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Species-Specific Biomass Allocation Shapes Seagrass Biomass Carbon in an Indonesian Coastal National Park: Evidence from West Bali National Park

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Abstract

Accurate estimation of biomass-based blue carbon stocks in tropical seagrass meadows requires consideration of species-specific differences in plant size, tissue carbon concentration, and biomass allocation between above- and below-ground compartments. However, these differences remain insufficiently incorporated into assessments of mixed-species seagrass meadows in Indonesian coastal protected areas. This study evaluated the influence of species identity and biomass allocation on biomass-based carbon stocks in West Bali National Park, Indonesia. Sampling was conducted at Labuan Lalang, Teluk Terima, and Karang Sewu and included the dominant species *Enhalus acoroides*, *Thalassia hemprichii*, and *Halophila ovalis*. A total of 63 sampling units generated 126 above- and below-ground compartment observations. Measured variables included shoot density, leaf morphology, biomass, organic carbon concentration (%Corg) estimated using loss on ignition, dry matter content, and biomass-based carbon stock. Organic carbon concentrations ranged from 9.28 to 39.02%. *Enhalus acoroides* had the highest total biomass (483.98 ± 245.55 g DW m^{-2}) and total biomass-based carbon stock (154.61 ± 77.38 g C m^{-2}), whereas *H. ovalis* had the highest shoot density but the lowest carbon stock (50.39 ± 15.38 g C m^{-2}). At the meadow scale, *E. acoroides* contributed 52.8 ± 9.2% of community biomass carbon from only 16.9 ± 6.6% of total shoots, while *H. ovalis* contributed 19.1 ± 6.7% of carbon despite representing 55.7 ± 11.2% of shoot abundance. The pooled negative correlation between shoot density and carbon stock ($\rho = -0.675$) disappeared in species-specific analyses, demonstrating Simpson's paradox. *Halophila ovalis* also exhibited significantly lower below-ground %Corg than above-ground tissues, consistent with its lower dry matter content and limited development of dense below-ground storage tissues. Mean community biomass carbon stock was 2.85 ± 0.97 Mg C ha^{-1}, with no significant differences among sites. These findings demonstrate that species identity and biomass allocation are stronger determinants of biomass-based carbon storage than shoot density or site alone, supporting species-sensitive blue carbon assessments in tropical coastal protected areas.

1. INTRODUCTION

Carbon dioxide (CO_2) is one of the major greenhouse gases in the atmosphere that significantly contributes to global climate change (Lin et al., 2025). The ocean represents the largest active carbon reservoir on Earth and plays a critical role in regulating atmospheric carbon through biological and physical processes (Song & Tu, 2025; S. J. Wang et al., 2014). One of the key strategies to mitigate carbon emissions is the conservation and management of ecosystems that function as natural carbon sinks, both terrestrial and marine.

Among coastal ecosystems, seagrass meadows are recognized as highly effective blue carbon systems due to their capacity to capture, store, and retain carbon over extended periods (Kumala et al., 2024; Pergent-Martini et al., 2021; Zou et al., 2021). This capability is largely attributed to their ability to trap organic matter and stabilize it within water-saturated sediments (Kaewsrikhaw et al., 2026; Ren et al., 2024; Samper-Villarreal et al., 2016). Carbon fixed through photosynthesis is stored in both above-ground biomass (leaves) and below-ground biomass (roots and rhizomes), with a substantial proportion eventually deposited and preserved in the sediment, resulting in long-term carbon sequestration (Asir et al., 2026; Engelbrecht et al., 2026; Kurniawan et al., 2026).

Seagrass ecosystems have considerable potential for carbon storage and play an important role in mitigating climate change (Pendleton et al., 2012; Waycott et al., 2009). Despite covering only a small fraction of the ocean's surface, seagrass meadows contribute significantly to global carbon sequestration through high productivity (Gomis et al., 2025) and efficient sediment trapping (Mejjad et al., 2025). The persistence of carbon within seagrass systems is influenced not only by total biomass but also by how carbon is allocated between different plant compartments, particularly between above-ground and below-ground tissues (Singh et al., 2022).

Despite extensive research on blue carbon ecosystems (Choesin et al., 2024; Dahl et al., 2022; Thorhaug et al., 2017a; Wasserman et al., 2023), limited studies have explicitly quantified how species-specific biomass allocation influences carbon storage efficiency in tropical seagrass meadows. In particular, the partitioning of carbon between above-ground and below-ground biomass remains underexplored, especially in protected areas where ecological processes may differ from more anthropogenically impacted coastal systems. In addition, variations in species morphology and growth strategies may lead to differences in carbon storage capacity, yet these relationships are not fully understood in site-specific contexts.

In Indonesia, several studies have estimated seagrass carbon stocks across different coastal regions (Hernawan et al., 2021; Irda et al., 2024; Kumala et al., 2024; Latifah et al., 2023; Ramadhan & Kurniawan, 2026). However, most assessments have focused on site-level carbon estimates, while comparatively few have examined how species composition, plant morphology, and allocation between above- and below-ground biomass jointly shape biomass-based carbon storage within formally protected coastal areas. This gap is particularly relevant in mixed-species meadows, where differences in plant size and growth strategy may cause shoot density to poorly represent carbon storage. West Bali National Park therefore provides an important case study because it contains diverse seagrass assemblages distributed across sites with contrasting local disturbance contexts within a nationally protected coastal landscape (Amarasinghe et al., 2021; Purnomo et al., 2017).

Therefore, this study evaluates how species-specific structural traits and biomass allocation influence biomass-based seagrass carbon stocks in West Bali National Park. Specifically, the study aimed to: (1) quantify shoot density, leaf morphology, and the allocation of biomass between above- and below-ground compartments in the dominant seagrass species; (2) estimate LOI-derived tissue organic carbon concentration and biomass-based carbon stocks across species and plant compartments; and (3) assess the relationships among structural attributes, biomass allocation, tissue carbon concentration, site context, and biomass-based carbon storage. The novelty of this study lies in integrating species identity, compartment-specific biomass allocation, and tissue carbon characteristics within the context of an Indonesian coastal national park. The findings are expected to provide a species-sensitive framework for interpreting biomass carbon in tropical mixed-species meadows and offers a more ecologically robust basis for seagrass monitoring and conservation-oriented blue carbon assessment in protected coastal areas.

2. MATERIALS AND METHODS

2.1 Site Location and Sampling Design

Sampling was conducted using a stratified purposive design to represent gradients of anthropogenic pressure across three sites in West Bali National Park: Labuan Lalang (high impact), Teluk Terima (moderate impact), and Karang Sewu (low impact) (Fig. 1). Site classification followed Watiniasih *et al.*, (2021), which categorizes coastal areas based on levels of human disturbance. Labuan Lalang (LBL) is characterized by intensive marine tourism activities and frequent boat traffic. Teluk Terima (TTR) represents a moderately impacted area with occasional fishing activity and proximity to small settlements. Karang Sewu (KSW), located in a semi-enclosed environment with minimal human access and low fishing intensity, was classified as a low-impact site.

At each site, three transects were established perpendicular to the shoreline, with 1 × 1 m quadrats subdivided into 25 subquadrats of 20 × 20 cm (Fig. 2). Seven spatially separated replicate locations containing all three focal seagrass species were selected per site for destructive biomass sampling. One sample of each species was collected at each replicate location, yielding 21 sampling units per species and 63 species-level biological sampling units across the three sites. Each sampling unit was separated into paired above-ground (AG) and below-ground (BG) compartments, generating 126 compartment-level observations. Because all three species were sampled within the same replicate locations, their values were also combined to generate 21 community-level observations (seven per site). Sampling was conducted during low tide to ensure optimal visibility and accessibility of seagrass meadows. The study focused on three dominant seagrass species, namely *Enhalus acoroides*, *Thalassia hemprichii*, and *Halophila ovalis*. In situ collection was conducted using destructive sampling, where entire plants (including leaves, rhizomes, and roots) were carefully harvested by hand from selected subplots for biomass and carbon analysis.

2.2 Data collection

2.2.1 Seagrass Density

Seagrass density was determined by counting the number of shoots of each species within 1 × 1 m quadrats. The density (D_i), expressed in shoot m⁻², was calculated as the number of shoots (n_i) per unit area (A) using the following equation:

$$D_i = \sum \frac{n_i}{A}$$

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2.2.2 Seagrass Leaf Area and Leaf Area Index (LAI)

Leaf Area Index (LAI) was used to estimate leaf surface area contributing to photosynthetic capacity (Jiang et al., 2020). Higher LAI values indicate greater leaf area and potential for carbon-rich biomass production (Lebrasse et al., 2022; Wicaksono, 2015). Leaf length (cm) and maximum leaf width (cm) were measured from representative shoots of each seagrass species collected at each sampling quadrat. The estimated leaf area per shoot (cm² shoot⁻¹) was calculated as the product of leaf length and maximum leaf width

$$\varvec{E}\varvec{s}\varvec{t}\varvec{i}\varvec{m}\varvec{a}\varvec{t}\varvec{e}\varvec{d}\ \varvec{L}\varvec{e}\varvec{a}\varvec{f}\ \varvec{A}\varvec{rea}$$

LAI was subsequently calculated by multiplying the estimated leaf area per shoot by shoot density within each quadrat, thereby expressing the total one-sided leaf area per unit ground surface area (F. Short & Coles, 2001), as follows: .

$$\varvec{L}\varvec{e}\varvec{a}\varvec{f}\ \varvec{A}\varvec{r}\varvec{e}\varvec{a}\ \varvec{I}\varvec{n}\varvec{d}\varvec{e}\varvec{x}\ (\varvec{L}\varvec{a}$$

where LA is the estimated leaf area per shoot (cm² shoot⁻¹), D is shoot density (shoots m⁻²), and 10,000 is the conversion factor from cm² to m². Consequently, LAI is expressed as m² leaf area m⁻² ground area. Estimated leaf area and LAI were used to characterize species-specific canopy structure, with estimated leaf area describing leaf morphology at the individual shoot level and LAI integrating leaf size and shoot density to represent canopy development.

