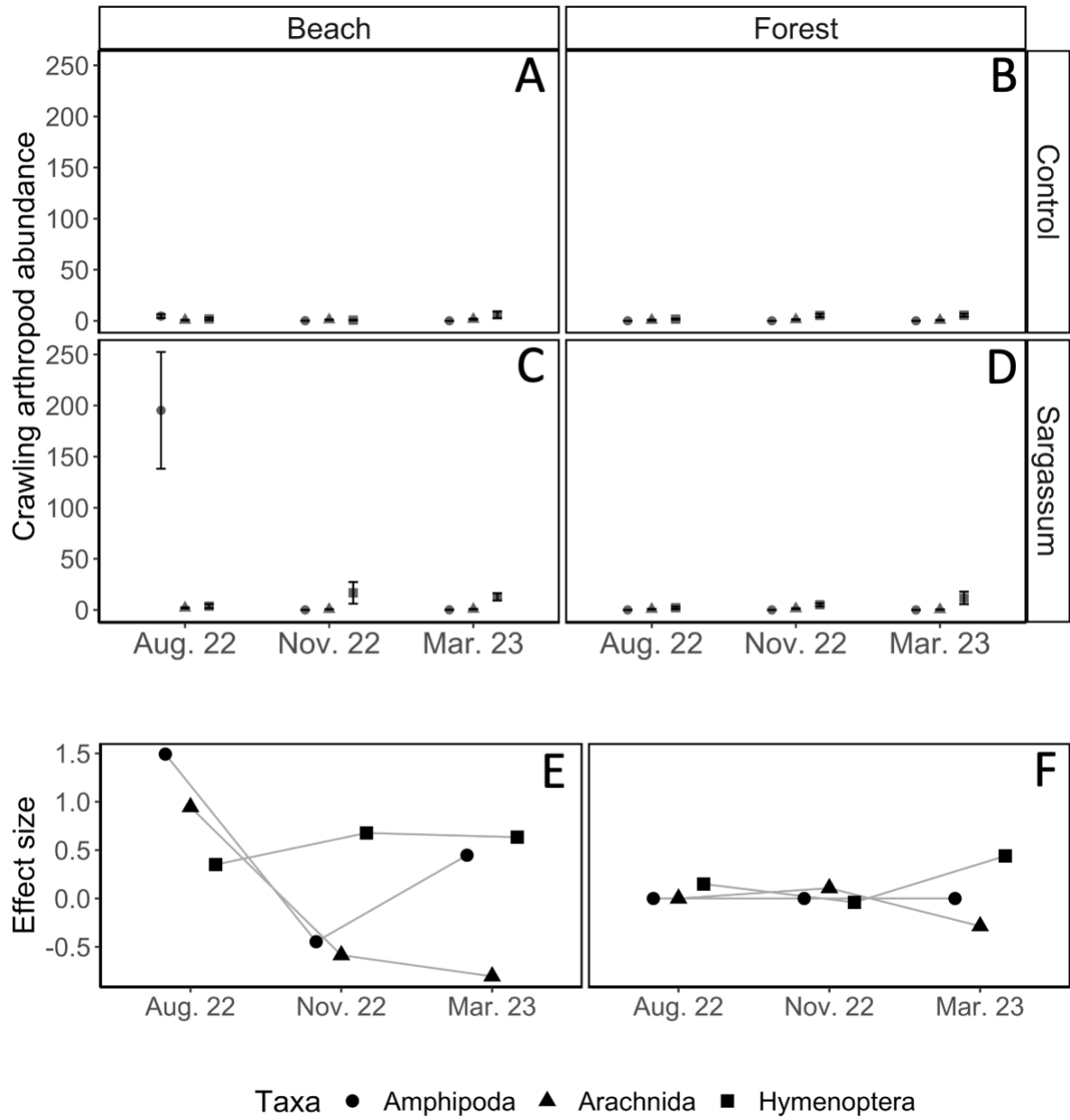
Figure 8
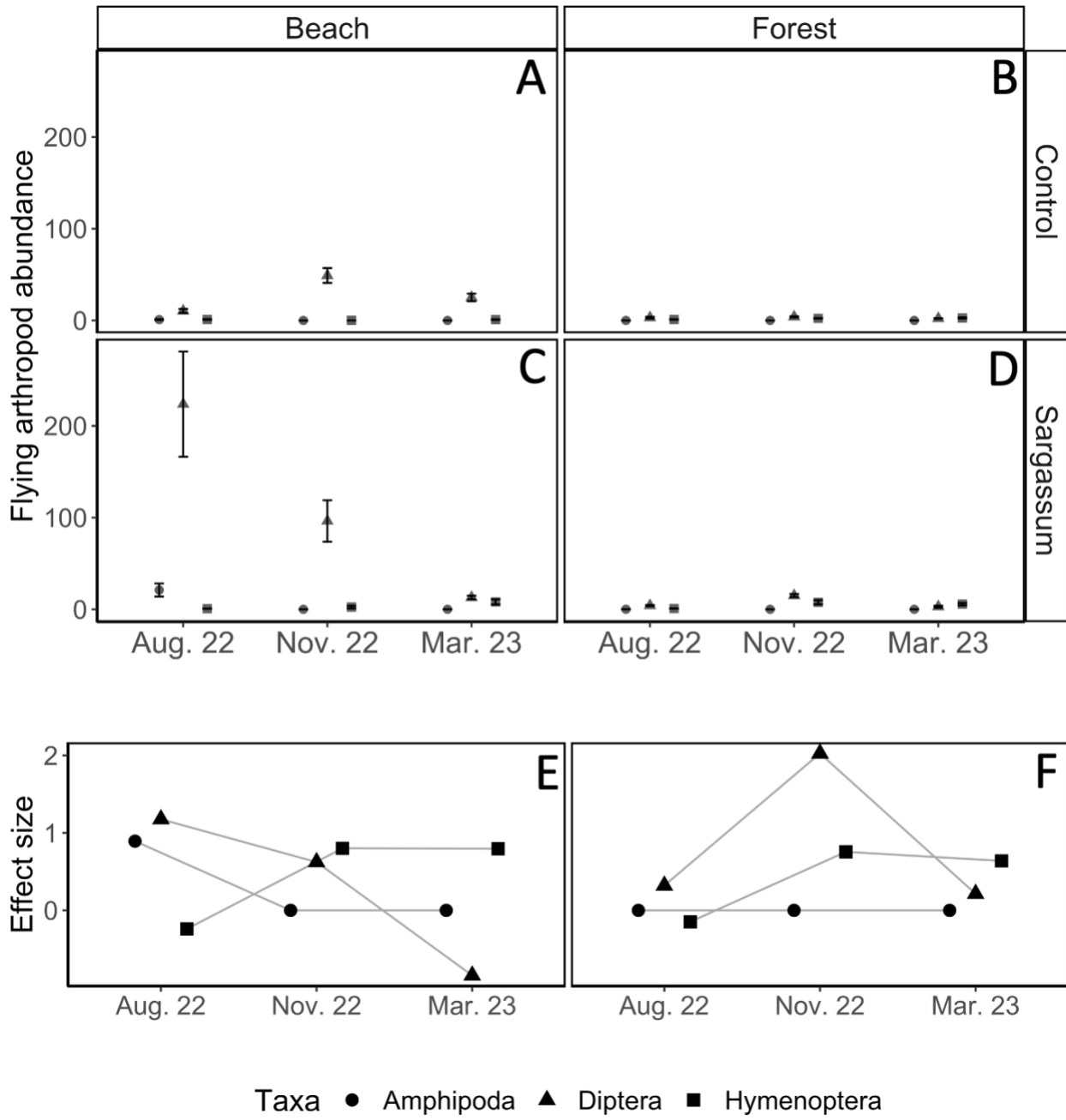
