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Contrasting Growth Responses of Invasive and Native Alternanthera to Micro- and Macroplastics Across Aquatic and Terrestrial Conditions

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Abstract

Global plastic pollution and biological invasions are two defining drivers of the Anthropocene, yet how they interact to reshape plant communities across diverse ecosystems remains poorly understood. Here, we experimentally tested whether microplastics act as habitat-dependent ecological filters that differentially alter the growth performance of the globally invasive *Alternanthera philoxeroides* (Mart.) Griseb. and its native congener *A. sessilis* (L.) R. Br. ex DC. Using a fully crossed factorial design, we exposed both species to three polymer types (PE, Nylon/PA6, Biodegradable plastic bags (PBAT and PLA) and two particle sizes (micro- vs. macro-) under aquatic and terrestrial conditions. By integrating absolute and relative effect sizes, we uncovered a striking habitat-switch in growth performance patterns. Statistical analyses revealed a significant three-way Treatment × Habitat × Species interaction on total biomass ($p < 0.001$), demonstrating a striking habitat-dependent shift in performance. In aquatic environments, specific plastic treatments (e.g., macro-PE and micro-Bio) significantly increased the total biomass of the invader *A. philoxeroides* ($p < 0.05$), exhibiting positive relative effect sizes, whereas the native *A. sessilis* showed a significant reduction in aboveground biomass under nylon exposure. Conversely, under terrestrial conditions, neither species showed a significant change in total biomass relative to its control, so relative responses were described as trends. Notably, macro-sized plastics generally inhibited the invader's growth (relative effect sizes < 0), whereas the native species maintained neutral or slightly positive responses. Specifically, *A. philoxeroides* showed no clear overall response, whereas *A. sessilis* tended to increase under macro-Bio and macro-PE and to decrease under micro-PE. Overall, this study demonstrates that the effects of microplastics are not uniform but highly context-dependent, potentially accelerating aquatic invasions while imposing constraints in terrestrial systems. These findings highlight the urgent need to incorporate habitat heterogeneity and pollutant characteristics into ecological risk assessments and biosecurity management.

Keywords: microplastics; biological invasion; habitat dependency; *Alternanthera philoxeroides*; plant growth response; ecological modulators

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1. Introduction

We are living in what some have called the Plastic Age [1]. Global plastic production has surged over the past few decades, causing widespread environmental accumulation, most notably as microplastics (MPs), particles smaller than 5 mm. These contaminants pervade nearly every ecosystem, from deep-sea sediments to agricultural soils [2–6]. The increasing presence of microplastics in both aquatic and terrestrial environments poses significant ecological risks [3,5]. While the microplastic impacts on animal physiology and lower trophic levels are well documented [6–8], their effects on plants remain poorly understood, despite the foundational role plants play in ecosystem functioning and primary productivity [9–11].

Plants are directly exposed to microplastics in their growth environment, whether in soil, water, or sediment. In terrestrial systems, microplastics primarily alter soil structure (changing bulk density, water retention, and aggregation), thereby indirectly affecting root development and nutrient availability [9,10,12]. These changes often impair seedling establishment and growth and can even suppress reproductive output [13–16]. Conversely, in aquatic habitats, microplastics influence plants primarily through physical and chemical pathways: suspended particles reduce light availability for photosynthesis, cause physical damage to tissues, and may interact with biofilms to deliver adsorbed pollutants [17–21]. This dichotomy implies that terrestrial plants likely experience chronic stress from altered soil structure, whereas aquatic plants face acute physiological disruption, suggesting the microplastic effects are strongly habitat-dependent.

Crucially, these habitat-specific stressors do not affect all plants equally; rather, they often disproportionately favor invasive species over their native counterparts [22,23]. In terrestrial ecosystems, microplastics alter soil physicochemical properties and microbial communities, which can inadvertently benefit invasive plants [12]. Due to their higher phenotypic plasticity and rapid resource-acquisition traits, invasive species are often better equipped to exploit the modified soil microenvironments or even utilize plastic additives, thereby outcompeting native plants [22,24]. For instance, microplastics have been shown to significantly enhance the biomass and competitive dominance of terrestrial invaders, particularly under fluctuating environmental conditions [22,23,25]. Conversely, in aquatic habitats, the physical smothering and chemical toxicity induced by microplastics impose severe constraints on photosynthesis and gas exchange. Native aquatic plants, particularly sensitive submerged macrophytes, often suffer significant growth inhibition under such stress. In contrast, invasive aquatic species, characterized by robust clonal integration and stress-tolerance mechanisms, frequently exhibit greater resilience, allowing them to maintain growth and even expand their dominance in microplastic-polluted waters [26]. Consequently, microplastic pollution may act as a novel anthropogenic disturbance that exacerbates biological invasions across both terrestrial and aquatic environments by shifting the performance balance in favor of invaders with high phenotypic plasticity [22,23].

To disentangle how these habitat-specific stressors interact with species traits, comparative studies of closely related invasive and native species are essential. The amphibious plant genus *Alternanthera* offers an ideal model system. The invasive *A. philoxeroides* (Mart.) Griseb. (alligator weed) is globally notorious for its rapid clonal spread and high phenotypic plasticity across both aquatic and terrestrial settings [27,28]. In contrast, its congener *A. sessilis* (L.) R. Br. ex DC. (sessile joyweed) is a native species in Asian wetlands, occupying similar riparian zones but typically exhibiting lower performance dominance [29,30]. Since invasive species often possess superior resource-acquisition and stress-tolerance traits [23,31], they may respond more favorably to, or be more resilient to, anthropogenic disturbances such as microplastic pollution compared to their native counterparts.