2.2.3 Biomass Determination and Calculation

Biomass samples were collected from 20 × 20 cm subplots within each quadrat. One representative subplot (20 × 20 cm) was randomly selected within each quadrat for biomass sampling. All seagrass material within the selected subplot was harvested, including leaves, rhizomes, and roots (Engelbrecht et al., 2026).

Collected samples were gently cleaned using a razor blade to remove epiphytes and adhering sediments without damaging plant tissues (Atmaja et al., 2021). The samples were then separated into two compartments: above-ground (AG), consisting of leaves, and below-ground (BG), consisting of roots and rhizomes (Fig. 3).

Each sample was oven-dried at 60°C for a minimum of 24 h until constant weight was achieved and subsequently weighed using an analytical balance with a precision of 0.0001 g. The dry weight of each component was recorded to determine biomass. Biomass was expressed as dry weight per unit area (g DW m⁻²) (Short *et al.*, 2016) using the following equation:

$$B = \frac{W}{A}$$

where *B* is biomass (g DW m^{-2}), *W* is dry weight (g), and *A* is the sampling area (0.04 m^2). The resulting biomass dataset comprised 63 species-level biological sampling units, each separated into paired AG and BG compartments for subsequent laboratory analyses.

2.2.4 Carbon Content and Carbon Stock Analysis

Carbon content of seagrass biomass was determined using the Loss on Ignition (LOI) method, following standardized procedures with empirical conversion refinement adapted from Fourqurean *et al.*, (2012) and Sophianto *et al.*, (2020). This approach is widely applied in blue carbon studies due to its operational efficiency and strong correlation with organic carbon content.

Oven-dried biomass samples (aboveground and belowground fractions) were first weighed to obtain dry weight (DW). Subsequently, samples were combusted in a muffle furnace at 500°C for 4 hours to remove organic matter. After cooling in a desiccator, the remaining ash weight was recorded. The percentage of organic matter (OM) was calculated using the formula as follows:

$$Loss\ on\ Ignition\ \ (LOI)\ (\%) = \frac{Dry\ weight\ \ (g) - Ash\ weight\ \ (g)}{Dry\ weight\ \ (g)}\ x\ 100$$

2.2.5 Organic Carbon Concentration

To improve accuracy in estimating organic carbon, OM values derived from LOI were converted into organic carbon content (%Corg) using empirical relationships. Following Nava-Félix *et al.*, 2025 and Zhao *et al.*, (2025), LOI-derived organic matter was first normalized, and carbon content was estimated using a conversion factor accounting for incomplete combustion and compositional variability. The final %Corg was calculated using the established regression model from the previous study by Fourqurean *et al.*, (2012):

$\%C_{org}$ = 0,40 x %*LOI* – 0,21 if LOI < 20%
$\%C_{org}$ = 0,43 x %*LOI* – 0,33 if LOI > 20%

2.2.6 Carbon Storage Estimation

Carbon stock (C) for each biomass component was calculated as:

C (g C m^{-2}) = ($\%C_{org}$ / 100) × B

where %Corg is the organic carbon content (%) and B is biomass (g DW m^{-2}). Total carbon stock was obtained by summing aboveground and belowground carbon pools. To ensure analytical reliability, all measurements were conducted in replicate, and samples were cooled in a desiccator prior to weighing to prevent moisture absorption.

2.3 Data analysis

All statistical analyses were conducted using Python with the SciPy, NumPy, and Pandas libraries. Prior to statistical analyses, biomass- and carbon-related variables were recalculated from the raw laboratory measurements to derive biomass, organic carbon concentration, and biomass-based carbon stock for each above-ground (AG) and below-ground (BG) compartment. Structural variables, including shoot density and estimated leaf area index (LAI) were also calculated.

Differences among seagrass species were evaluated using the Kruskal–Wallis H test, as several ecological variables did not satisfy the assumptions of normality and homogeneity of variance. When significant overall differences were detected, pairwise comparisons were performed using the Mann–Whitney U test, and p-values were adjusted using the Bonferroni correction to account for multiple comparisons.

Comparisons between AG and BG compartments within each species were performed using the paired Wilcoxon signed-rank test. This analysis was applied to biomass, organic carbon concentration, and biomass-based carbon stock to determine whether significant differences existed between above- and below-ground tissues.

Associations between structural variables and biomass-based carbon stock were evaluated using Spearman's rank correlation coefficient (ρ) because several variables exhibited non-normal distributions. Correlation analyses were conducted for pooled data (all species combined) between shoot density, estimated leaf area, estimated leaf area index (LAI), total biomass, below-ground biomass fraction, and total carbon stock. Additional species-specific Spearman correlation analyses were performed to examine the relationship between total biomass and total carbon stock within each seagrass species.

To complement the non-parametric correlation analyses, simple linear regression was performed separately for each species to describe the relationship between total biomass (independent variable) and total carbon stock (dependent variable). The goodness-of-fit was evaluated using the coefficient of determination (R^2), and statistical significance was assessed from the regression p-value.

All statistical tests were conducted using a significance level of α = 0.05. Descriptive statistics are presented as mean ± standard deviation (SD). Biomass-based carbon stock estimates reported in this study represent living seagrass biomass only and do not include sediment organic carbon, sediment bulk density, carbon burial rates, or ecosystem-scale carbon storage.

3. RESULTS

3.1 Species-Specific Structural Attributes

Structural characteristics differed significantly among the three seagrass species but were generally consistent across the three study sites (Fig. 4A–C; Table S1). Across all sites, *Halophila ovalis* exhibited the highest shoot density (166.10 ± 56.34 shoots m^{-2}), followed by *Thalassia hemprichii* (79.43 ± 29.86 shoots m^{-2}), whereas *Enhalus acoroides* had the lowest shoot density (49.57 ± 22.06 shoots m^{-2}). Shoot density differed significantly among species (Kruskal–Wallis, H = 43.01, p < 0.001), whereas no significant differences were detected among sites (H = 1.09, p = 0.580) (Table S2). Each species was represented by 21 species-level sampling units distributed across the three study sites.

In contrast to shoot density, estimated leaf area and leaf area index (LAI) increased with plant size. *Enhalus acoroides* exhibited the highest estimated leaf area (27.00 ± 11.69 cm^2 $shoot^{-1}$), followed by *T. hemprichii* (3.87 ± 2.30 cm^2 $shoot^{-1}$) and *H. ovalis* (0.76 ± 0.28 cm^2 $shoot^{-1}$). A similar pattern was observed for LAI, with *E. acoroides* showing the highest value (0.1395 ± 0.0891), followed by *T. hemprichii* (0.0289 ± 0.0143) and *H. ovalis* (0.0130 ± 0.0066). Both estimated leaf area (Kruskal–Wallis, H = 54.75, p < 0.001) and LAI (H = 42.12, p < 0.001) differed significantly among species but not among sites (Table S2).

The three sampling sites were characterized by distinct substrate types, with muddy sediment at Labuan Lalang (LBL), sandy sediment at Teluk Terima (TTR), and mixed mud–sand sediment at Karang Sewu (KSW). Because substrate type was inherently associated with site identity, it was not included as an independent explanatory factor in the statistical analyses. The observed differences in structural attributes among species were further reflected in their biomass allocation patterns, as presented in the following section.

3.2 Species-Specific Biomass Allocation

Species differed markedly in biomass production and biomass allocation between above- and below-ground compartments (Fig. 5). *Enhalus acoroides* exhibited the highest total biomass (483.98 ± 245.55 g DW m^{-2}), followed by *Thalassia hemprichii* (270.60 ± 125.26 g DW m^{-2}) and *Halophila ovalis* (189.62 ± 52.07 g DW m^{-2}). Total biomass differed significantly among species (Kruskal–Wallis, H = 28.28, p < 0.001), whereas no significant differences were detected among study sites (H = 0.98, p = 0.614) (Table S2). Pairwise Mann–Whitney U tests with Bonferroni correction indicated that total biomass of *E. acoroides* was significantly greater than that of both *T. hemprichii* and *H. ovalis*, whereas no significant difference was detected between *T. hemprichii* and *H. ovalis* (Table S3).

Species also differed in the proportion of biomass allocated below ground (Figure S1A; Tables S3 and S14). *Enhalus acoroides* allocated the largest fraction of total biomass to below-ground tissues (60.33 ± 5.58%), followed by *T. hemprichii* (57.28 ± 7.50%), whereas *H. ovalis* exhibited a nearly equal distribution between above- and below-ground biomass, with 49.01 ± 8.50% of total biomass occurring below ground. Within-species comparisons showed that below-ground biomass was significantly greater than above-ground biomass in *E. acoroides* and *T. hemprichii* (p < 0.001), whereas no significant difference was observed in *H. ovalis* (p = 0.892) (Figure S1; Table S4).

Across study sites, mean total biomass was lowest at Labuan Lalang (277.59 ± 144.95 g DW m^{-2}), intermediate at Teluk Terima (318.72 ± 236.51 g DW m^{-2}), and highest at Karang Sewu (347.88 ± 218.37 g DW m^{-2}).

3.3 Species-specific organic carbon concentration

LOI-derived organic carbon concentration (%Corg) across all seagrass biomass samples ranged from 9.28 to 39.02%, with an overall mean of 29.76 ± 4.67% (Fig. 6; Table S5). The distributions of LOI values and the corresponding converted %Corg estimates are presented in Figure S3. Organic carbon concentration differed significantly among species (Kruskal–Wallis, H = 31.11, p < 0.001), but not between above- and below-ground compartments when all samples were pooled (Wilcoxon signed-rank test, W = 979, p = 0.843, n = 63 paired observations) or among study sites (Kruskal–Wallis, H = 0.14, p = 0.930) (Tables S2, S4, and S5).

