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Experimental tests of snail grazing on turtle grass, *Thalassia testudinum*: evidence of resilience in short-term plant function to scarring of live tissues

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Keywords: *Thalassia testudinum*, *Tegula fasciata*, seagrass resilience, invertebrate grazing, fungal infection, top-down control

Abstract

In coastal ecosystems, the intricate interactions among grazers, microorganisms, and plants play a crucial role in shaping plant health and ecosystem dynamics. Recent work has shown that snail grazing on live seagrass tissue creates wounds that can facilitate fungal infection, suggesting a pathway by which invertebrate grazers may exert top-down control over seagrass growth. However, whether density-dependent snail grazing translates into measurable impacts on fungal infection and seagrass health under field conditions remains untested. To address this gap, we conducted field surveys and experiments to examine how fungal infection in *Thalassia testudinum* blades and seagrass health varies with different densities of the herbivorous smooth tegula, *Tegula fasciata* snail in Bocas del Toro on the Caribbean coast of Panama. Field surveys documented snail scarring on seagrass blades and that density of smooth tegula in seagrass beds was positively associated with both scarring prevalence and increased brown tissue (indicative of fungal infection) in seagrass blades. Our six-week experimental manipulation testing densities of tegula snails (0, 1, 2, 4, and 6 snails per 625 cm^2) revealed no significant effects of snail density on seagrass metrics including biomass, productivity, shoot density, or degree of fungal

colonization, despite visible emergence of radulation scars on blades. The only significant treatment effect was on total shoot number, where treatments with natural snail density (1 snail per 625 cm^2) produced more shoots than treatments with the highest snail density (6 snails per 625 cm^2). Although snail presence increased scarring on new growth blades relative to snail-free controls, tissue damage did not translate into detectable effects on seagrass biomass, productivity, or fungal colonization. These results suggest that *T. testudinum* can effectively compensate for snail grazing over short timescales, as it does with other grazers, such as turtles. Fungal biomass did not increase significantly with snail density or scarring presence, indicating that the grazer-pathogen facilitation pathway documented in other marine plant systems may not operate over short experimental timescales in turtlegrass. Together, these findings suggest a degree of ecological co-tolerance between *T. testudinum* and invertebrate grazers, though whether this resilience holds under sustained grazing pressure or compounding environmental stressors warrants further investigation.

Introduction

In terrestrial systems, grazers can have large and diverse effects on plant communities. Studies across multiple habitats have demonstrated grazers' ability to influence plant biomass and primary production (Bruno et al. 2008; He and Silliman 2016), leaf abscission rates (Mingo and Oesterheld 2009), nutrient content in leaves (Zieman et al. 1984), flowering rates (Brys et al. 2011), clonal propagation (Maschinski and Whitham 1989), as well as plant diversity and succession (Huntly 1991). Mechanisms of control can be direct, through the consumption of plant tissue, and/or through myriad indirect pathways. One powerful indirect pathway of grazer control on plant growth is facilitation of fungal infection of live plant tissues via grazer-induced wounding (Taylor and Bardner 1968; Silliman and Newell 2003; Daleo et al. 2009; Eigenbrode et al. 2018; Gossner et al. 2021). This grazer-pathogen-plant interaction often leads to suppressed plant growth and can make plants more susceptible to environmental stressors such as drought (He et al. 2013) and warming (Graham et al. 2024).

Understanding of herbivore impacts in seagrass ecosystems has undergone substantial revision over recent decades (Nowicki et al. 2018; Valentine & Heck 2021). Early paradigms emphasized bottom-up and epiphyte grazer control of seagrass growth, positioning small invertebrate mesograzers primarily as mutualists that facilitate seagrass health by removing epiphytic algae and thereby reducing competition for light and nutrients (Hughes et al. 2004; Heck & Valentine 2006; Reynolds et al. 2014; Duffy et al. 2015).

More recently, emerging evidence from both seagrass and other marine systems suggests that the traditional beneficial view of mesograzers may be incomplete. In seagrass ecosystems, multiple studies now document cases where small invertebrates directly consume live seagrass tissue—including leaves, reproductive structures, and seeds—and can facilitate secondary damage through facilitation of fungal infection in grazer-induced wounds (Valentine & Duffy 2007; Carr & Boyer 2014; Boyd et al. 2022). For examples, non-native amphipod outbreaks have been shown to consume eelgrass leaves, spathes, and whole fruits at rates that could remove all seeds from a meadow within weeks (Carr & Boyer 2014), while gastropod grazing on turtlegrass blades has been documented to create scars that may facilitate fungal growth in live tissue (Boyd et al. 2022).

These patterns parallel well-documented grazer-pathogen facilitation in other marine foundation species. In salt marsh systems, snail grazing on *Spartina* facilitates fungal colonization, and the combination of grazing and infection substantially reduces plant production (Silliman & Newell 2003; Daleo et al. 2009; Freitas et al. 2014). Similarly, in eelgrass (*Zostera marina*) meadows, grazing scars increased wasting disease caused by *Labyrinthula zosterae*, with some herbivores passing live pathogen cells in feces and thereby amplifying disease transmission (Graham et al. 2024). Across marine systems, the strength of these grazer-pathogen-plant interactions appears highly context-dependent, driven by grazer identity (including non-native or outbreaking species), grazer density, predator control, habitat complexity, and environmental stressors (Alberti et al 2007; Valentine & Duffy 2007; Carr & Boyer 2014).

Despite this growing body of evidence from other marine ecosystems, direct experimental tests of whether gastropod grazing on live seagrass tissue facilitates fungal infection and impacts seagrass health remain rare, particularly in tropical systems. This knowledge gap is particularly important given that historical overexploitation has dramatically reduced populations of megaherbivores and predators that control consumers, elevating the relative importance of mesograzers in contemporary seagrass food webs (Martínez-Crego et al. 2016). These shifts may have created novel grazing dynamics that differ fundamentally from the evolutionary context in which these systems developed.