However, most relevant studies have examined either aquatic or terrestrial systems in isolation, and few have compared congeneric invasive and native species across both habitat types under standardized conditions. This leaves unclear whether species-specific growth responses to microplastics are consistent across habitats or habitat-dependent. To address this gap, we compare congeneric invasive and native species in terms of their species-specific growth responses to multiple plastic types across aquatic and terrestrial conditions. The congeneric pairing reduces phylogenetic confounding, and the parallel two-habitat design allows us to test the habitat dependence of these responses. In this study, we experimentally exposed *A. philoxeroides* and *A. sessilis* to varying microplastic types and sizes under both aquatic and terrestrial conditions. This full-factorial design allows us to determine whether the renowned plasticity of invasive species provides a potential competitive advantage under microplastic stress. Specifically, we address the following hypotheses: (1) The effects of microplastics on plant growth are strongly habitat-dependent; (2) the invasive *A. philoxeroides* will demonstrate higher phenotypic plasticity and stress tolerance than the native *A. sessilis*, resulting in less growth inhibition (or even compensatory growth) under microplastic exposure; (3) smaller microplastic particles exert stronger negative effects than larger particles, but this size effect will be species- and habitat-dependent, with the native species being more susceptible to smaller particles while the invasive species may buffer or reverse these negative effects.

2. Results

2.1. Biomass Accumulation and Allocation Patterns (Raw Data)

2.1.1. Aboveground Biomass

Microplastic exposure significantly altered aboveground biomass, driven by significant main effects of treatment and species (both $p < 0.001$). Furthermore, these effects were strongly modulated by habitat, as evidenced by significant two-way interactions for habitat × species ($p < 0.001$) and treatment × habitat ($p = 0.005$), as well as a significant three-way treatment × habitat × species interaction ($p < 0.001$; Table S1).

In aquatic habitats, the invasive *A. philoxeroides* generally outperformed the native *A. sessilis*, accumulating significantly greater biomass under all treatments except CK and MicroPE. (Figure 1). Notably, *A. philoxeroides* exhibited a trend toward increased growth under plastic exposure relative to its plastic-free control, with a significant stimulation observed in the macro-PE and MicroBio treatments. Conversely, the native *A. sessilis* showed limited responsiveness, except under the MacroNylon and MicroNylon treatments, where it experienced significant biomass reductions.

In terrestrial habitats, treatment effects were subdued. No significant differences were detected under the control or macroplastic treatments, whereas the invasive *A. philoxeroides* maintained significantly higher biomass than the native *A. sessilis* under the MicroBio, MicroNylon, and MicroPE treatments. Neither species showed significant deviations from their respective controls (Figure 1).