Compartment-specific patterns in %Corg differed among species. *Enhalus acoroides* had a higher mean %Corg in below-ground tissues (33.58 ± 3.08%) than in above-ground tissues (30.72 ± 2.84%). *Thalassia hemprichii* exhibited similar %Corg values in the two compartments, whereas *Halophila ovalis* had a lower mean below-ground %Corg (24.80 ± 5.83%) than above-ground %Corg (28.70 ± 3.41%). Within-species paired comparisons showed that below-ground %Corg was significantly higher than above-ground %Corg in *E. acoroides* (Wilcoxon signed-rank test, W = 22, p < 0.001), did not differ significantly between compartments in *T. hemprichii* (W = 113, p = 0.946), and was significantly lower than above-ground %Corg in *H. ovalis* (W = 27, p = 0.001) (Tables S4 and S5).

Dry matter content (DMC) also differed between compartments in a species-specific manner (Tables S6 and S7; Figure S4). Below-ground DMC was significantly higher than above-ground DMC in *E. acoroides* (0.190 ± 0.030 versus 0.118 ± 0.040 g DW g^{-1} WW; W = 0, p < 0.001) and *T. hemprichii* (0.145 ± 0.033 versus 0.097 ± 0.028 g DW g^{-1} WW; W = 14, p < 0.001). In contrast, DMC did not differ significantly between below- and above-ground tissues of *H. ovalis* (0.138 ± 0.065 versus 0.123 ± 0.041 g DW g^{-1} WW; W = 81, p = 0.243).

Across all samples, DMC was positively correlated with %Corg (Spearman's ρ = 0.364, p < 0.001; Table S7). Significant positive correlations were also detected separately for *E. acoroides* (ρ = 0.408, p = 0.007) and *T. hemprichii* (ρ = 0.394, p = 0.010), whereas no significant relationship was observed for *H. ovalis* (ρ = 0.127, p = 0.424). Site-specific distributions of tissue %Corg are presented in Figure S5. A sensitivity analysis demonstrated that the lower below-ground %Corg observed in *Halophila ovalis* remained consistent across all exclusion criteria and remained significant after excluding samples with ash contents exceeding 50% (*n* = 17, Wilcoxon signed-rank test, *W* = 27, *p* = 0.017; Table S15). Ash content also differed among species. In *E. acoroides*, below-ground tissues contained significantly lower ash than above-ground tissues (− 6.65 percentage points; *W* = 22, *p* < 0.001), whereas no significant compartmental difference was detected in *T. hemprichii* (+ 0.18 percentage points; *W* = 112.5, *p* = 0.917). In contrast, *H. ovalis* exhibited significantly higher ash content in below-ground tissues (+ 9.06 percentage points; *W* = 27, *p* = 0.001). Below-ground ash content of *H. ovalis* did not differ significantly among study sites (Kruskal–Wallis, *H* = 2.10, *p* = 0.350) (Table S16).

3.4 Carbon stock of seagrass meadows

Biomass-based carbon stocks differed significantly among species (Fig. 7). *Enhalus acoroides* had the highest total biomass-based carbon stock (154.61 ± 77.38 g C m^{-2}), followed by *Thalassia hemprichii* (79.57 ± 31.74 g C m^{-2}) and *Halophila ovalis* (50.39 ± 15.38 g C m^{-2}). Total biomass-based carbon stock differed significantly among species (Kruskal–Wallis, H = 36.98, p < 0.001). Pairwise Mann–Whitney U tests with Bonferroni correction identified significant differences among all species pairs, including between *T. hemprichii* and *H. ovalis* (adjusted p = 0.005), although these two species did not differ significantly in total biomass.

Below-ground tissues accounted for 62.40 ± 5.73% of the total biomass-based carbon stock in *E. acoroides*, 57.22 ± 7.90% in *T. hemprichii*, and 44.75 ± 10.32% in *H. ovalis*. Within-species comparisons showed that below-ground carbon stocks were significantly higher than above-ground carbon stocks in *E. acoroides* and *T. hemprichii* (both p < 0.001). No significant difference between compartments was detected in *H. ovalis* (p = 0.060).

Mean total biomass-based carbon stocks did not differ significantly among study sites (Kruskal–Wallis, H = 0.67, p = 0.714) (Figure S6; Table S2).

3.5 Relationships Between Structural Attributes and Biomass-Based Carbon Stocks

Relationships between structural attributes and total biomass-based carbon stock varied among the measured variables (Fig. 8; Figures S7–S8; Tables S8–S10). Across all species, total biomass exhibited the strongest positive correlation with total biomass-based carbon stock (Spearman's ρ = 0.960, p < 0.001). Estimated leaf area (ρ = 0.729, p < 0.001), leaf area index (LAI) (ρ = 0.610, p < 0.001), and below-ground biomass fraction (ρ = 0.473, p < 0.001) were also positively correlated with biomass-based carbon stock (Table S8).

In contrast, shoot density showed a significant negative correlation with biomass-based carbon stock when all species were analyzed together (ρ = −0.675, p < 0.001). However, this relationship was not observed within individual species. Species-specific analyses yielded non-significant correlations for *Enhalus acoroides* (ρ = −0.291, p = 0.201), *Thalassia hemprichii* (ρ = −0.147, p = 0.524), and *Halophila ovalis* (ρ = 0.158, p = 0.493), with the correlation becoming positive in *H. ovalis*. This contrast between pooled and species-specific analyses is consistent with Simpson's paradox, in which the pooled trend reflects species composition rather than consistent within-species relationships (Figure S8; Table S9).

Figure 8 illustrates the relationship between total biomass and total biomass-based carbon stock for the three dominant seagrass species. Regression statistics for each species are presented in Table S10, whereas site-specific biomass-based carbon stocks are provided in Figure S6.

3.6 Community Biomass-Based Carbon Stocks and Species Contributions

The proportional contribution of each species differed markedly between shoot abundance and biomass-based carbon stock (Fig. 9; Table S12). Mean community biomass-based carbon stock was 284.57 ± 97.18 g C m^{-2}, equivalent to 2.85 ± 0.97 Mg C ha^{-1}, and did not differ significantly among study sites (Kruskal–Wallis, *H* = 0.72, *p* = 0.698). *Enhalus acoroides* contributed 52.8 ± 9.2% of the community biomass-based carbon stock while accounting for only 16.9 ± 6.6% of total shoot abundance, resulting in a carbon-to-shoot contribution ratio of 3.13. In contrast, *Halophila ovalis* contributed only 19.1 ± 6.7% of community biomass-based carbon stock despite representing 55.7 ± 11.2% of total shoots, corresponding to a ratio of 0.34. *Thalassia hemprichii* exhibited nearly proportional contributions to biomass-based carbon stock and shoot abundance, contributing 28.0 ± 5.9% of community carbon while representing 27.5 ± 10.0% of total shoots (ratio = 1.02).

Species-specific allometric characteristics were consistent with these differences in community contribution (Table S13). Root-to-shoot ratios differed significantly among species (Kruskal–Wallis, H = 17.88, p < 0.001), decreasing from 1.588 ± 0.522 in *E. acoroides* to 1.407 ± 0.400 in *T. hemprichii* and 1.013 ± 0.331 in *H. ovalis*. Biomass-based carbon stored per shoot varied by more than an order of magnitude, ranging from 3.806 ± 2.154 g C $shoot^{-1}$ in *E. acoroides* to 0.330 ± 0.128 g C $shoot^{-1}$ in *H. ovalis*. Among all variables examined, carbon stock per shoot exhibited the strongest species effect (Kruskal–Wallis, H = 48.13, p < 0.001), exceeding that observed for total biomass (Table S14).

4. DISCUSSION

4.1 Functional differences among species drive biomass-based carbon storage

The present study demonstrates that species identity and biomass allocation are the primary determinants of biomass-based carbon storage in tropical mixed-species seagrass meadows. Although *Halophila ovalis* exhibited the highest shoot density, *Enhalus acoroides* stored more than three times as much biomass-based carbon because of its substantially larger biomass and greater allocation to below-ground tissues. These findings indicate that biomass-based carbon storage is governed more by species-specific functional traits than by shoot abundance alone. At the community scale, this contrast became particularly evident: *E. acoroides* contributed more than half of the total biomass-based carbon stock while representing less than one-fifth of total shoot abundance, whereas *H. ovalis* accounted for more than half of all shoots but contributed less than one-fifth of community biomass-based carbon. Consequently, monitoring programs that rely primarily on shoot density may substantially underestimate the carbon contribution of large-bodied species while overestimating that of small-bodied species.

This pattern reflects a fundamental ecological trade-off between plant size and abundance. Small-bodied seagrass species generally maximize space occupancy by producing numerous shoots with relatively low biomass per individual, whereas large-bodied species invest in fewer but substantially larger shoots supported by extensive rhizome and root systems. Such differences in biomass allocation strongly influence biomass-based carbon storage because below-ground tissues constitute the principal long-term biomass reservoir in many tropical seagrasses (Githaiga et al., 2017; Mishra et al., 2023). In the present study, *E. acoroides* allocated over 60% of its biomass below ground, whereas *H. ovalis* exhibited a nearly equal distribution between above- and

below-ground compartments. These contrasting allocation strategies explain why shoot abundance alone provides only a limited representation of biomass-based carbon storage.

The observed size–abundance relationship agrees with previous studies of tropical seagrass ecosystems. High shoot densities have frequently been associated with small-bodied species rather than high biomass or carbon storage (Vieira et al., 2018). Conversely, large species such as *E. acoroides* and *Thalassia hemprichii* typically accumulate greater below-ground biomass because of thicker rhizomes, larger root systems, and greater structural investment (Kilminster et al., 2015). Similar species-dependent differences in biomass production and carbon storage have also been documented in Indonesian seagrass meadows (Angrelina et al., 2022; Rahman et al., 2023), suggesting that functional differences among species consistently outweigh simple abundance metrics across tropical regions.