Given the importance of seagrass as a foundation species in the Caribbean and evidence that invertebrate grazers can have cryptic but strong top-down control in other marine systems (Brearley and Walker 1995; Nakaoka et al. 2002; Silliman and Newell 2003; Fredriksen et al. 2004; Shaver et al. 2020), we investigated whether commonly occurring snails that graze live turtlegrass can facilitate fungal infection and impact seagrass health. We conducted field surveys and a six-week manipulative experiment in Bocas del Toro on the Caribbean coast of Panama. Surveys quantified natural patterns of snail abundance and

seagrass scarring to identify relationships between grazers and plant damage. We then experimentally manipulated Smooth Tegula snail density across five levels (0, 1×, 2×, 4×, and 6× natural density) to test density-dependent effects on fungal infection, seagrass biomass, productivity, and shoot density. Our findings suggest that T. testudinum tolerates invertebrate grazing pressure over short timescales, highlighting the resilience of tropical seagrass to small-scale consumer impacts and the importance of experimental scale in detecting top-down control.

Methods

Snail Density & Scarring Surveys

To determine ambient snail density, surveys were conducted in seagrass beds in Bocas del Toro on the Caribbean coast of Panama (n=5, 9°21'03.67"N 82°15'26.35"W). At this site, surveys with 15 random quadrats (25 × 25 cm) were surveyed during the day (12:00–16:00 h) and again at night (19:00–20:00 h) (Boyd et al. 2022). Within each quadrat, all snails on the turtlegrass blades, at the sediment surface, and within the top 2.5 cm of sediment in each quadrat were collected, enumerated, identified, and categorized by taxonomic group (Boyd et al. 2022). All turtlegrass blades from each quadrat were collected and processed in the lab to determine scarring prevalence. For processing, the total number of blades per quadrat was counted, and for each blade within a quadrat the following variables were measured: blade height (cm) and width (cm), number of scars, scar length (cm) and width (cm), blade greenness (%). Blade surface area was calculated as height × width (cm^2), and scar surface area was estimated as number of scars per blade x scar length × 0.1 cm (assumed scar width, approximating the width of longitudinal vascular bundles along which snail radulae typically graze). Scarring intensity was expressed as the proportion of total blade area scarred (total scar area ÷ total blade area) and analyzed at the per-blade level.

Field Experiment

To examine the effects of tegula density on turtlegrass fungal infection, we employed a field experiment (n=8 per treatment) and manipulated grazing Smooth Tegula densities using established snail-caging methodologies (Silliman and Zieman 2001). There were five levels of grazing snail density (0, 1, 2, 4, and 6 snails per 625 cm^2), in addition to the control and cage control plots . To generate the five levels of snail densities, cages were stocked with the appropriate snail density, and these densities were monitored daily and maintained throughout the experiment. Cages were 25 x 25 cm, 30 cm tall, built with PVC poles and ¼ inch mesh galvanized hardware cloth, to prevent snails from escaping or entering the cages (Fig. 1).

Cages were roofless so as not to impede sunlight while the zinc coating on the cages deterred snails from crawling on the cages. Experimental cages were deployed in a low-flow, protected bay to minimize interactions with water flow, and cages were cleaned daily to prevent algal accumulation on the cages. To standardize initial conditions across treatments, cages were deployed and maintained without snails for 14 days prior to the start of the experiment. During this period, all seagrass within the cages was cut down to ~2.5 cm above the sediment and allowed to regrow without grazer presence, ensuring similar baseline conditions across all experimental units. Following this standardization period, the experiment ran for 30 days from May-July 2023, during which plots were stocked with appropriate snail densities. Turtlegrass blades (n=4) were collected on Day 0 and Day 30 of the experiment from each plot to determine fungal biomass (based on ergosterol concentration), as well as grazing scar size and abundance on each blade using established methods (Silliman and Newell 2003). To examine seagrass growth rates, 3 × 3 cm growth plots were established within each cage at the midpoint of the experiment (approximately Day 17). Within each growth plot, turtlegrass was cut to 1–2 cm above the sediment and allowed to regrow; after 8 days, turtlegrass (n=4) was collected from each growth plot to assess growth rates ($cm^2 \cdot day^{-1}$) and scarring prevalence. After 8 days, turtlegrass (n=4) was collected from each growth plot to assess growth rates ($cm \cdot day^{-1}$) and scarring prevalence. On Day 30 of the experiment, all turtlegrass and snails were collected from each cage and transported to the lab for processing.

Turtlegrass and Epiphyte Samples

From each quadrat/cage, the total number of turtlegrass blades sampled during each collection was counted and separated into groups labeled as ‘Alive’ (green) and ‘Dead’ (brown). To focus analyses on photosynthetically active tissue, blades were designated as 'Alive' if at least 80% of blade area was green and 'Dead' if below this threshold; dead blades were excluded from further measurement. For each alive blade, percent green tissue was subsequently recorded as a continuous variable by visually estimating the proportion of green relative to brown tissue. For each blade, morphological measurements included seagrass length (cm) and seagrass width (cm) for each blade. Following those measurements, the percent green was determined by comparing the green and brown sections as a measure of how alive the seagrass blade was. The number of grazing scars present and the length (cm) of each scar was recorded for each seagrass blade. The width for each scar was assumed to be 0.1cm. Finally, epiphyte biomass samples were collected from each turtlegrass blade. The epiphyte biomass samples were predominantly composed of algae and associated epibionts, which were gently scraped and washed off each blade. All seagrass and epiphyte samples were stored in aluminum pouches and dried in an oven for ~48-72 hours at 70 °C to determine dry mass (g).

Rhizome Samples

At the end of the experiment, rhizome samples (n=5) were collected from each cage to assess how snail density treatments affected belowground biomass and resource allocation. During the 'Post' sample processing, rhizome length (cm), width (cm), and the number of alive seagrass blades attached to the rhizome were recorded for each of the five samples. After taking the baseline seagrass and scaring measurements (as described above), turtlegrass, epiphyte, and rhizome samples were stored in aluminum pouches and dried in an oven to a constant mass (i.e., ~48-72 hours) at 70 °C before biomass measurements (g) were recorded.