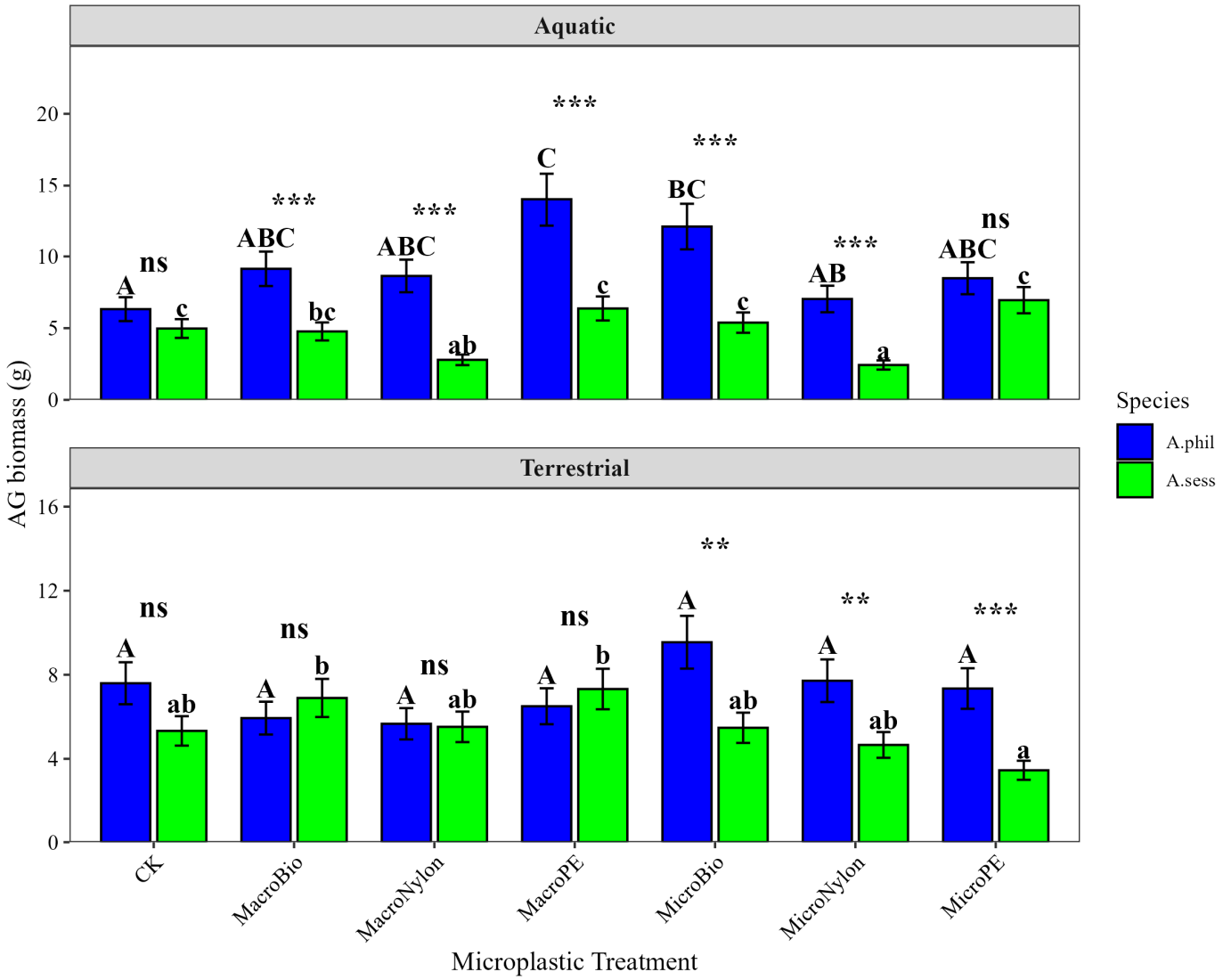

Figure 1. Effects of microplastics on aboveground biomass of *A. philoxeroides* and *A. sessilis*. Blue and green bars represent *A. philoxeroides* and *A. sessilis*, respectively. Data are presented as mean ± standard error (SE). Different uppercase letters (A, B, C) above the blue bars indicate significant differences among treatments for *A. philoxeroides*, while different lowercase letters (a, b, c) above the green bars indicate significant differences among treatments for *A. sessilis* ($p < 0.05$). Asterisks denote significant differences between the two species within the same treatment (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$), and "ns" indicates no significant difference ($p > 0.05$). Abbreviations: CK, control; Macro, macro-sized particles; Micro, micro-sized particles; Bio, biodegradable plastic; PE, polyethylene; Nylon, nylon. The same annotation is used in Figures 1–4.

2.1.2. Belowground Biomass

Belowground biomass was significantly affected by all three main factors (treatment: $p = 0.002$; habitat: $p < 0.001$; species: $p = 0.005$). However, these effects were strongly modulated by complex interactions, particularly the three-way treatment × habitat × species interaction ($p < 0.001$), alongside significant two-way interactions of treatment × species ($p = 0.007$) and habitat × species ($p < 0.001$; Table S1).

In aquatic environments, the native *A. sessilis* generally exhibited higher root allocation than *A. philoxeroides*, a difference that was statistically significant under the CK, MacroPE, MicroPE, and MicroBio treatments, whereas the opposite pattern was observed under the MacroNylon treatment (where *A. sessilis* allocated less biomass to roots). However, neither species showed significant plastic-induced changes relative to controls.