Our findings further extend those reported by previous studies, who likewise identified *E. acoroides* as contributing disproportionately more biomass-based carbon than *H. ovalis* in Indonesian seagrass ecosystems (Cereno et al., 2000; Maulita et al., 2023; Stankovic et al., 2017; Tupan & Wawo, 2020). However, the biomass-based carbon stocks recorded in the present study were considerably higher than those previously reported. Such differences are expected because biomass-based carbon estimates are influenced by local environmental conditions (Gorman & Leal, 2026; Vadillo Gonzalez et al., 2026), meadow composition (Asir et al., 2026), sampling design, compartment definitions (Samper-Villarreal et al., 2016), and analytical methodology. Hence, comparisons among studies should emphasize ecological patterns rather than absolute carbon values.

Collectively, these findings demonstrate that biomass-based blue carbon assessments should explicitly incorporate species composition and biomass allocation rather than assuming equivalent carbon contributions among shoots or species (Ramadhan et al., 2026; Wasserman et al., 2023). The evidence from West Bali National Park indicates that species identity exerts a stronger influence on biomass-based carbon storage than shoot density alone, highlighting the importance of species-sensitive approaches for improving blue carbon inventories and ecological assessments of tropical mixed-species seagrass meadows.

4.2 Species composition determines how shoot density reflects biomass-based carbon storage

The negative relationship observed between pooled shoot density and biomass-based carbon stock should not be interpreted as evidence that denser seagrass meadows inherently store less carbon. Rather, the relationship reflects differences in species composition among sampling units rather than a direct biological effect of shoot density. Meadows dominated by *Halophila ovalis* contained numerous small shoots with relatively low biomass, whereas those dominated by *Enhalus acoroides* supported fewer but substantially larger individuals with much greater biomass-based carbon storage. These findings indicate that structural attributes associated with plant size, including leaf area, canopy development, and below-ground biomass allocation, provide more informative indicators of biomass-based carbon storage than shoot density alone. Consequently, shoot abundance should be interpreted as a measure of population structure rather than as a direct proxy for biomass-based carbon storage.

An important contribution of this study is the demonstration that ecological relationships depend strongly on the scale at which they are analyzed. When observations from all species were pooled, shoot density showed a moderately strong negative correlation with biomass-based carbon stock ($\rho = -0.675$). However, this relationship disappeared after accounting for species identity and even reversed direction in *H. ovalis*. This pattern represents a classic example of Simpson's paradox, in which an apparent trend at the pooled level results from differences among groups rather than from processes operating within the groups themselves. In ecological studies, such scale-dependent relationships are well recognized because interspecific variation frequently dominates community-level analyses, whereas intraspecific relationships reflect different biological mechanisms. Our findings therefore demonstrate that species composition can fundamentally alter the apparent relationship between seagrass structural attributes and biomass-based carbon storage if species identity is ignored.

These results have important implications for tropical seagrass monitoring and blue carbon assessment. Standard monitoring protocols generally prioritize species occurrence, percentage cover, and shoot density because these variables are rapid, inexpensive, and standardized for long-term ecological monitoring (Short & Coles, 2001). While these indicators remain indispensable for evaluating seagrass distribution, condition, and temporal change, they may not adequately represent biomass-based carbon storage in mixed-species meadows where species differ markedly in morphology and biomass allocation. In the present study, leaf area, leaf area index (LAI), total biomass, and below-ground biomass allocation consistently showed stronger associations with biomass-based carbon stock than shoot density alone. Integrating these structural attributes alongside species composition would therefore provide a more biologically meaningful framework for estimating biomass-based blue carbon in tropical seagrass ecosystems (Krause et al., 2025; Wang et al., 2026; Wang & Sha, 2026).

The broader methodological implications of these findings are consistent with previous regional and global studies of seagrass blue carbon. Fourqurean et al., (2012) demonstrated that global variation in living seagrass biomass carbon is strongly influenced by species composition, with large-bodied species contributing disproportionately to biomass carbon storage. Likewise, Collier et al. (2021) showed that below-ground biomass in tropical seagrasses reflects interactions among plant morphology, environmental conditions, and community composition (Kumala et al., 2024; Vonk et al., 2015). Our study extends these findings by demonstrating that species composition not only influences the magnitude of biomass-based carbon storage but can also modify the apparent direction of statistical relationships between structural attributes and carbon storage. This distinction highlights the importance of interpreting biomass-based blue carbon estimates within an explicit species-specific framework, particularly in tropical mixed-species seagrass meadows where morphological diversity is exceptionally high (Ambo-Rappe et al., 2013; De los Santos et al., 2016).

These findings align with the broader understanding that seagrass carbon storage is governed by a coupled biological–sediment system, where plant structure influences both carbon input (Samper-Villarreal et al., 2016) and retention (Atmaja et al., 2025). Previous studies have highlighted that below-

ground biomass plays a critical role in maintaining sediment carbon stocks by promoting organic matter accumulation and reducing carbon loss through physical disturbance (Meng et al., 2021; Tsegay & Meng, 2021). Overall, the results emphasize that carbon storage in seagrass ecosystems cannot be adequately assessed by above-ground biomass alone. Instead, below-ground biomass represents a key pathway for long-term carbon sequestration, and its contribution must be explicitly considered in blue carbon evaluations.

4.3 Structural investment underlies species differences in tissue carbon concentration

Tissue organic carbon concentration varied among species and biomass compartments, indicating that carbon content cannot be assumed to be uniform across tropical seagrass tissues. *Enhalus acoroides* contained more carbon in below-ground than above-ground tissues, *Thalassia hemprichii* showed little compartmental difference, and *Halophila ovalis* exhibited the opposite pattern. These differences were nevertheless smaller than the interspecific variation in biomass, suggesting that biomass quantity and allocation exerted a stronger influence on area-based carbon stock than tissue carbon concentration alone.

The lower below-ground carbon concentration of *H. ovalis* may reflect its contrasting tissue construction strategy. As a small, rapidly spreading species, *H. ovalis* develops relatively thin roots and rhizomes with limited structural investment (Roberts, 1993; Wu et al., 2026), whereas larger and more persistent species such as *E. acoroides* allocate more material to dense below-ground tissues (Syed et al., 2019). This interpretation is supported by the dry matter content (DMC) patterns: below-ground tissues were denser than above-ground tissues in the two larger species, and DMC was positively related to carbon concentration in those species but not in *H. ovalis*. These results suggest that tissue carbon concentration is partly linked to structural investment, although the strength of this relationship appears species-dependent.

The values observed in West Bali National Park were broadly consistent with Indonesian and global reports (Table 1). Rahmawati et al. (2019) documented comparable species-level patterns across Indonesia, including lower carbon concentrations in *H. ovalis* than in *E. acoroides* and *T. hemprichii*. Higher values reported by Wawo et al. (2014) should be interpreted cautiously because they were obtained using the Walkley–Black method rather than LOI-based conversion. Likewise, values reported from the northern Mexican Caribbean were lower on average but remained within a comparable range for living seagrass tissues (Nava-Félix et al., 2025). Together, these comparisons indicate that reported tissue carbon concentrations reflect both biological variation and analytical methodology.

Table 1
Organic carbon concentrations reported for seagrass tissues from West Bali National Park and selected Indonesian and global studies.

Study/location	Species	Above-ground Corg (%)	Below-ground Corg (%)	Overall value or range	Methodological notes and comparability
Present study, West Bali National Park, Indonesia	*Enhalus acoroides*	30.72 ± 2.84	33.58 ± 3.08	Species- and compartment-specific values	LOI-derived Corg estimates; directly comparable among samples within the present study
Present study, West Bali National Park, Indonesia	*Thalassia hemprichii*	30.42 ± 4.21	30.34 ± 3.37	Species- and compartment-specific values	LOI-derived Corg estimates; directly comparable among samples within the present study
Present study, West Bali National Park, Indonesia	*Halophila ovalis*	28.70 ± 3.41	24.80 ± 5.83	Species- and compartment-specific values	LOI-derived Corg estimates; directly comparable among samples within the present study
(Rahmawati et al., 2019), national Indonesian compilation	Mixed Indonesian seagrass species	32.6 ± 0.6	33.5 ± 0.6	Overall mean: 33.3 ± 0.5	Data derived using LOI and CN analysis; national reference values not consistently separated by species and compartment
(Rahmawati et al., 2019), national Indonesian compilation	*Enhalus acoroides*	Not separated	Not separated	35% DW; range 29–44%	Species-level reference for Indonesia
(Rahmawati et al., 2019), national Indonesian compilation	*Thalassia hemprichii*	Not separated	Not separated	33% DW; range 19–52%	Species-level reference for Indonesia
(Rahmawati et al., 2019), national Indonesian compilation	*Halophila ovalis*	Not separated	Not separated	27% DW; range 18–38%	Species-level reference for Indonesia
(Wawo et al., 2014) Kotania Bay, West Seram, Indonesia	*Enhalus acoroides*	41.86	47.03	Species- and compartment-specific values	Walkley–Black method; not directly equivalent to LOI-derived estimates
(Wawo et al., 2014) Kotania Bay, West Seram, Indonesia	*Thalassia hemprichii*	40.33	42.72	Species- and compartment-specific values	Walkley–Black method; not directly equivalent to LOI-derived estimates
(Wawo et al., 2014) Kotania Bay, West Seram, Indonesia	*Halophila ovalis*	37.86	38.12	Species- and compartment-specific values	Walkley–Black method; not directly equivalent to LOI-derived estimates
(Nava-Félix et al., 2025), northern Mexican Caribbean	*Thalassia testudinum* and *Syringodium filiforme*	Not reported separately	Not reported separately	18.2–27.4%; mean 22.7%	Global tissue-Corg reference; different species, region, and potentially analytical context

A methodological limitation is that LOI estimates organic matter rather than elemental carbon directly. Conversion from LOI to Corg may therefore introduce uncertainty related to species, tissue type, ash content, and the selected conversion equation (Sparkes et al., 2026). The sensitivity analysis supports the robustness of the main compartment patterns, but direct CN or CHN analysis would be required to validate absolute carbon concentrations (Kuveke et al., 2022) and the proposed relationship between DMC and tissue carbon content.