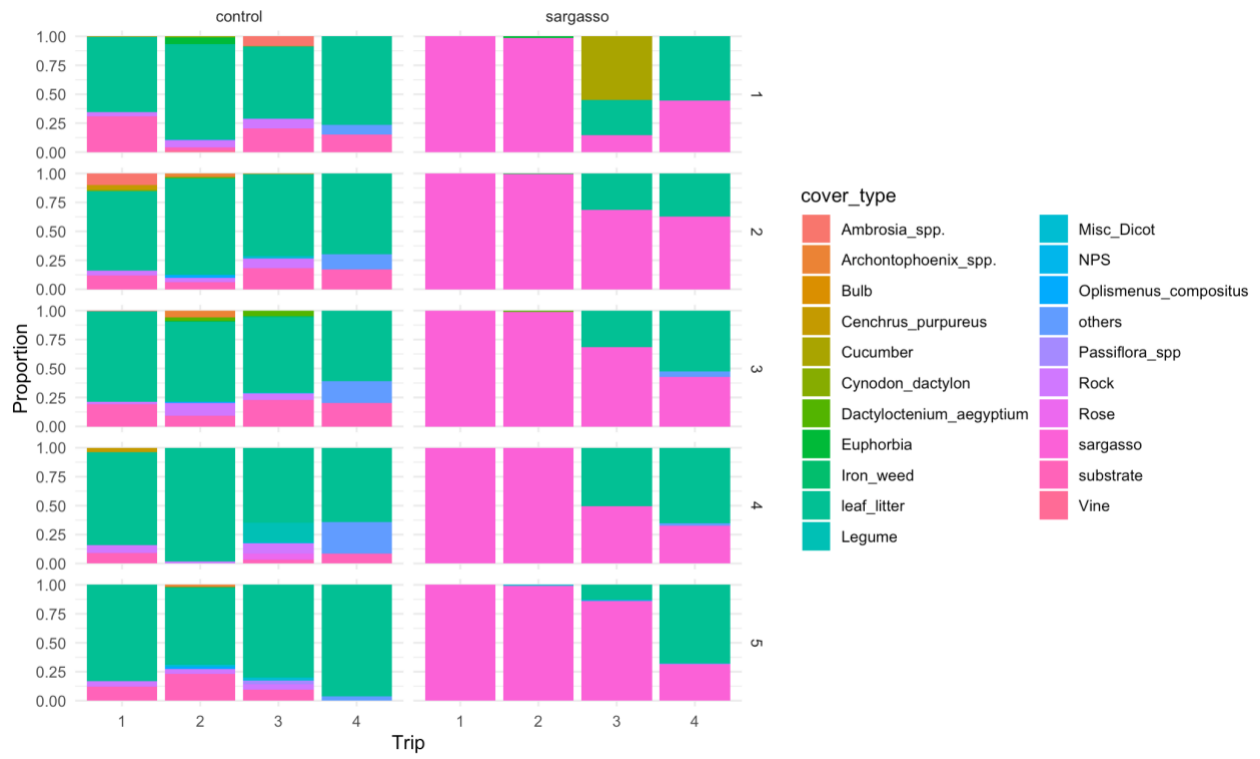**Appendix figures**