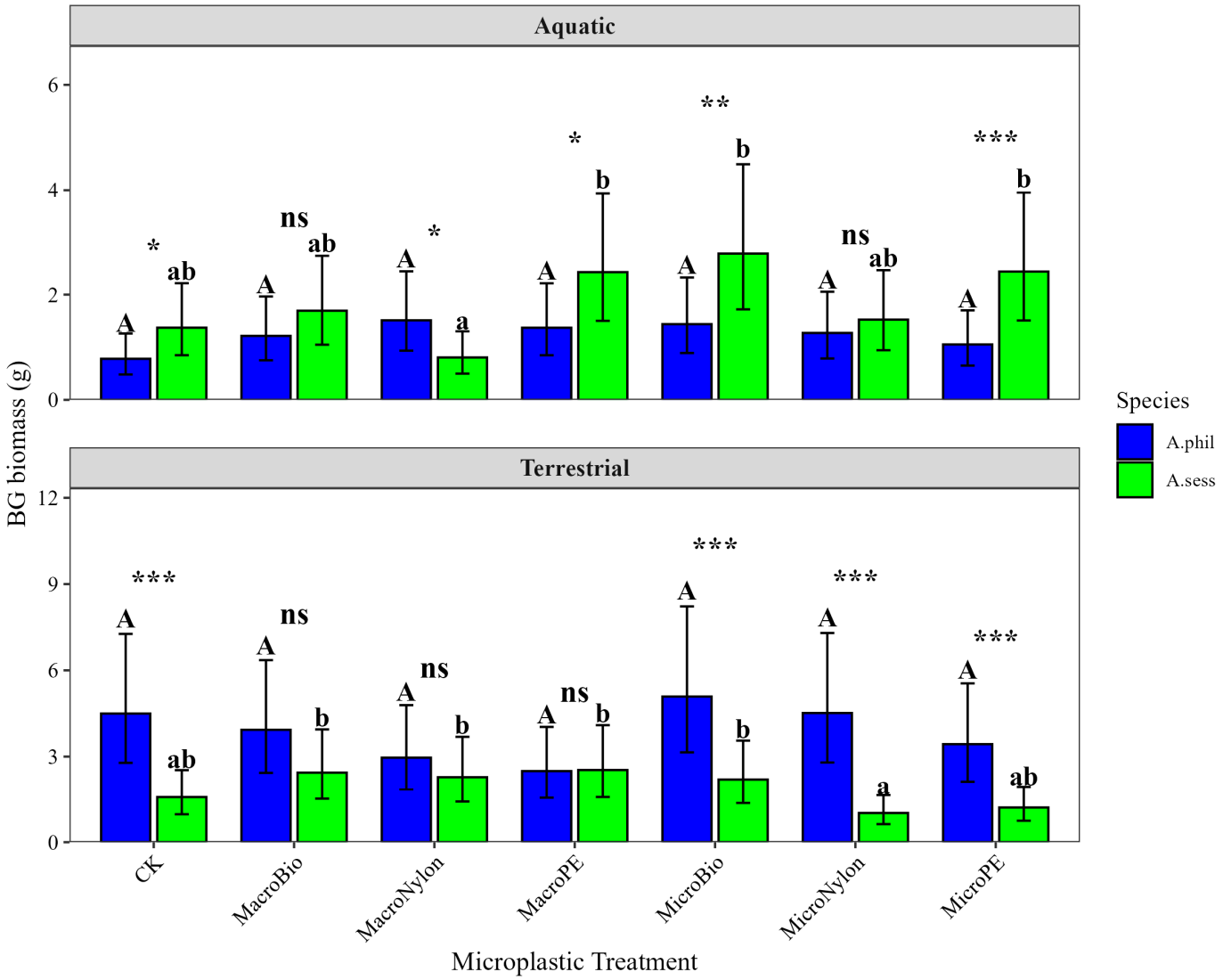

Figure 2. Effects of microplastics on belowground biomass of *A. philoxeroides* and *A. sessilis*.

In terrestrial environments, the pattern reversed: *A. philoxeroides* developed significantly larger root systems than *A. sessilis* in the control, MicroBio, MicroNylon, and MicroPE treatments. Similar to aquatic findings, no plastic treatment significantly altered belowground biomass relative to controls for either species (Figure 2).

2.1.3. Total Biomass

Total biomass patterns largely mirrored those of aboveground biomass, with significant main effects of treatment and species (both $p < 0.001$). These effects were further modulated by habitat, as indicated by a significant treatment × habitat interaction ($p < 0.001$), and by the combined influence of habitat and species, as shown by a significant three-way treatment × habitat × species interaction ($p < 0.001$; Table S1).

In aquatic habitats, *A. philoxeroides* maintained a clear growth advantage over *A. sessilis* in all treatments except the CK and MicroPE treatments. Crucially, MacroPE and MicroBio exposure significantly stimulated total biomass production in *A. philoxeroides* relative to its control, whereas *A. sessilis* remained unaffected by any treatment.

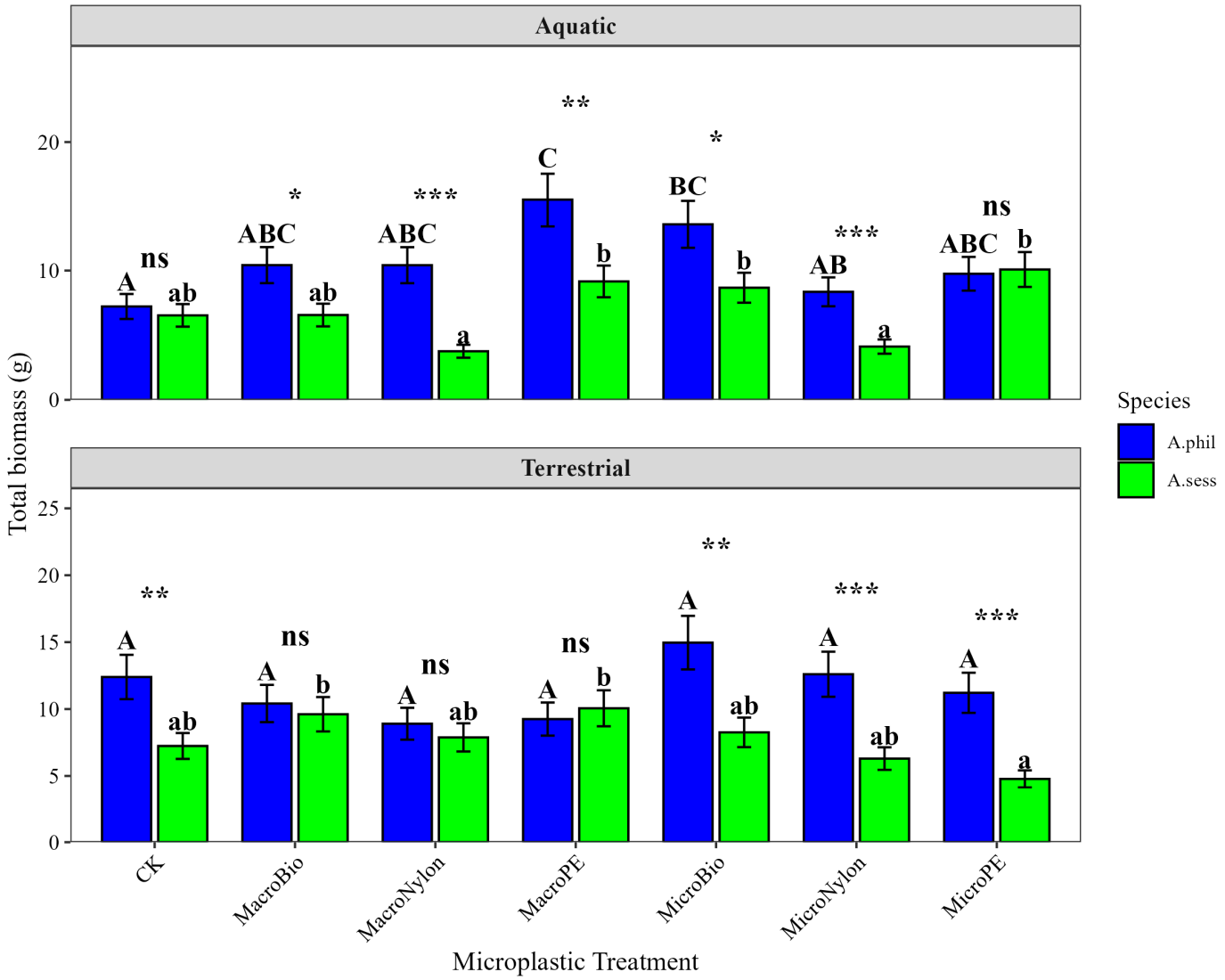

Figure 3. Effects of microplastics on total biomass of *A. philoxeroides* and *A. sessilis*.