Overall, tissue carbon concentration in tropical seagrasses is both species-specific and method-sensitive. However, biomass-based carbon stock per unit area depends on the combined effects of tissue carbon concentration, total biomass, and biomass allocation. In the present study, variation in biomass and below-ground allocation was more consequential than variation in tissue carbon concentration, reinforcing the need to interpret Corg values within the broader context of species identity and plant structure.

4.4 Implications for biomass-based carbon monitoring in Indonesian Coastal National Parks

Site category did not significantly affect total biomass or total biomass-based carbon stock, indicating that species identity and biomass allocation explained more variation than the broad site classifications used in this study. Because pressure category and substrate type were intrinsically associated with each site, they should be interpreted as contextual attributes rather than independently replicated causal factors. Site-level patterns in biomass and carbon stock are presented in Figure S2, while community-level values are summarized in Table S11.

This finding has direct implications for monitoring within coastal protected areas. National parks are commonly subdivided into spatial management zones based on ecological sensitivity and desired resource conditions, with accessibility and the type or intensity of visitor use also informing their delineation (Geneletti & van Duren, 2008; Grêt-Regamey et al., 2017). Although these categories remain useful for conservation planning, they may not fully explain variation in biomass-based carbon storage within mixed-species seagrass meadows. Monitoring programs should therefore record species composition and above- and below-ground biomass allocation alongside conventional indicators of site condition. Without species-level information, dense meadows dominated by small-bodied species may be overestimated as high-carbon habitats, whereas less dense meadows dominated by larger species may be undervalued (Belshe et al., 2018; Gomis et al., 2025). At sites exposed to boat traffic or anchoring, maintaining rhizome-root integrity and sediment stability is particularly important because mechanical disturbance can create scars, promote sediment erosion, and reduce associated carbon stocks (Sejati et al., 2020; Serrano et al., 2016; Thorhaug et al., 2017b).

The estimated community-level biomass carbon stock of 2.85 ± 0.97 Mg C ha^{-1} was approximately 1.13 times the global mean for living seagrass biomass reported by Fourqurean et al., (2012), placing the meadows of West Bali National Park slightly above the global average. This estimate provides a useful baseline for future monitoring. Species contributions were also consistent across the three site categories, with *E. acoroides* accounting for approximately 51–55% of community biomass carbon at each site. This consistency suggests that species identity and community size structure may be more reliable predictors of biomass-based carbon storage than broad pressure categories used for spatial zoning. Site-level carbon contributions are presented in Figure S9, while species-, site-, and compartment-specific values are provided in Figure S6.

The management implication is not to prioritize *E. acoroides* at the expense of other species. Seagrass meadows, including mixed-species assemblages, provide multiple ecosystem functions, including habitat and nursery provision, sediment stabilization, nutrient cycling, and support for associated biodiversity (Atmaja et al., 2021, 2024; Duffy, 2006; Mtwana Nordlund et al., 2016). Rather, the findings demonstrate that biomass-carbon monitoring in Indonesian coastal national parks should be species-sensitive. Protected meadows should be evaluated not only through occurrence, cover, or shoot density, but also through species composition and the distribution of biomass between above- and below-ground compartments. The species-sensitive assessment framework proposed in Figure S10 provides a conceptual basis for incorporating these attributes into future monitoring.

Overall, West Bali National Park illustrates how species composition and biomass allocation can strongly influence estimates of seagrass biomass carbon in tropical coastal protected areas. By positioning the park as a case study, this study demonstrates that species-based approaches can improve the interpretation of biomass carbon stocks in mixed-species meadows commonly found across Indonesian coastal conservation areas.

4.5 Limitations and future study

Several limitations should be considered when interpreting the present findings. First, this study quantified carbon stored only in living seagrass biomass and did not include sediment organic carbon, sediment depth, dry bulk density, carbon burial rates, or meadow area. Consequently, the estimates represent biomass-based carbon storage rather than total ecosystem blue carbon or long-term carbon sequestration. Second, tissue organic carbon concentration was estimated using LOI-derived conversion equations rather than direct elemental analysis. Although LOI provides a practical and resource-efficient approach for studies with limited analytical capacity, the resulting tissue Corg concentrations and biomass carbon stocks should be regarded as provisional operational estimates until validated against direct carbon measurements using a CN/CHN elemental analyzer (Serrano et al., 2023; Yeemin et al., 2024). In addition, pressure category and substrate type were site-specific attributes and therefore could not be statistically separated from site identity. Finally, the study represents a single temporal snapshot and does not capture seasonal, interannual, or disturbance-driven variation in seagrass morphology, canopy development, biomass allocation, and carbon storage (Lebrasse et al., 2022; Macreadie et al., 2015).

Future research should integrate biomass measurements with sediment carbon inventories, including sediment coring, dry bulk density, sediment depth, direct elemental carbon analysis, meadow-area mapping, and long-term monitoring to quantify ecosystem-scale blue carbon more comprehensively. Experimental designs incorporating independent replication of disturbance gradients and substrate types would further improve understanding of environmental controls on biomass allocation and carbon storage. Such integration would facilitate the transition from species-sensitive biomass assessment to spatially explicit blue carbon monitoring capable of supporting long-term conservation and management of Indonesia's coastal national parks.

5. CONCLUSION

This study demonstrated that biomass-based carbon storage in the mixed-species seagrass meadows of West Bali National Park is strongly species-dependent, with species identity and biomass allocation exerting a greater influence than shoot density or broad site categories. Larger species, particularly *Enhalus acoroides*, contributed disproportionately to biomass carbon storage through greater biomass production and below-ground allocation, whereas smaller species such as *Halophila ovalis* exhibited high shoot density but substantially lower biomass carbon storage. Differences in tissue organic carbon concentration among species further reflected contrasting patterns of structural investment, reinforcing that biomass quantity and allocation contribute more to biomass-based carbon storage than tissue carbon concentration alone. These findings demonstrate that species composition should be explicitly incorporated into biomass carbon assessments, as shoot density alone is not a reliable proxy for carbon storage in tropical mixed-species seagrass meadows.

By using West Bali National Park as an Indonesian coastal national park case study, this study provides empirical evidence that species-sensitive biomass assessment can improve interpretation of seagrass carbon stocks in tropical protected areas. Nevertheless, the findings represent carbon stored in living seagrass biomass rather than total ecosystem blue carbon because sediment carbon pools, sediment properties, meadow extent, burial processes, and temporal carbon accumulation were not evaluated. Future research should integrate species-specific biomass measurements with sediment carbon inventories, spatial mapping, and long-term monitoring to develop comprehensive ecosystem-scale blue carbon assessments that better support conservation planning and climate change mitigation in Indonesia's coastal national parks.

DECLARATIONS

Declarations OF GENERATIVE AI

During the preparation of this work the author(s) used ChatGPT in order to improve the grammatical quality of the manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

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Figures

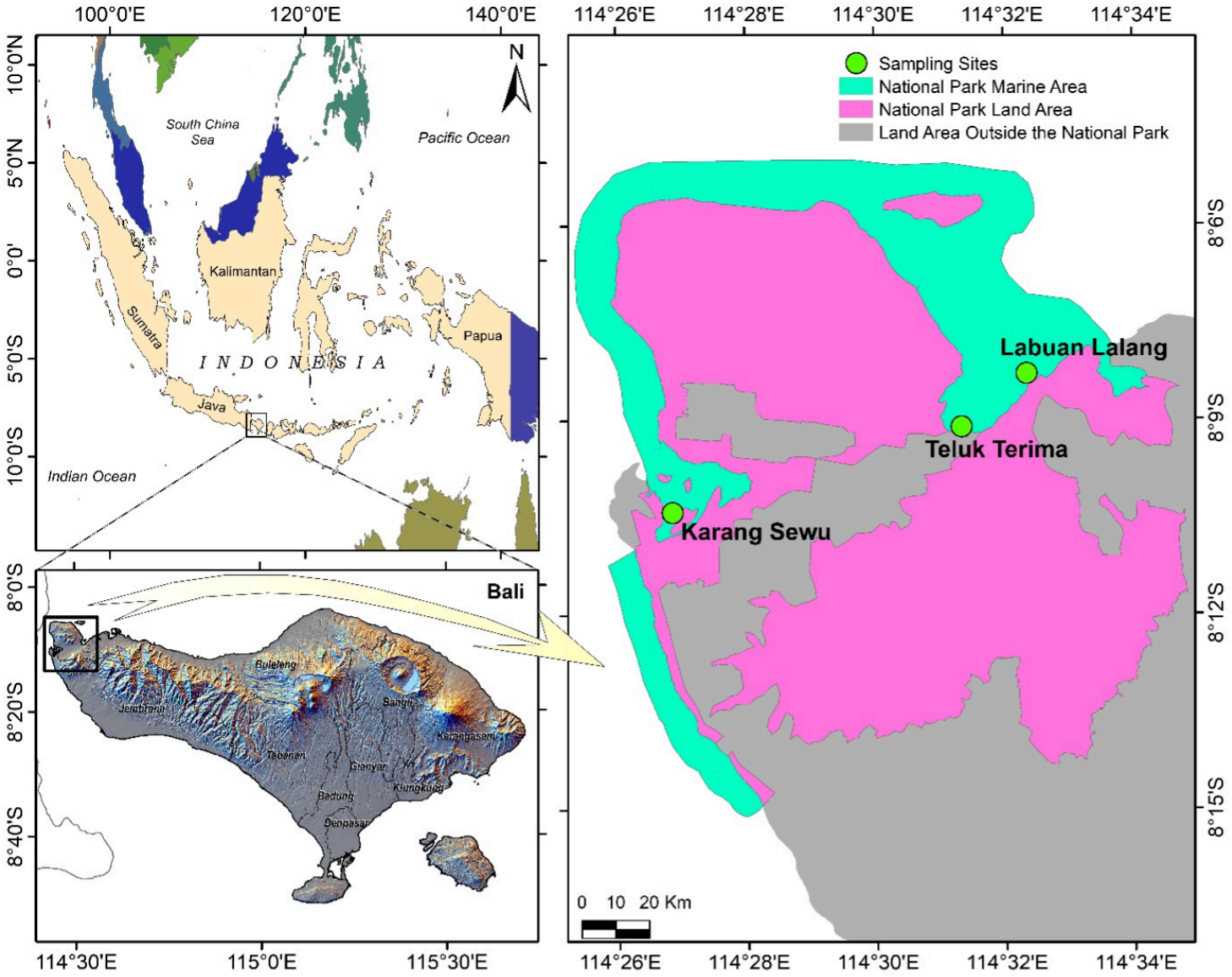


Figure 1

Geographic location of seagrass sampling stations across West Bali National Park, Bali, Indonesia