Figure S1
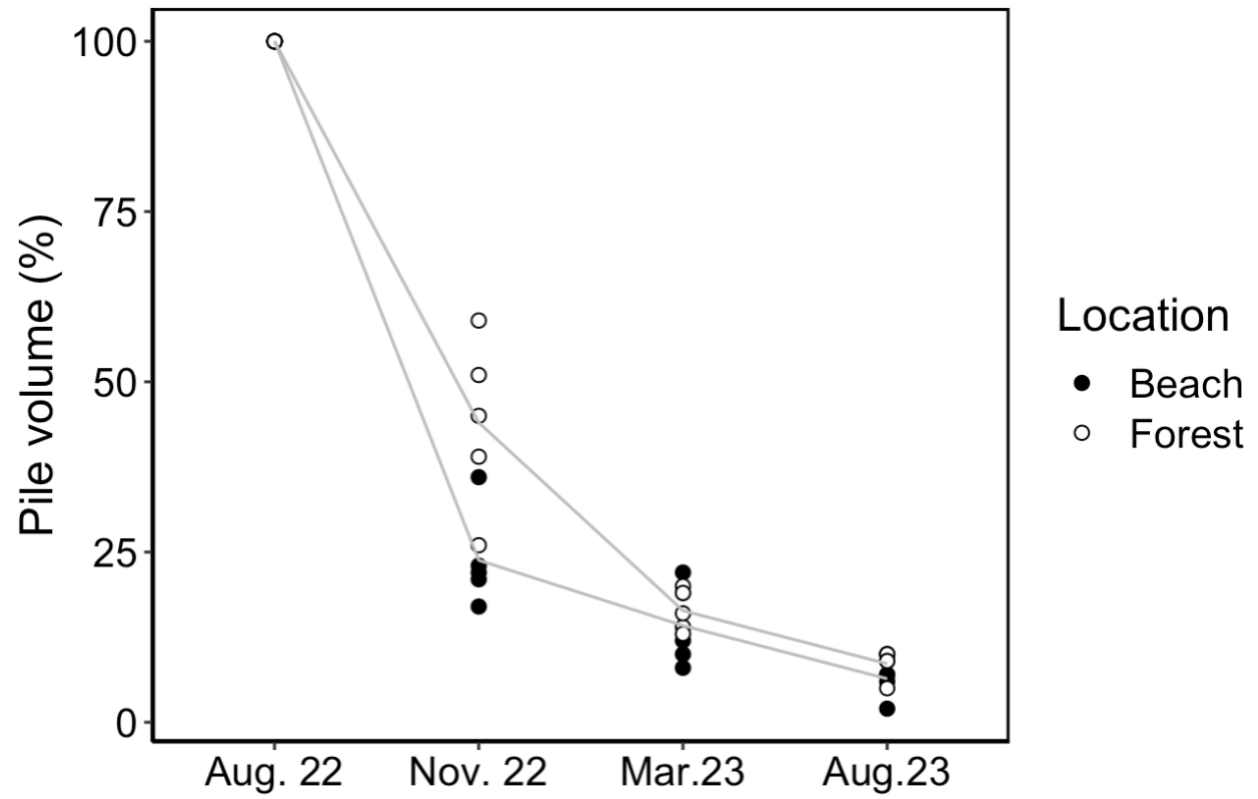
Figure S2

Figure S3

Figure S4

Figure S5

Figure S6