In terrestrial habitats, the total biomass of *A. philoxeroides* remained significantly higher than that of *A. sessilis* in the CK, MicroBio, MicroNylon, and MicroPE treatments. No significant differences were observed for either species compared to controls (Figure 3).

2.1.4. Shoot-to-Root Ratio (SR)

Biomass allocation, expressed as the shoot:root ratio, differed markedly between habitats and species (both $p < 0.001$) and was further modulated by significant treatment × species and habitat × species interactions (both $p < 0.001$; Table S1).

In aquatic habitats, *A. philoxeroides* consistently allocated more resources aboveground, maintaining a significantly higher SR than *A. sessilis* across all treatments except MacroNylon and MicroNylon. Compared with their respective controls, neither *A. philoxeroides* nor *A. sessilis* showed significant differences.

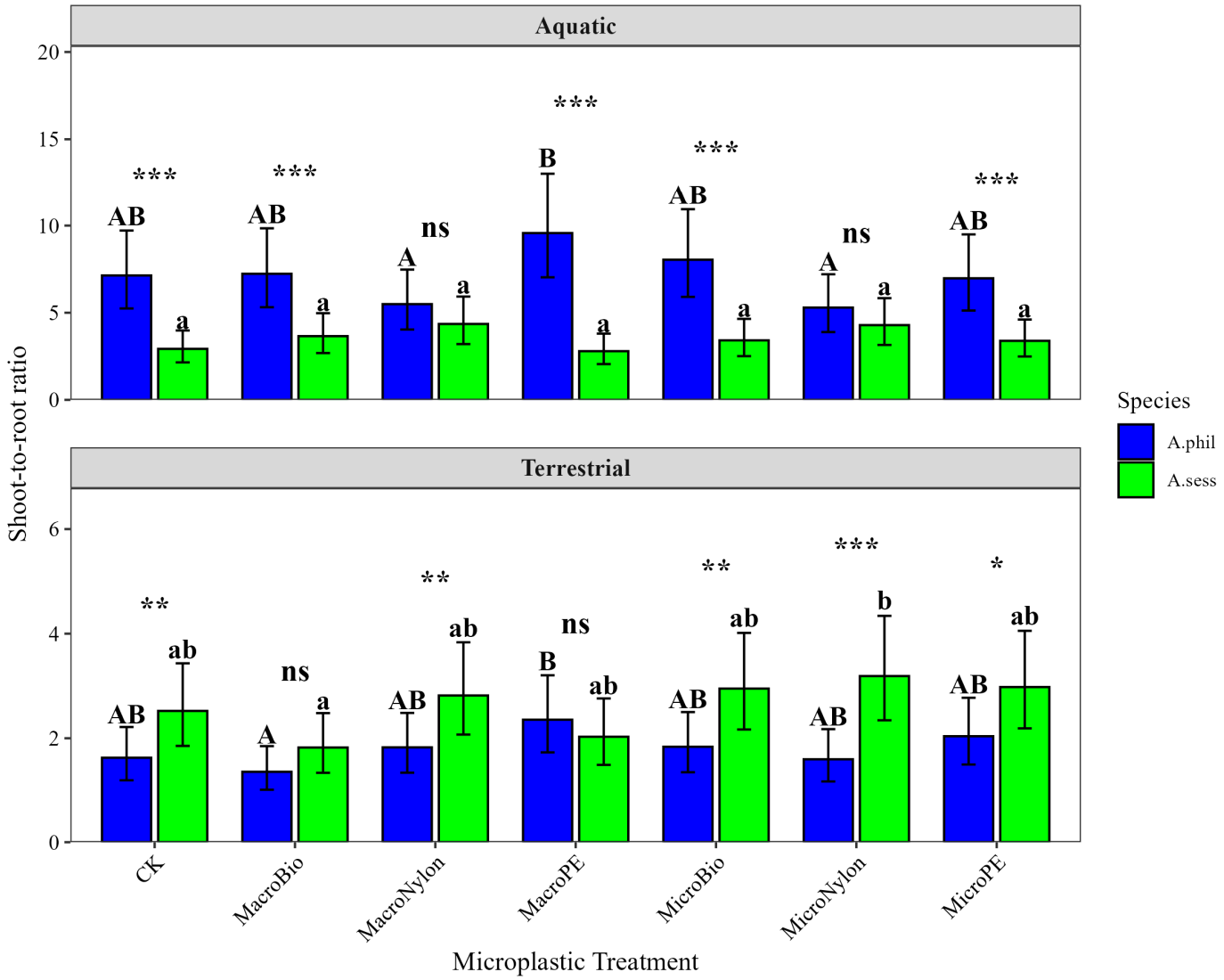

Figure 4. Effects of microplastics on shoot:root of *A. philoxeroides* and *A. sessilis*.

In terrestrial habitats, the invasive *A. philoxeroides* generally displayed a lower SR than the native *A. sessilis* in all treatments except MicroBio and MicroPE. Relative to their respective controls, no treatment significantly altered SR for either species. (Figure 4).

2.2. Relative Magnitude of Microplastic Effects (Effect Sizes)

2.2.1. Responses of Aboveground Biomass (Rela AG)

The relative impact of microplastics on aboveground growth was highly context-dependent, with significant main effects of species, habitat, and plastic type (all $p < 0.001$). This context dependence was further reflected in significant two-way interactions for species × habitat, habitat × plastic type, and plastic type × plastic size (all $p < 0.001$), as well as significant higher-order interactions involving species × habitat × plastic size ($p < 0.001$) and species × habitat × plastic type × plastic size ($p = 0.030$; Table S2).