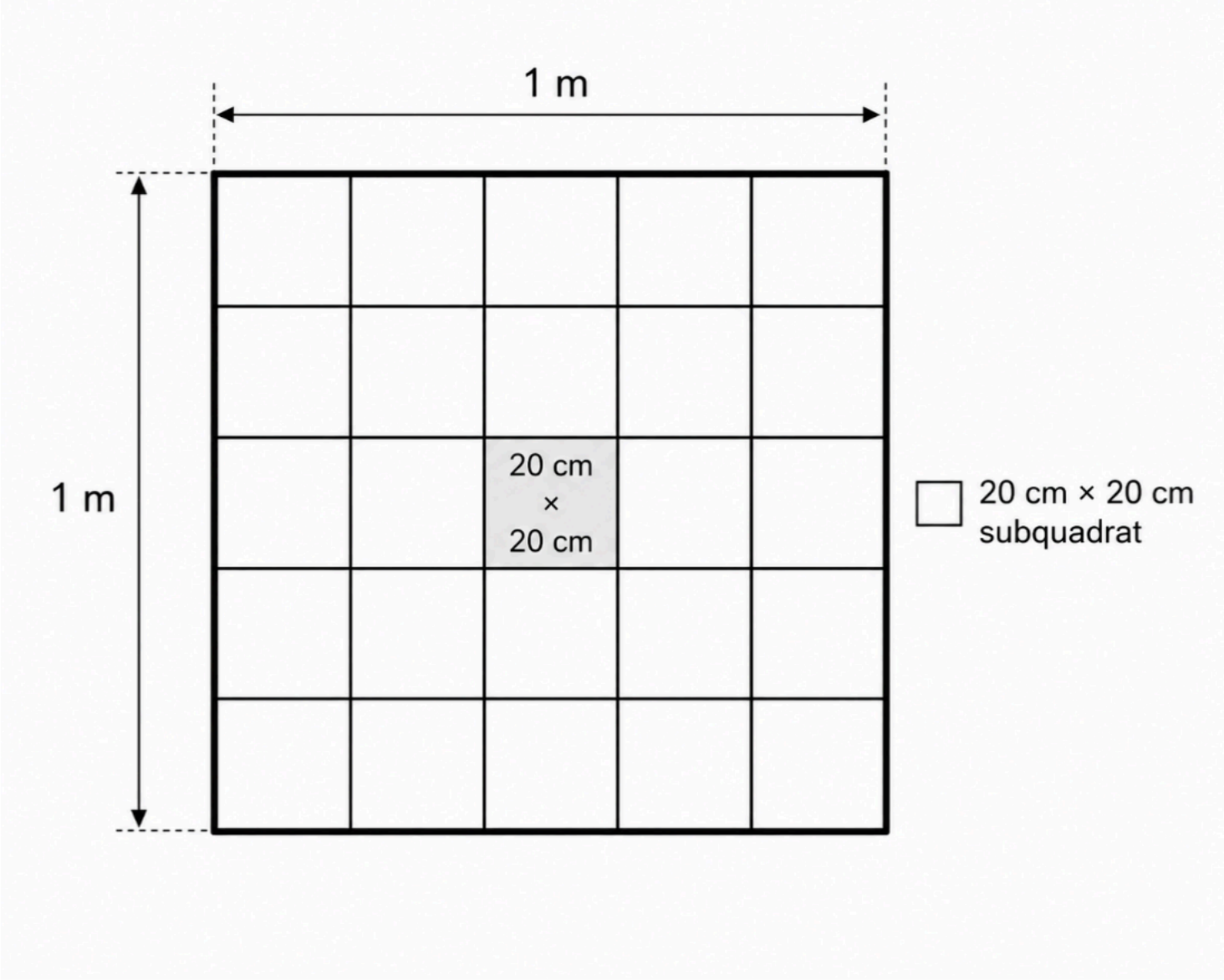


Figure 2

Schematic representation of the 1 × 1 m quadrat subdivided into 25 subquadrats of 20 × 20 cm each.

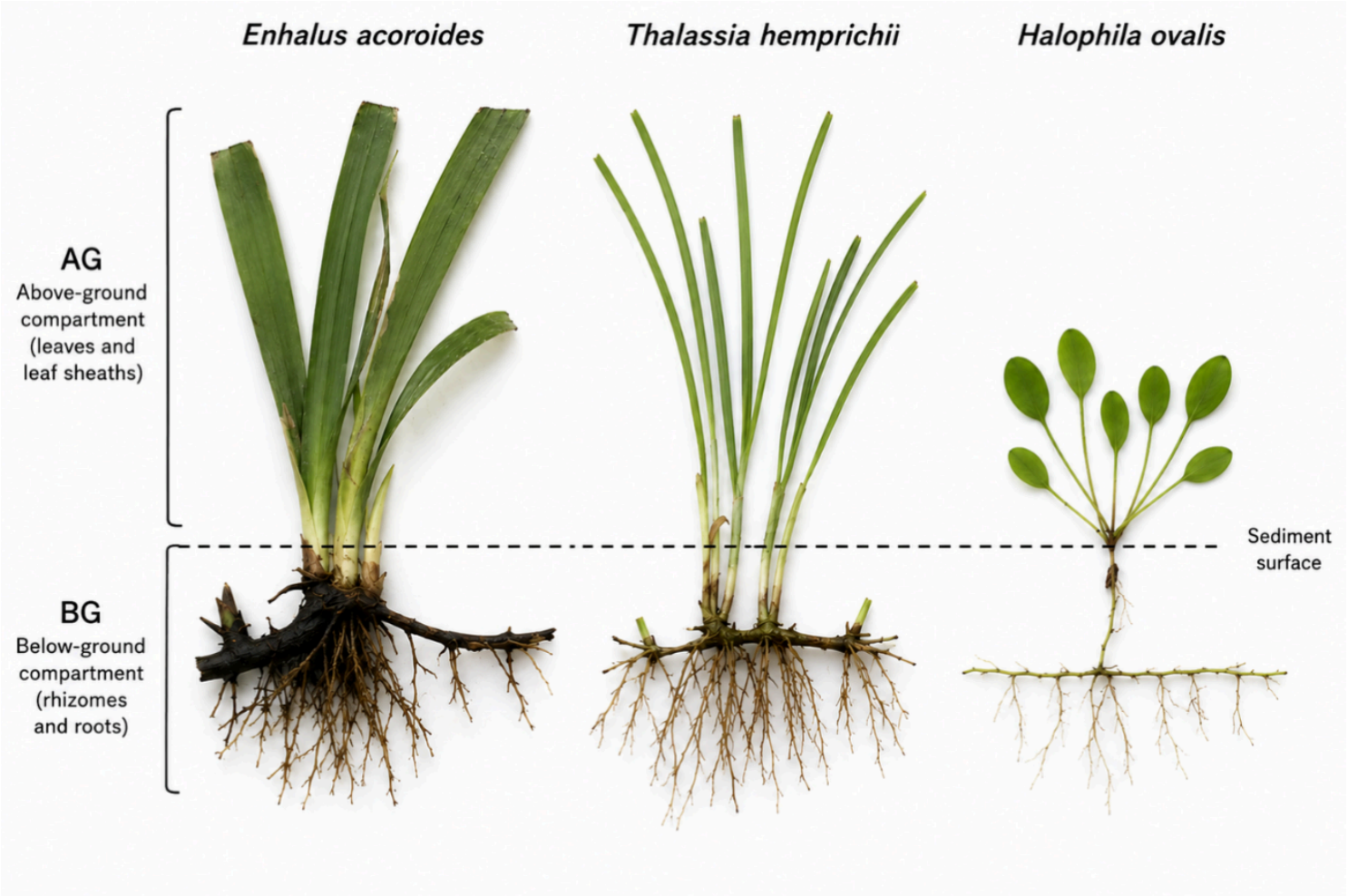


Figure 3

Schematic representation of above-ground and below-ground biomass compartments in the three dominant seagrass species examined in this study.