Fungal Samples

Four turtlegrass blades (per cage) collected at Day 0 (pre) and Day 30 (post) were used for fungal biomass analysis. The same morphological measurements (seagrass length (cm), width (cm), scar number, and scar length (cm)) were recorded for each turtlegrass blade. For fungal biomass analysis, two 3-cm sections were cut from each turtlegrass blade (n=4): leaving a total of eight 3 cm sections per cage/sample. In parallel, the same morphological measurements were recorded for each 3-cm section. Four 3-cm sections of seagrass (one from each blade) were preserved in 20-mL vials with 15 mL of methanol and stored at -20 °C. The corresponding four 3-cm sections were oven-dried to determine dry mass as described above. Samples preserved in methanol were shipped on ice to Coastal Carolina University for fungal biomass analysis based on quantifying ergosterol concentration in plant tissues. Ergosterol is a sterol found in fungal membranes, which is widely used as a specific biomarker for estimating fungal biomass in various environmental samples (Gulis and Bärlocher 2017). Lipids were extracted from turtlegrass samples in methanolic KOH, partitioned in pentane, and redissolved in methanol. Samples were prepared for high-performance liquid chromatography (HPLC) by filtering through PTFE syringe filters into HPLC vials. HPLC was run isocratically using methanol as a mobile phase and a C_{18} reverse-phase column as described by Gulis and Bärlocher (2017). Ergosterol concentrations in turtlegrass (µg/g) were calculated based on the area of the ergosterol peak, data from external ergosterol standards, and plant sample dry mass.

Statistical Analysis

Survey data were analyzed using two regression models with stepwise AIC-based model selection. To model scarring prevalence, a beta-binomial regression was used to account for overdispersed binomial data, with the response variable structured as a two-column matrix of success/failure counts (scarred vs. unscarred blades). To model the proportion of brown tissue (calculated as 1 − percent green), beta regression was used with a boundary-adjusted response variable. Both models initially included all

potential ecological predictors: densities of six snail species (Smooth Tegula (*Tegula fasciata*), Stocky Cerith (Cerithium litteratum), Dark Cerith (*Cerithium atratum*), Ivory Cerith (Cerithium eburneum), Emerald Nerite (*Smaragdia viridis*), and Long-Spined Star snails (*Lithopoma phoebium*)), time of day (day/night), total seagrass blade area, mean blade length, and proportion of blade area scarred (where applicable). The final scarring model retained five predictors: Smooth Tegula density, Dark Cerith density, Emerald Nerite density, time of day, and total seagrass area. The final brown tissue model retained three predictors: Smooth Tegula density, mean blade length, and proportion of scarred area. Model diagnostics for both models were assessed using simulated residuals via the DHARMa package, which confirmed appropriate model fit.

Seagrass morphological responses were analyzed using generalized linear models (GLMs) appropriate to each response variable's distribution. In all models, snail density treatment (five levels: 0, 1×, 2×, 4×, and 6× natural density) was included as the sole fixed factor. Proportion of the scarred area was analyzed using beta GLM. Total seagrass biomass was analyzed using gamma GLM with log link. Live blade counts were analyzed using negative binomial GLM due to Poisson overdispersion. Total shoot counts were analyzed using Poisson GLM with log link. Rhizome measurements (length and biomass) were analyzed using ANOVA.

Productivity (growth rate) was calculated as increase in blade growth area (seagrass surface area (cm^2) ÷ 8 days) averaged across blades per cage to yield per-cage mean growth rate ($cm^2 \cdot day^{-1}$). Assumptions were evaluated using Shapiro-Wilk tests on log-transformed values and Levene's test for homogeneity of variance. Growth rates were analyzed using Gaussian GLM, with Kruskal-Wallis test as nonparametric confirmation. Scarring on new growth was expressed as the per-cage ratio of total scar surface area to total blade surface area and analyzed using a binomial GLM with denominator weights, appropriate for proportional response data. A quasi-binomial GLM was fit to account for potential overdispersion, with Kruskal-Wallis test as nonparametric confirmation

For fungal analyses, cages were classified as scarred or unscarred based on whether any scar area was recorded in post-experiment samples. Fungal biomass (ergosterol) was quantified as corrected ergosterol per g seagrass dry mass (µg/g) and compared between scarred and unscarred cages using a Wilcoxon rank-sum test, and across snail density treatments within each scar group using Kruskal-Wallis tests. Non-normalized corrected ergosterol per g was compared between scarred and unscarred cages using Wilcoxon rank-sum test, and across treatments within scar groups using Kruskal-Wallis tests.

Post-hoc pairwise comparisons for significant effects were conducted using Tukey's HSD tests. All analyses were performed in R v4.6.

Results

FIELD SURVEY RESULTS

Snail Distribution and Scarring Patterns

Our surveys revealed an average tegula snail density of 1.69 ± 1.03 (mean ± SD, n=13) per 0.25m² quadrat, with Cerith snails being more abundant (Dark Cerith: 6.54 ± 7.25, n=26; Stocky Cerith: 3.69 ± 4.71, n=16; Ivory Cerith: 2.06 ± 2.59, n=16).

The beta-binomial regression revealed several significant predictors of seagrass blade scarring intensity (Fig. 2). Smooth Tegula density showed a significant positive relationship with scars per blade (Estimate = 0.16 ± 0.07 SE, z = 2.46, p=0.014). In contrast, Dark Cerith density exhibited a significant negative relationship with scarring intensity (Estimate = -0.03 ± 0.01 SE, z = -2.77, p=0.006). The average number of scars per blade decreased with increasing total seagrass surface area (Estimate = -0.001 ± 0.0003 SE, z = -3.97, p<0.001). Ivory Cerith density showed a negative but non-significant trend with scarring (Estimate = -0.07 ± 0.04 SE, z = -1.60, p=0.109).

The final beta regression model revealed three significant predictors of brown tissue percentage in seagrass blades (Fig. 3). Brown tissue increased significantly with the proportion of scarred blade area (Estimate = 46.72 ± 6.54 SE, z = 7.15, p<0.001), mean blade length (Estimate = 0.035 ± 0.010 SE, z = 3.67, p<0.001), and the density of smooth tegula (Estimate = 0.070 ± 0.029 SE, z = 2.45, p=0.014).

EXPERIMENTAL RESULTS

Seagrass Morphological Responses to Grazer Manipulation

The proportion of seagrass area scarred did not differ among treatments (Fig. 4a; Beta GLM, Wald $\chi^2(4)=1.99$, p=0.738). Total seagrass biomass showed no significant treatment effects (Fig. 4b; Gamma GLM: $\chi^2(4)=0.545$, p=0.463). Live blade counts per cage showed no significant treatment effect (Fig. 4c; Negative binomial GLM: $\chi^2(4)=3.419$, p=0.491). However, the total number of post-experiment shoots

per cage showed a significant treatment effect (Fig. 4d; Poisson GLM: $\chi^2(4)=11.108$, $p=0.025$), with post-hoc comparisons revealing significantly more shoots in natural density treatments compared to 6× density treatments (Tukey's test, $p=0.017$). All other pairwise contrasts were not significant. Rhizome measurements showed no significant treatment effects for either length (ANOVA: $F(4,35)=0.588$, $p=0.673$) or biomass ($F(4,35)=0.547$, $p=0.703$).