Overall, *A. philoxeroides* exhibited a "benefit-in-water, cost-on-land" strategy: it showed positive relative effect sizes (stimulation) in aquatic habitats across all plastic types but negative effects (inhibition) in terrestrial habitats under macro-sized plastic treatments (MacroBio, MacroNylon, and MacroPE), with only a slightly positive effect under MicroBio (Figure 5).

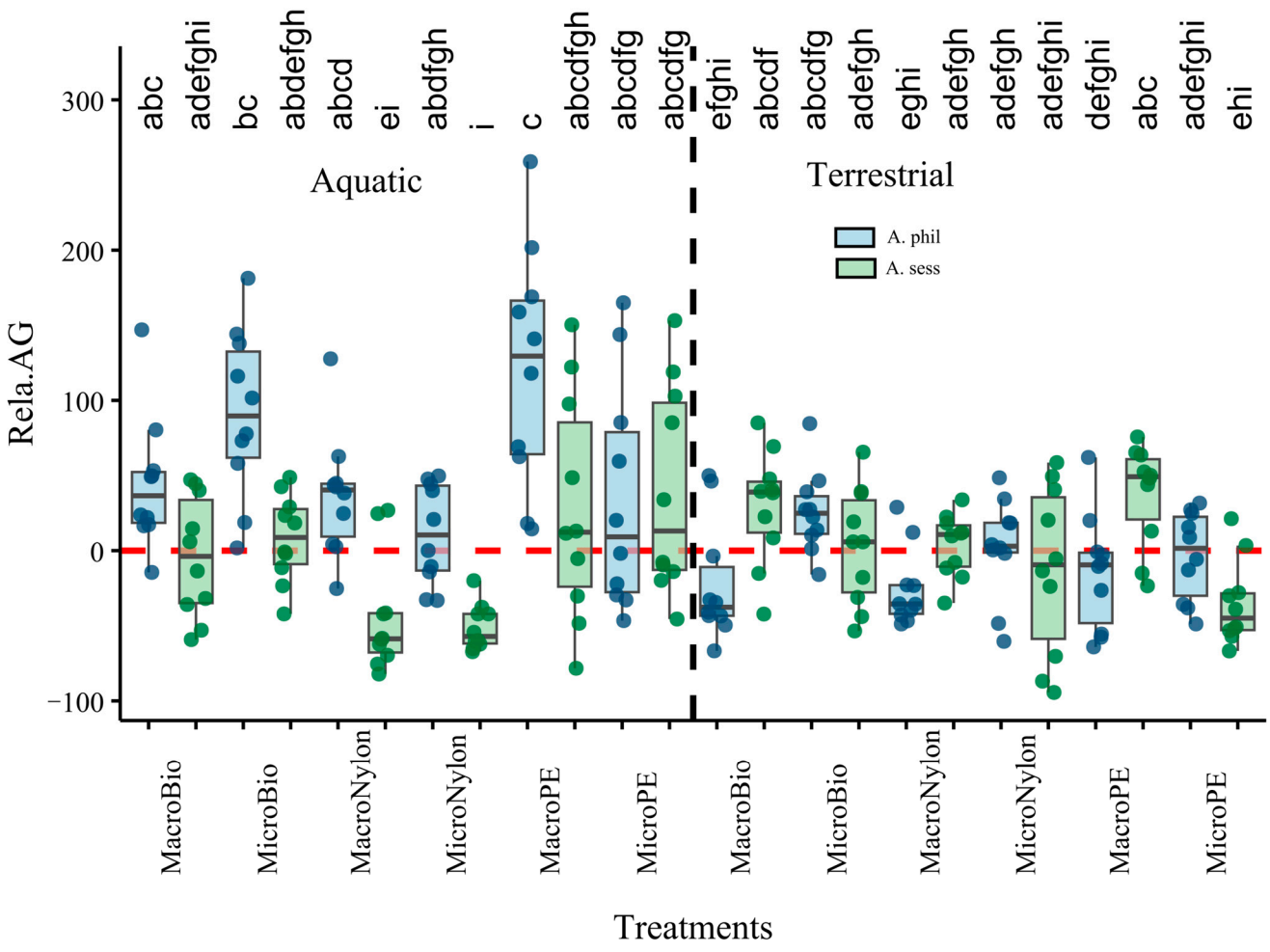

Figure 5. Relative effects of microplastics on aboveground biomass of *A. philoxeroides* and *A. sessilis.* The black dashed line separates habitats, with the aquatic habitat on the left and terrestrial habitat on the right. The red dashed line denotes the zero-effect baseline; *A. philoxeroides* is represented by light blue boxes and dark blue points, and *A. sessilis* by light green boxes and dark green points. Box plots display the median (central horizontal line), interquartile range (box edges), and whiskers extending to 1.5 times the interquartile range, while scattered points represent individual data replicates. Different lowercase letters indicate significant differences among the six plastic treatments within the same habitat and species; they do not indicate significant departures from the control (CK) or from the zero-effect baseline. Comparisons with CK are based on the raw-data model, in which CK is included as a treatment level. Relative effect sizes > 0 indicate a positive effect (stimulation), whereas values < 0 indicate a negative effect (inhibition) relative to the control. The same annotation is used in Figures 5–8.