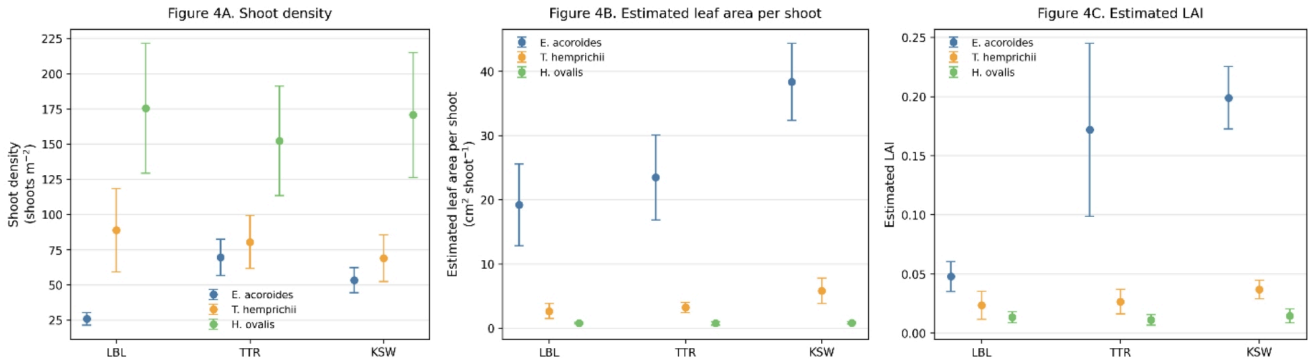


Figure 4

Species-specific structural attributes of seagrass at the three sampling sites in West Bali National Park. (A) Shoot density (shoots m^{-2}), (B) estimated leaf area per shoot (cm^2 $shoot^{-1}$), and (C) estimated leaf area index (LAI). Error bars represent 95% confidence intervals.

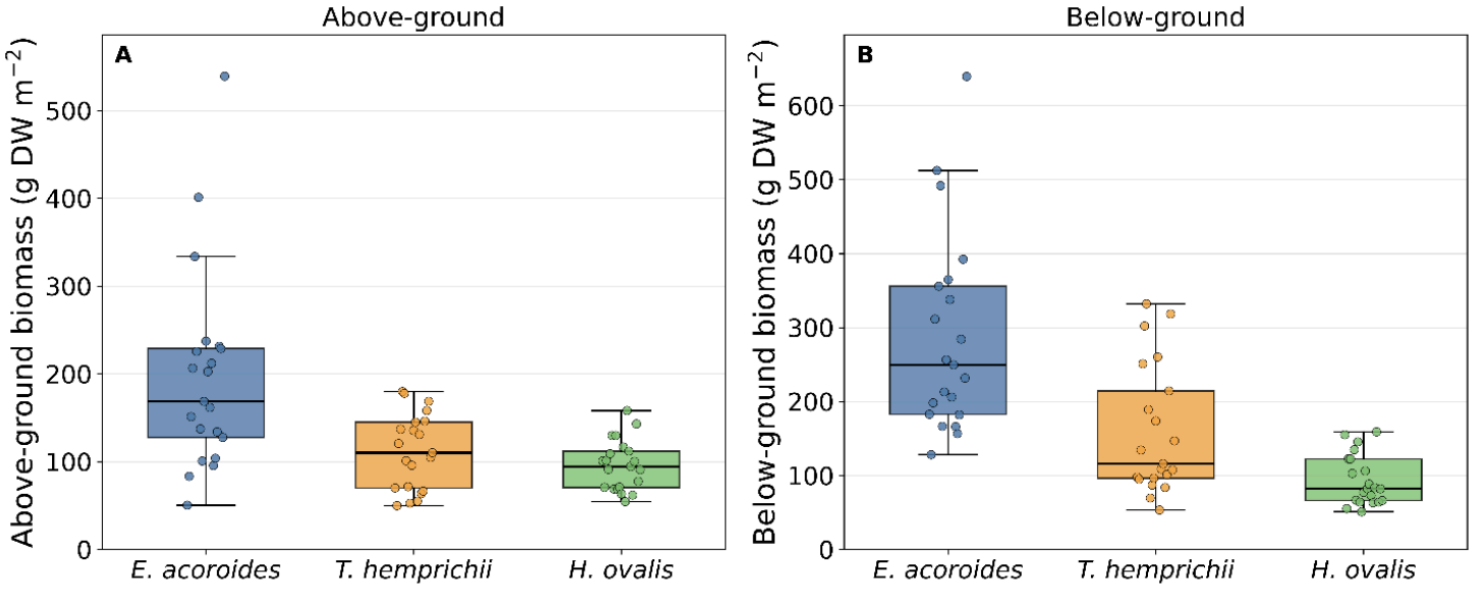


Figure 5

Above-ground (AG) and below-ground (BG) biomass of *Enhalus acoroides, Thalassia hemprichii,*and *Halophila ovalis* across the three study sites. Biomass was calculated from dry weight per 0.04 m² subplot and expressed as g DW m⁻².

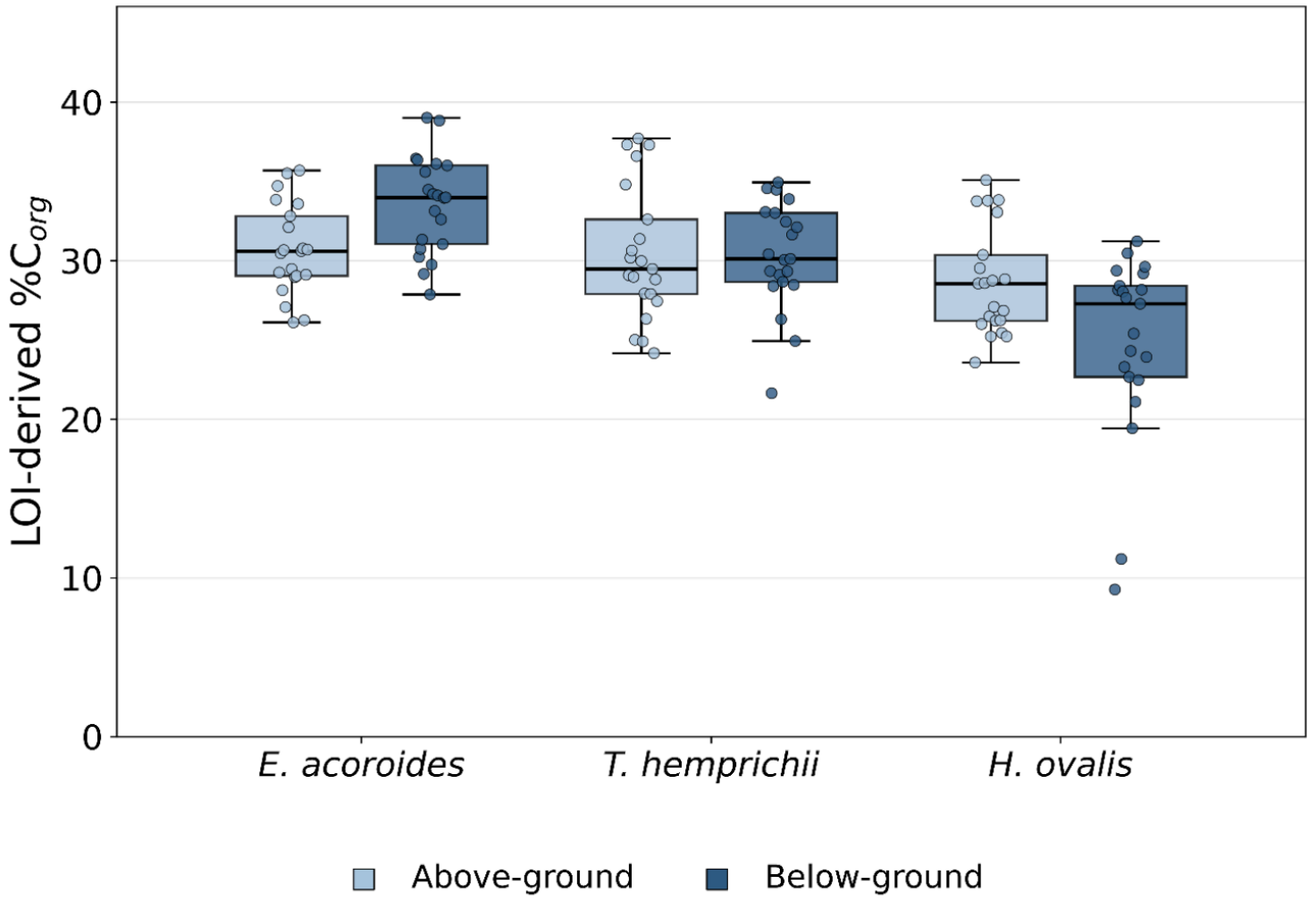


Figure 6

LOI-derived organic carbon concentrations (%Corg) in the above- and below-ground tissues of the three dominant seagrass species.