Productivity and Growth Responses to Grazer Manipulation

Seagrass growth rates showed no significant differences between treatments (Fig. 5a; $F(4,32)=0.501$, $p=0.736$). While snail inclusion treatments exhibited more scars on new growth blades compared to exclusion treatments, the proportion of scarred area did not significantly differ among treatments (Fig. 5b; binomial GLM: $\chi^2(4)=7.17$, $p=0.127$, dispersion≈1.11; quasi-binomial: $F(4,31)=1.288$, $p=0.296$). Zero scarring was consistently observed in control cages (7/7) and absent scarring was frequent in low-density treatments (>80% of cages at 1× and 2× natural density).

Fungal Infection Analysis to Grazer Manipulation

Fungal biomass showed no significant relationship with snail density or scarring. Corrected ergosterol per g of seagrass dry mass was similar in scarred (31.8 ± 3.0 µg/g SE) and unscarred cages (27.2 ± 2.4 µg/g SE), with no statistically significant difference detected (Fig. 6a; Wilcoxon rank-sum $W = 142$, $p=0.209$). Ergosterol did not differ significantly across snail density treatments within scarred or unscarred cage groups (Fig. 6b; Kruskal-Wallis: unscarred $\chi^2(4) = 6.267$, $p = 0.180$; scarred $\chi^2(4) = 5.492$, $p=0.241$).

Figures

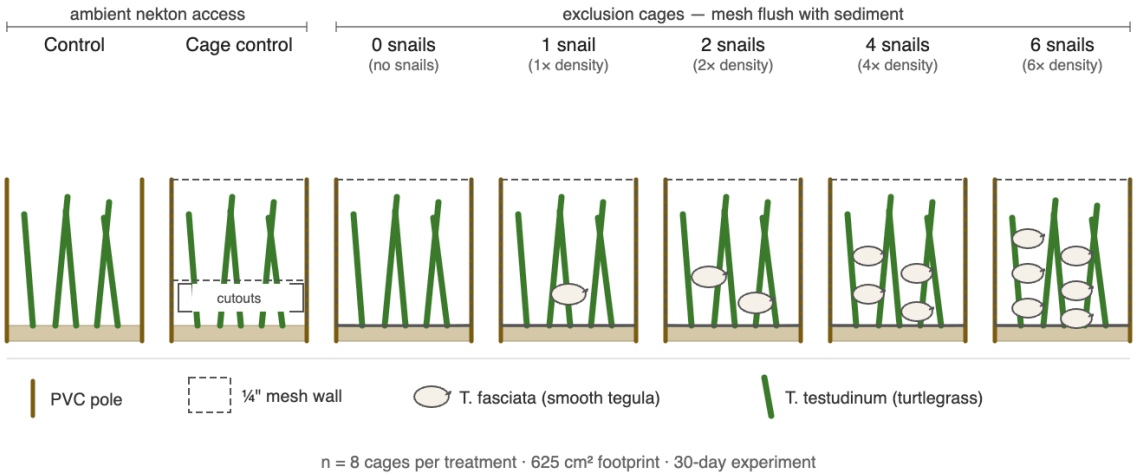


Figure 1. Experimental design. Cages (25 × 25 cm, 30 cm tall, ¼" galvanized mesh on PVC poles) were deployed in *Thalassia testudinum* beds in Bocas del Toro, Panama. Control plots had no enclosure. Cage controls had mesh walls with cutout openings near the sediment surface to allow free organism movement. Exclusion cages had mesh flush with the sediment, preventing snail entry or exit. Five snail density treatments (0, 1, 2, 4, and 6 *T. fasciata* per 625 cm²) were maintained for 30 days (May–July 2023).

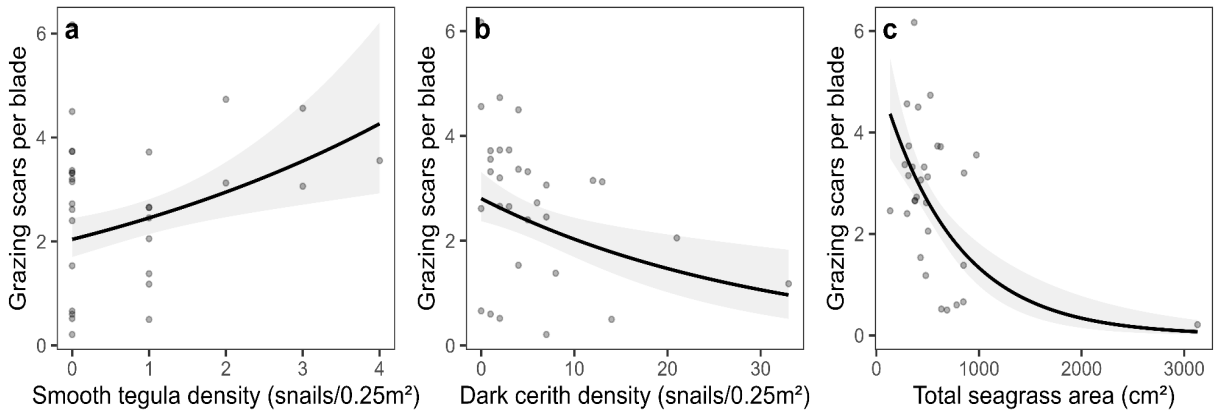


Figure 2. Partial effects of environmental predictors on seagrass blade scarring intensity. Model predictions (lines) with 95% confidence intervals (shaded ribbons) from a beta-binomial generalized linear mixed model show the relationship between average number of scars per blade and (a) smooth tegula density, (b) dark cerith density, and (c) total surface area of seagrass blades. All predictions are

shown while holding other variables at their mean values. Points represent observed data from survey plots.