In contrast, *A. sessilis* displayed an opposing pattern. In aquatic habitats, its growth was inhibited by nylon at both size classes, whereas PE exerted a positive effect. In terrestrial habitats, *A. sessilis* benefited from MacroBio and MicroBio treatments as well as from MacroNylon and MacroPE, but its growth was inhibited by micro-sized nylon and PE.

Particle size further modulated these effects. In terrestrial habitats, MicroBio and MicroNylon exerted positive effects on *A. philoxeroides*, thereby alleviating the inhibition caused by their macro-sized counterparts (MacroBio and MacroNylon)(Figure 5).

2.2.2. Responses of Belowground Biomass (Rela BG)

Responses of belowground biomass (Rela BG) were driven primarily by habitat and plastic type, with significant main effects of habitat ($p < 0.001$) and plastic type ($p = 0.018$). These effects were further modulated by species identity and plastic size, as indicated by significant species × habitat ($p = 0.001$), species × plastic type ($p < 0.001$), and plastic type × plastic size ($p = 0.015$) interactions, together with significant three-way interactions for species × habitat × plastic type ($p = 0.009$) and species × habitat × plastic size ($p < 0.001$; Table S2).

In aquatic settings, *A. philoxeroides* consistently exhibited positive root growth responses to all plastic treatments. *A. sessilis* also showed largely positive responses, except for an inhibitory effect from MacroNylon.

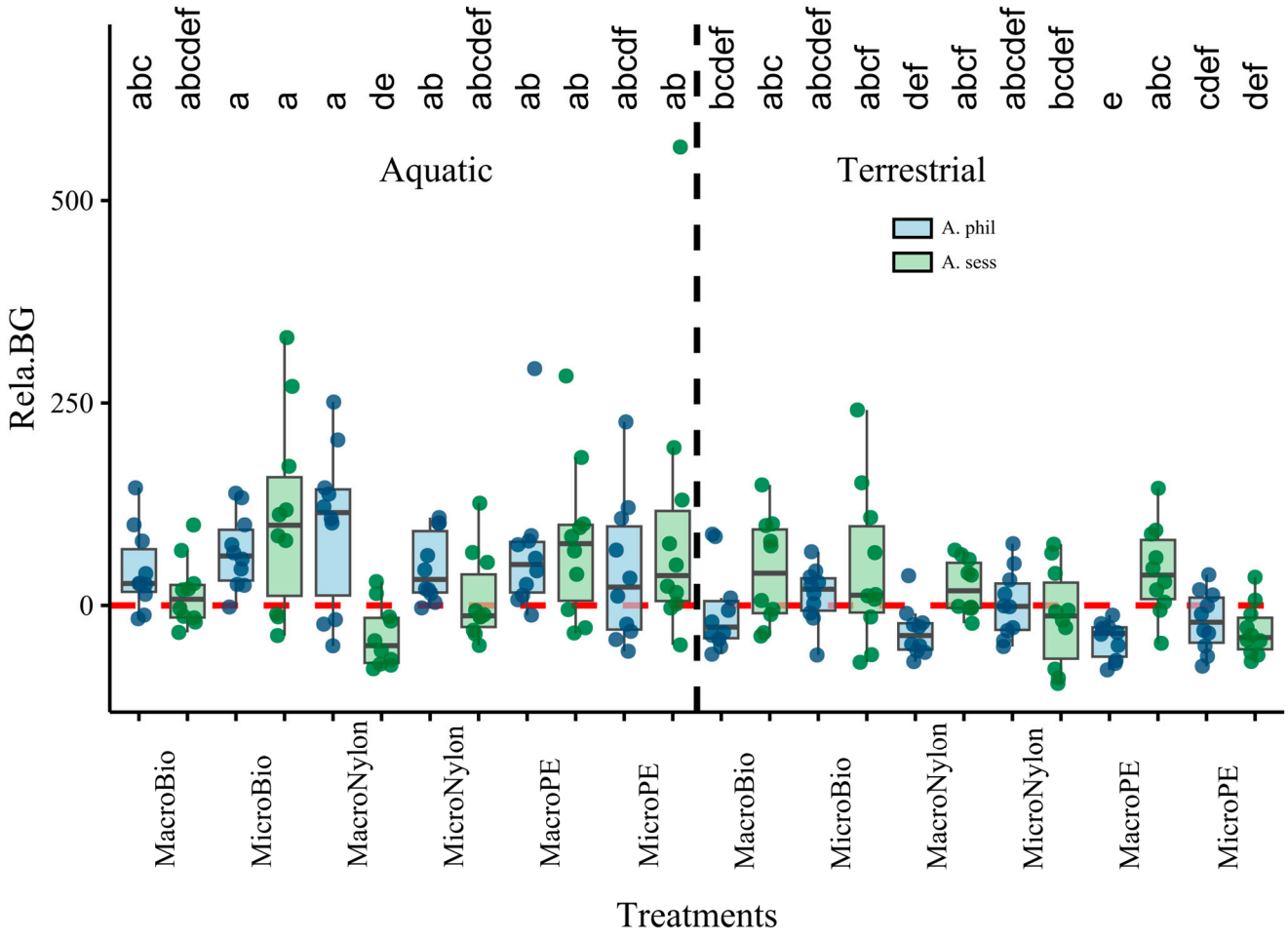

Figure 6. Relative effects of microplastics on belowground biomass of *A. philoxeroides* and *A. sessilis*. In terrestrial settings, root growth of *A. philoxeroides* was inhibited by MacroPE, MicroPE, MacroBio, and MacroNylon treatments but stimulated by MicroBio and MicroNylon. For *A. sessilis*, root growth was consistently stimulated by MacroBio and MicroBio, whereas the effects of nylon and PE were size-dependent, with macro-sized particles promoting and micro-sized particles inhibiting root growth (Figure 6).