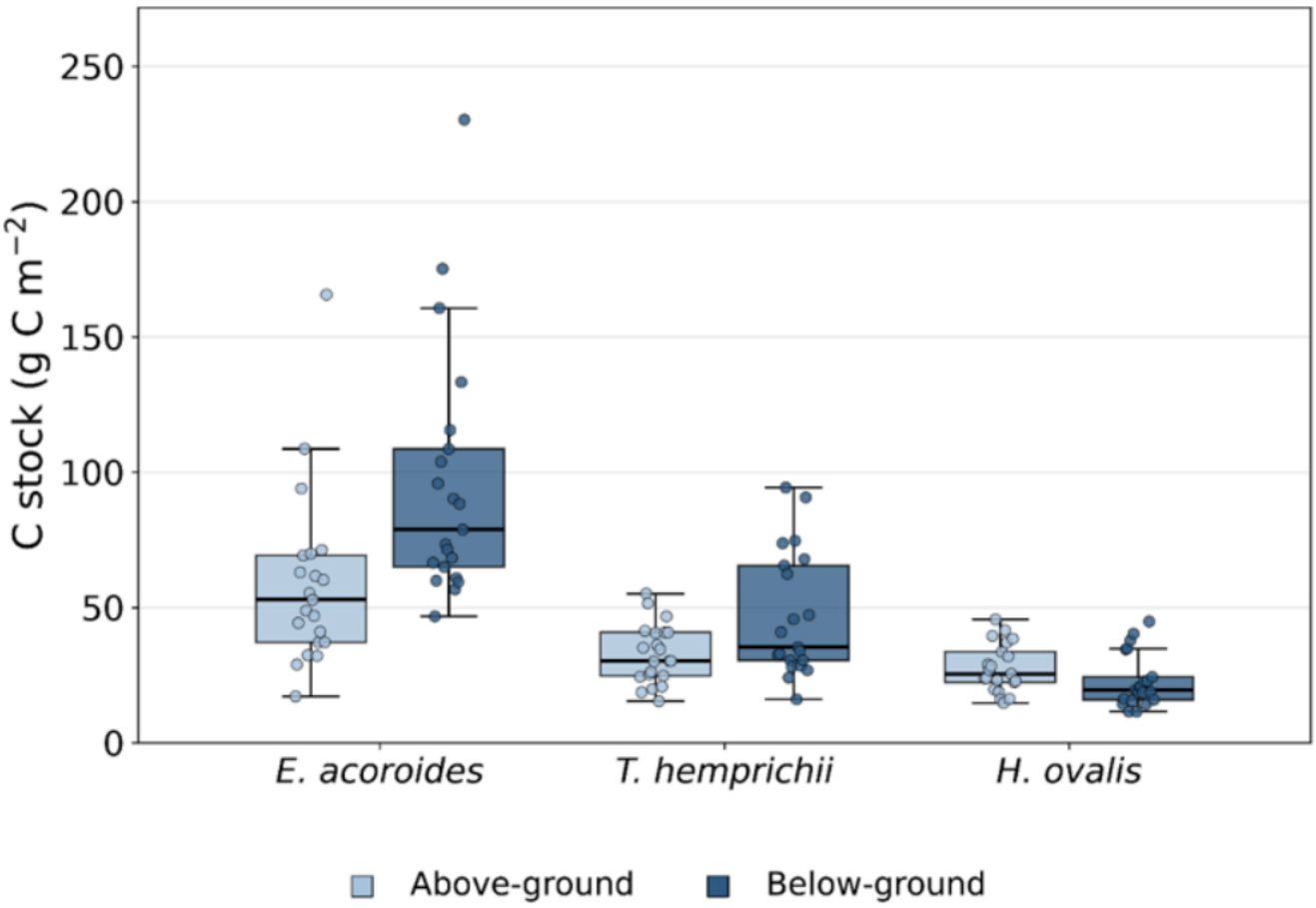


Figure 7

Above- and below-ground biomass-based carbon stocks of the three dominant seagrass species. Values represent carbon stored in living plant biomass only and exclude sediment carbon stocks.

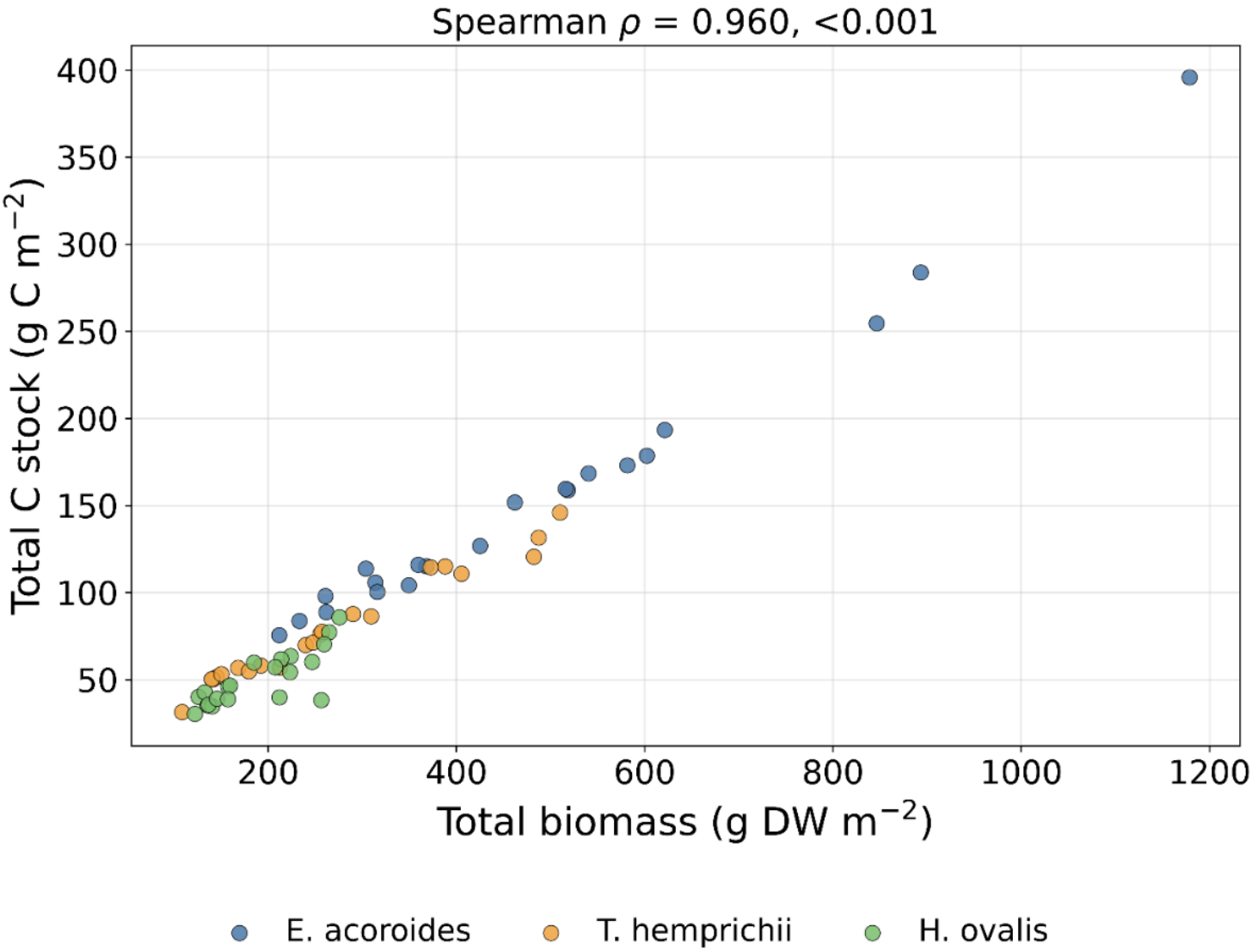


Figure 8

Relationship between total biomass and total biomass-based carbon stock for the three dominant seagrass species. Points are distinguished by species. Complete Spearman correlation coefficients are presented in Table S8.

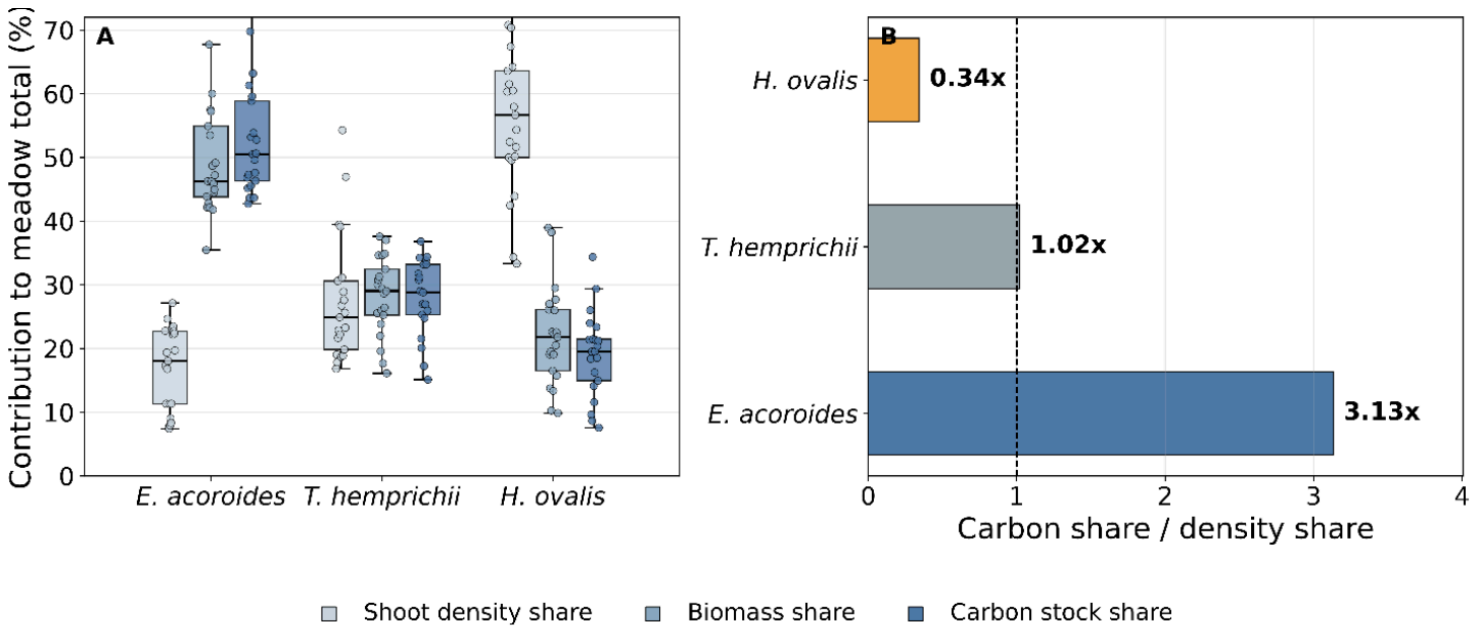


Figure 9

Mismatch between proportional shoot abundance, biomass, and biomass-based carbon stock of the three dominant seagrass species. (A) Species contributions to community shoot abundance, biomass, and biomass-based carbon stock (mean ± SD, *n* = 21 transect lines). (B) Ratio of proportional biomass-based carbon stock to proportional shoot abundance. The dashed line indicates equal proportional contributions of carbon stock and shoot abundance.

Supplementary Files

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