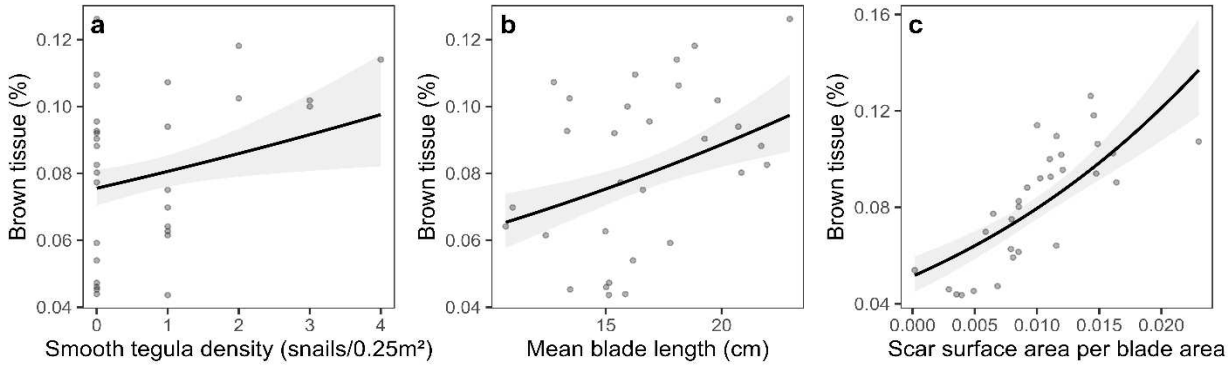


Figure 3. Partial effects of blade characteristics and grazing on brown (senescent) tissue percentage. Model predictions (lines) with 95% confidence intervals (shaded ribbons) from a generalized linear model show the relationship between brown tissue percentage and (a) smooth tegula density, (b) mean blade length, and (c) scar surface area per blade area. All predictions are shown while holding other variables at their mean values. Points represent observed data from survey plots.

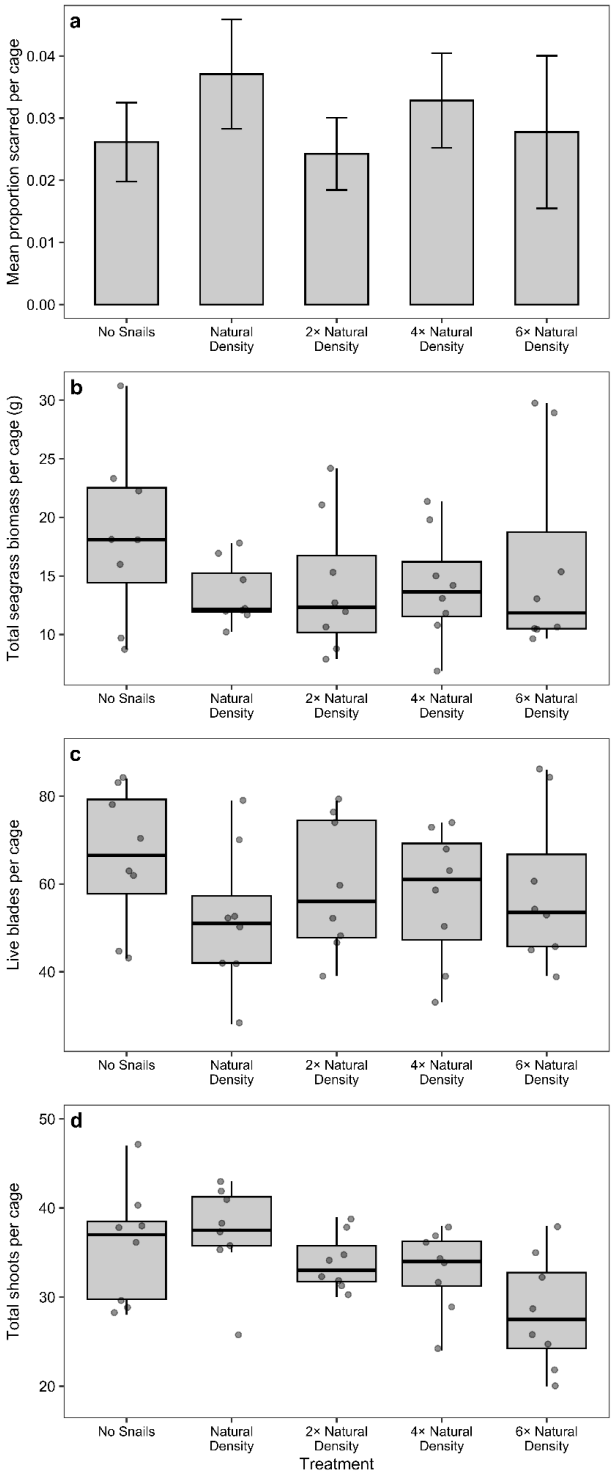


Figure 4. Seagrass morphological responses to snail density treatments (n = 8 cages per treatment). (a) Mean proportion of seagrass blade area scarred per cage (± SE). (b) Mean total seagrass biomass per cage (g, ± SE). (c) Live blade counts per cage. (d) Total shoot counts per cage. Boxes show medians and interquartile ranges; points represent individual cages. No significant treatment effects were detected for

scarring proportion, biomass, or live blade counts; shoot counts were significantly higher at natural snail density than at 6× natural density (Tukey's test, p = 0.017).

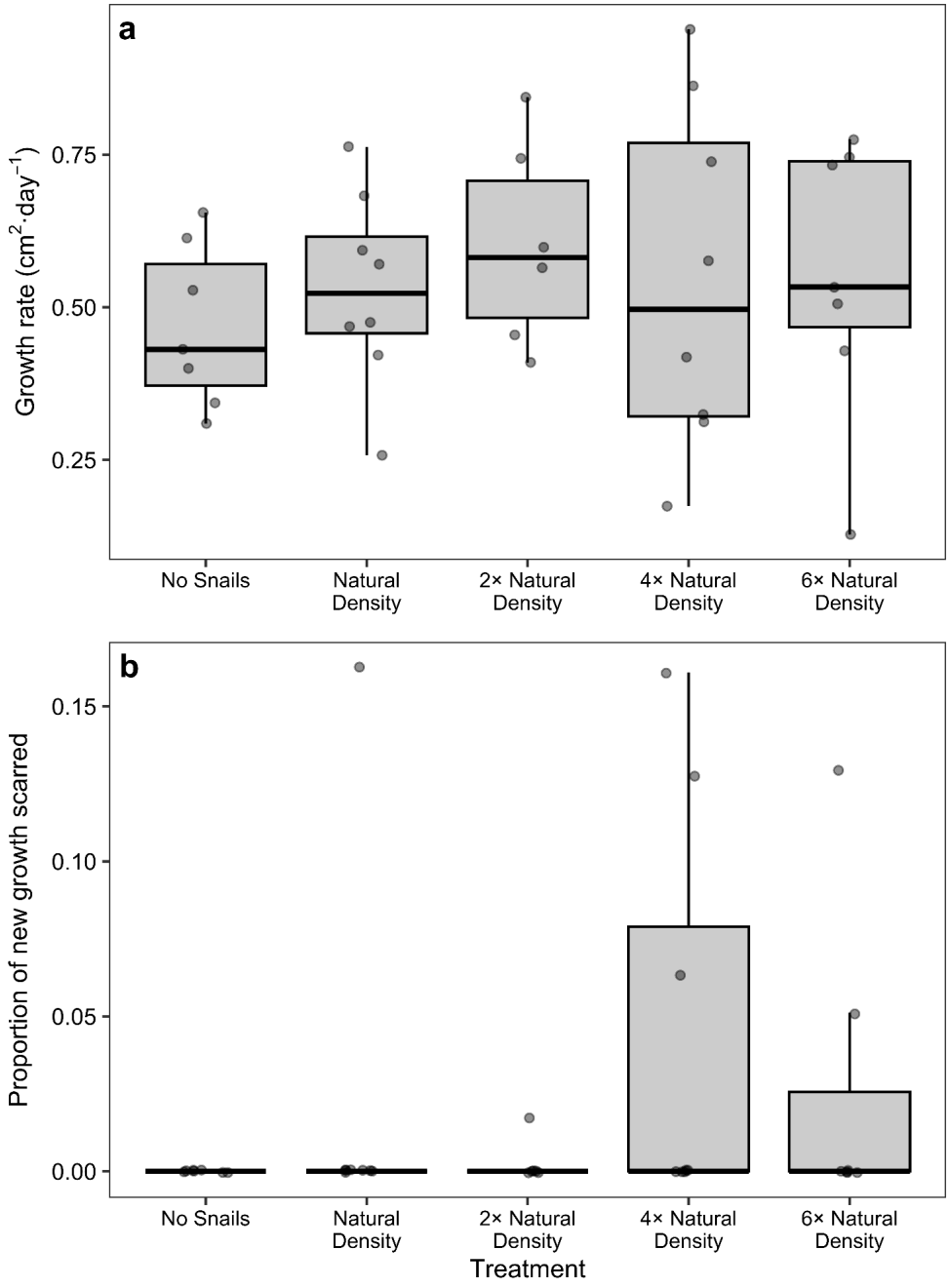
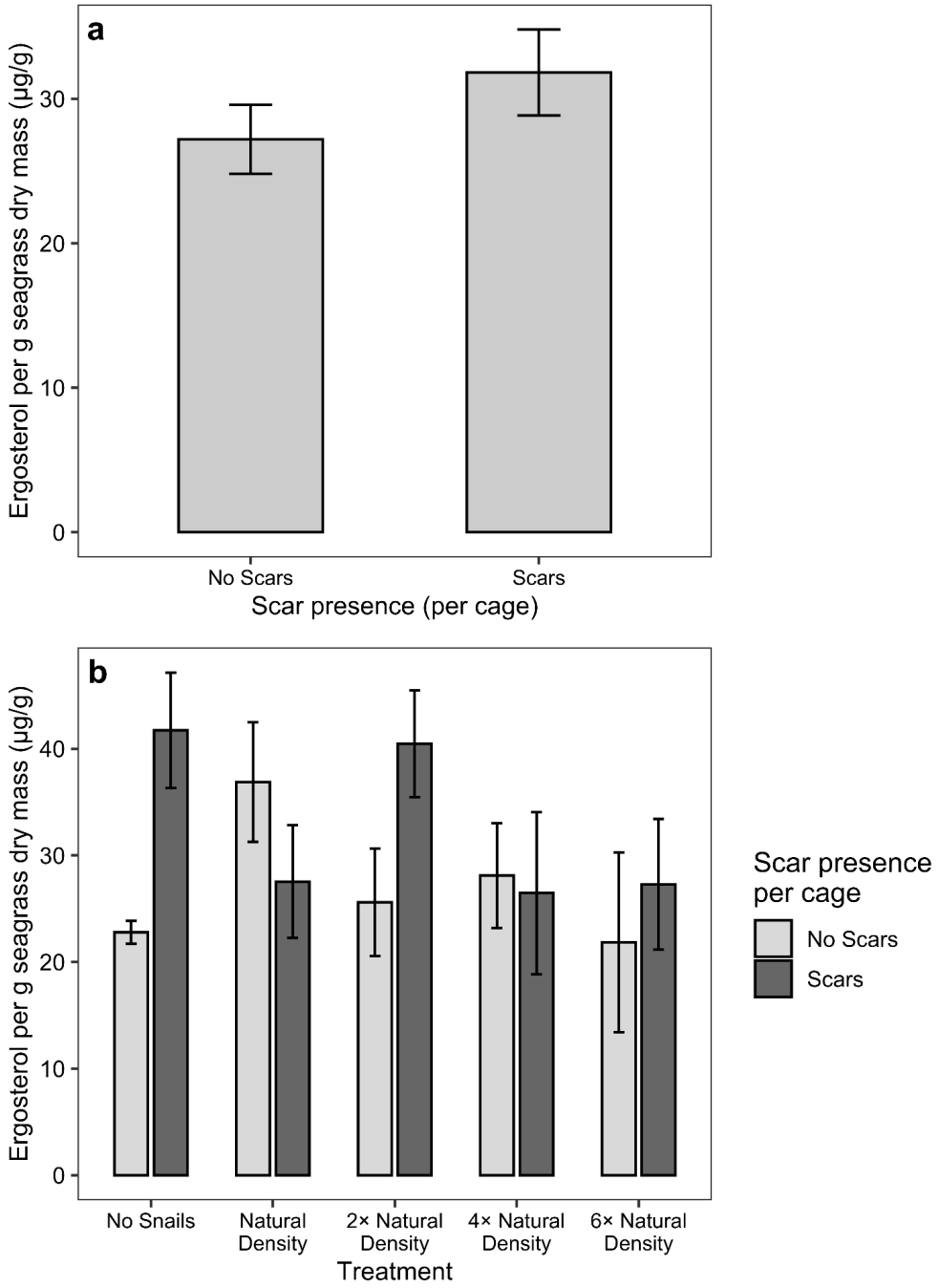


Figure 5. Seagrass productivity and scarring on new growth by snail density treatment. (a) Per-cage mean growth rate (cm²·day⁻¹), calculated as mean blade surface area divided by 8 days. (b) Proportion of new growth blade area scarred per cage (total scar surface area ÷ total blade surface area). Boxes show

309 medians and interquartile ranges; points represent individual cages. No significant treatment effects were
310 detected for either variable.

311



312

313 **Figure 6.** Fungal biomass by scar presence and snail density treatment. Fungal biomass is expressed as
314 corrected ergosterol per g seagrass dry mass (µg/g). (a) Mean ergosterol (± SE) in cages with and without

scarring, pooled across treatments. (b) Mean ergosterol (± SE) by snail density treatment, shown separately for scarred and unscarred cages. No significant effects of scar presence or snail density were detected.

Discussion

Despite visible scarring of turtlegrass blades by smooth tegula snails, our six-week experimental manipulation of snails in the field revealed no significant effects of snails on seagrass biomass, productivity, rhizome growth, or fungal infection. This null result was consistent across a wide range of snail densities (0 to 6x natural density) and multiple response variables, despite evidence from our surveys for greater occurrence of tissue scarring and browning in association with higher densities of tegula in natural settings. This suggests that turtlegrass health is resilient to tegula grazing impacts over short timescales and/or are effectively compensating for snail grazing.

This disconnect between the positive relationship in our survey of tegula density, scarring and leaf browning and our experimental results showing no effect of snails on seagrass health is well-documented across plant systems: visible tissue loss often fails to predict fitness or performance outcomes because plants can tolerate or even overcompensate for herbivory through morphological and physiological adjustments (Camargo 2020; Agrawal & Maron 2022; Evans et al. 2023). Our survey data confirmed that smooth tegula density was positively associated with scarring prevalence and increased brown tissue in blades ($p<0.001$), yet when tested experimentally, snail presence had no detectable effect on seagrass performance except for total shoot number, where natural density treatments produced more shoots than 6X density treatments ($p=0.017$). Seagrasses can compensate for leaf loss through multiple mechanisms including accelerated leaf elongation, increased shoot recruitment, and mobilization of rhizome-stored carbohydrates and nitrogen (Heck & Valentine 1995; Sanmartí et al. 2014; Rodriguez & Heck 2020). Moreover, clonal plants commonly redistribute resources from undamaged to damaged ramets via intact rhizome connections, supporting leaf and ramet production and increasing biomass under herbivory (Benot et al. 2013; Wang et al. 2017). This physiological integration can buffer local tissue loss at the genet level, allowing plants to tolerate grazing without measurable declines in whole-plant performance (Angelini et al. 2018; Liu et al. 2020). The seagrass shoot number response we observed may reflect either intraspecific competition among snails at high densities or density-dependent relief from intraspecific plant competition, as documented in other clonal systems where moderate biomass removal can reduce self-shading and stimulate compensatory growth (Valentine et al. 1997; Nolet 2004; Smith et al. 2024).

Alternatively, *Tegula fasciata* grazing may exert net neutral effects on *T. testudinum* at natural densities, where potential costs of tissue removal could be offset by indirect benefits. Grazing invertebrates can subsidize local nutrient availability through excretion and fecal deposition, potentially stimulating seagrass productivity and partially compensating for tissue loss. The observed reduction in shoot count at the highest snail density (6×) relative to the 1× treatment suggests that such compensation may have density-dependent limits, with net negative effects potentially emerging only when grazing pressure substantially exceeds ambient levels.

Meaningful impacts of tegula grazing may also require longer temporal scales to manifest than captured by our 30-day experiment. Our 30-day experimental duration was selected to encompass multiple complete leaf turnover cycles in *T. testudinum*, which produces new blades every 14–21 days in tropical conditions (Zieman 1975) and recovered to pre-cut height within the two-week standardization period preceding our experiment. However, rapid aboveground recovery may obscure the slower drawdown of belowground rhizome carbohydrate and nitrogen reserves, which can sustain leaf production under grazing pressure over weeks to months before compensatory capacity is exhausted (Heck & Valentine 1995; Rodriguez & Heck 2020). Seagrass compensatory responses are also season-dependent: grazing during high-productivity seasons more readily elicits compensation than grazing in low-productivity periods (Valentine et al. 2000; Sanmartí et al. 2014). In other marine grazing systems, significant effects on seagrass biomass and community structure often do not emerge until experiments extend well beyond our study duration. For example, simulated green turtle grazing experiments showed sustained compensatory growth over 16 months in some contexts (Moran & Bjorndal 2005; Scott et al. 2018), while multi-month dugong grazing studies documented no detectable declines in shoot density until 7 months and required 10 months to show significant reductions (Zimmerman et al. 1996). Over short timescales, seagrasses can maintain productivity by drawing on belowground rhizome reserves (Heck & Valentine 1995; Rodriguez & Heck 2020), but sustained grazing pressure can eventually deplete these carbohydrate and nitrogen pools, exhausting compensatory capacity and leading to meadow decline (Deyanova et al. 2017; Gulick et al. 2020). The temporal dynamics of compensation are particularly important for tropical seagrasses like *T. testudinum*, which exhibit rapid leaf turnover but may require multiple growing seasons for cumulative grazing effects to exceed compensatory thresholds (Garthwin et al. 2024; Smulders et al. 2024). Longer-term experiments (>6 months to 2 years) conducted across gradients of environmental stress are needed to distinguish between true short-term tolerance and delayed impacts that emerge once compensatory reserves are exhausted.

Notably, we found no evidence that snail grazing affects fungal biomass in turtlegrass, contrasting with well-documented grazer-pathogen facilitation in salt marsh systems where snail grazing wounds serve as

infection sites for pathogenic fungi (Silliman & Newell 2003; Daleo et al. 2009; Freitas et al. 2014). While scarred cages showed slightly elevated ergosterol levels compared to unscarred cages (31.8 vs 27.2 μg/g), this difference was not statistically significant ($p=0.209$), and no density-dependent patterns emerged. Interestingly, in our earlier experiment (Boyd et al. 2022), simulated invertebrate scarring did result in increased fungal biomass on turtlegrass. Despite this, grazer-pathogen facilitation has been demonstrated in other seagrass species: laboratory experiments with eelgrass (*Zostera marina*) showed that grazing scars created by isopods and snails increased wasting disease caused by *Labyrinthula zosterae*, and live pathogen cells were isolated from herbivore feces (Graham et al. 2024). However, two key factors may explain why we did not observe similar facilitation of fungus or other pathogens in our field experiment with turtlegrass. First, species-specific blade morphology may influence vulnerability to wound-mediated infection. *Thalassia testudinum* produces thick, robust blades (typically 4–12 mm wide) with substantial structural tissue, whereas *Zostera marina* has thinner, more delicate leaves (2–4 mm wide). Grazing scars of similar absolute size may represent a proportionally smaller tissue disruption and expose less vulnerable inner tissue in thick-bladed *Thalassia* compared to thin-bladed *Zostera*, potentially reducing infection risk. Second, controlled laboratory conditions used in prior studies may not reflect field dynamics, as in our study, where seagrasses have access to belowground resource reserves, more variable environmental conditions, and potentially different microbial communities that compete with or inhibit pathogens.

Beyond these seagrass-specific factors, broader evidence from terrestrial and marine plant systems suggests additional mechanisms that may have prevented wound-mediated fungal infection in our experiment. Wound characteristics strongly determine infection risk: larger, deeper wounds that expose inner tissues and remove protective barriers (as in Boyd et al. 2022) facilitate pathogen entry, whereas superficial scars may induce minimal local defense responses and heal rapidly (Gossner et al. 2021; Graham et al. 2023). Tegula grazing produces relatively small, shallow scars compared to the larger wounds created by crab burrowing or mammalian herbivores that have been shown to facilitate fungal colonization in *Spartina* marshes (Freitas et al. 2014). Wound healing rates and plant defenses determine how long wounds remain permissive to infection. Formation of suberized periderm, deposition of lignin and phenolics, and activation of oxidative enzymes can render wounds resistant to pathogens within 2–3 days in some systems (Ginzberg 2008; Daleo et al. 2009; Graham et al. 2024), and rapid wound responses in plants may close the critical infection window before pathogens establish. Environmental conditions further modulate both pathogen activity and host wound responses: temperature affects healing rates, moisture influences periderm formation, and pathogen pressure varies spatially and temporally (Daleo et al. 2009). Our experiment was conducted in a relatively low-flow, protected bay during the growing

season; conditions that may favor rapid wound healing and limit pathogen transmission compared to more stressful environments.

Our findings suggest that turtlegrass meadows may be resilient to small-scale invertebrate grazing, even at high densities, over short timescales, but this resilience may be compromised by environmental degradation under combined stressors or sustained grazing pressure over larger spatial scales. Plant tolerance to herbivory is strongly modulated by environmental conditions: temperature, drought, salinity, and nutrient loading each modify compensatory capacity, and combined stresses commonly reduce compensation and can shift interactions from neutral to destructive (Long & Porturas 2014; Valentine & Heck 2021). For example, warming reduced *Thalassia* belowground biomass by ~34% and productivity by ~74% in experimental studies, thereby reducing tolerance to grazing (Lacey 2012), while drought and elevated salinity suppressed compensatory responses in marsh grasses and interacted additively with high grazer densities to reduce biomass and recovery (Long & Porturas 2014; Smith et al. 2024). Eutrophication can increase epiphyte loads and shift competitive balance toward fast-growing opportunists, but grazing can also mitigate some eutrophication effects by removing epiphytes and stimulating nutrient export (Hughes et al. 2004; Christianen et al. 2012). Predator loss represents another critical context modifier: predator removal often increases herbivore density or alters herbivore community composition, increasing top-down pressure and shifting systems from compensatory to degradative states, with effects that can match or exceed eutrophication impacts (Silliman & Bertness 2002; Moksnes et al. 2008; Jaschinski & Sommer 2008). Future work should also examine whether predator control of tegula populations influences grazing pressure, whether grazing effects interact synergistically with warming, eutrophication, or disease outbreaks, and whether spatial refugia (areas with favorable light, temperature, or salinity) can maintain compensatory capacity and serve as restoration targets (Burnell et al. 2013; Smulders et al. 2024).

Conclusion

The six-week experimental manipulations of smooth tegula snail density revealed no significant effects on turtlegrass biomass, productivity, or fungal infection, despite visible scarring of seagrass blades. These results suggest either that *T. testudinum* possesses effective compensatory mechanisms that maintain growth under grazing pressure, or that impacts require longer timescales to manifest, as documented in other marine herbivore systems where effects emerge only after multiple growing seasons. Future studies conducted over extended periods (>6 months to 2 years) could distinguish between these alternatives and clarify whether cumulative grazing pressure eventually exceeds compensatory capacity. Furthermore, the sensitivity of grazing effects to environmental conditions in other seagrass and vegetated ecosystems

suggests that habitat degradation could compromise the resilience of seagrass to grazing detected in our study, reinforcing the need to maintain healthy and intact ecosystems. Our findings demonstrate that *T. testudinum* can maintain biomass, productivity, and tissue integrity under invertebrate grazing pressure at ecologically relevant densities, suggesting that tropical seagrass meadows may possess greater inherent resilience to small-scale consumer impacts than previously recognized, a capacity that may become increasingly important as anthropogenic stressors continue to reshape coastal ecosystems.

Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

A.D.B. conceived and designed the study, conducted fieldwork, led data collection and analysis, and wrote the manuscript. B.R.S. contributed to experimental design and provided overall project oversight. M.T. and C.S. provided logistical support, site selection, and oversight at the Smithsonian Tropical Research Institute in Panama. V.G. conducted fungal biomass analysis via ergosterol quantification. A.H.A. contributed to experimental design, manuscript feedback, and STRI coordination. A.J.M. and I.R.Y. provided field support throughout the experiment, including sample processing and data collection; I.R.Y. also contributed to drafting portions of the Methods section. D.P. and J.P.M. contributed to data analysis and manuscript preparation. All authors read and approved the final manuscript.

Data Availability

The datasets generated and analyzed during this study are available from the corresponding author on reasonable request.

Ethics Approval

No ethics approval was required as experimental work was conducted with unregulated invertebrate species (*Tegula fasciata*) in the field.

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