2.2.3. Responses of Total Biomass (Rela Total)

Responses of total biomass (Rela Total) were governed by significant main effects of species ($p = 0.006$), habitat ($p < 0.001$), and plastic type ($p < 0.001$), and were further modulated by significant two-way interactions for species × habitat, habitat × plastic type, and plastic type × plastic size (all $p < 0.001$), as well as a significant three-way species × habitat × plastic size interaction ($p < 0.001$; Table S2).

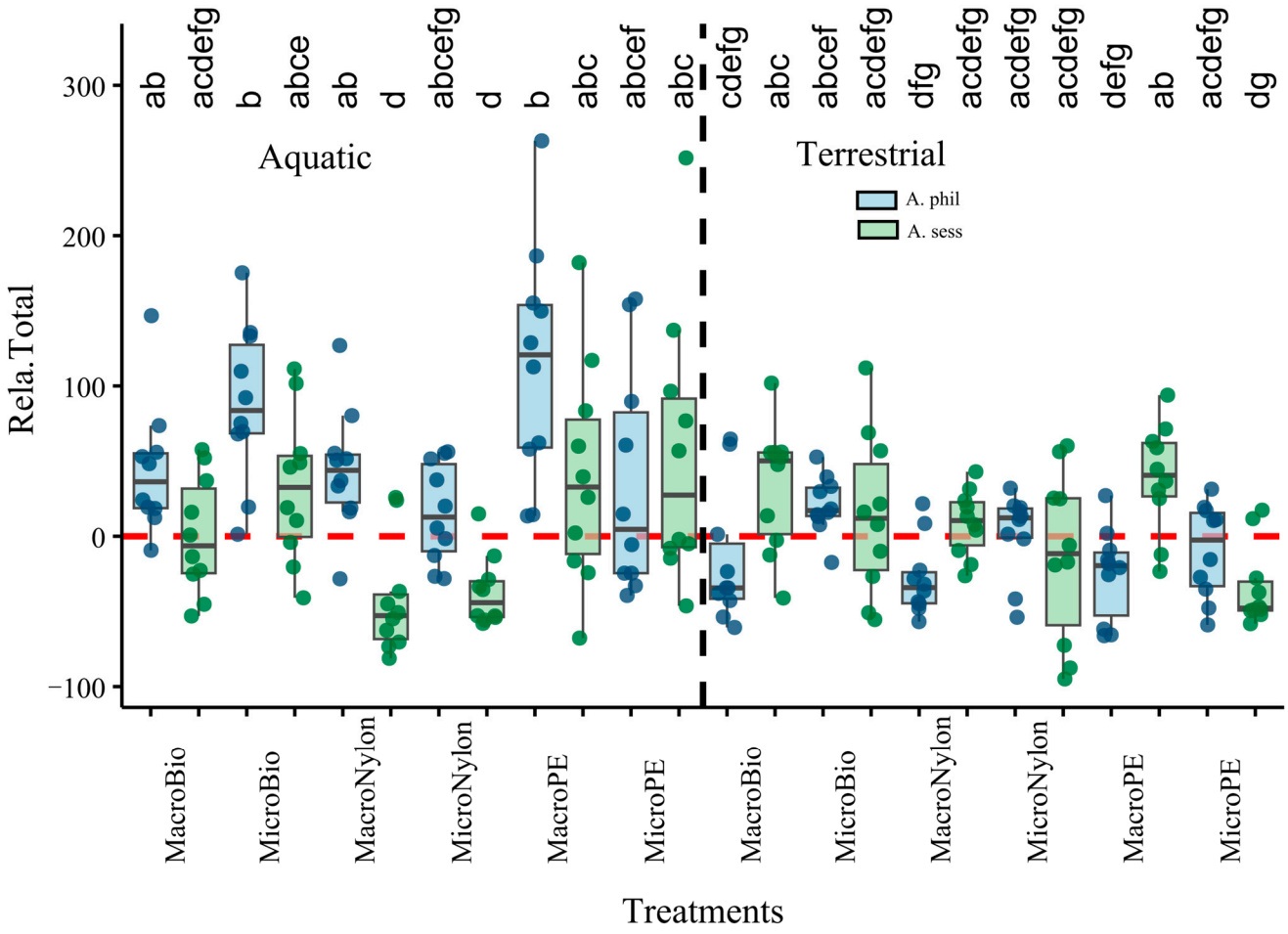

Figure 7. Relative effects of microplastics on total biomass of *A. philoxeroides* and *A. sessilis*.

A. philoxeroides consistently exhibited positive responses to plastic exposure in aquatic environments across all plastic types, whereas in terrestrial habitats it experienced growth inhibition, particularly under PE at both sizes and under MacroBio and MacroNylon.

Conversely, *A. sessilis* showed a more resilient or positive response profile in terrestrial habitats compared to aquatic ones, where it was notably inhibited by nylon. Size-dependent effects were evident in terrestrial habitats, where micro-sized particles generally induced more negative (or less positive) effects than macro-sized counterparts for *A. sessilis* under Nylon and PE treatments (Figure 7).

2.2.4. Responses of Shoot-to-Root Ratio (Rela SR)

Responses of the shoot-to-root ratio (Rela SR) were predominantly structured by species-specific interactions, with significant species × habitat and species × plastic type interactions (both $p < 0.001$), a significant species × plastic size interaction ($p = 0.021$), and a significant species × plastic type × plastic size interaction ($p = 0.026$; Table S2).

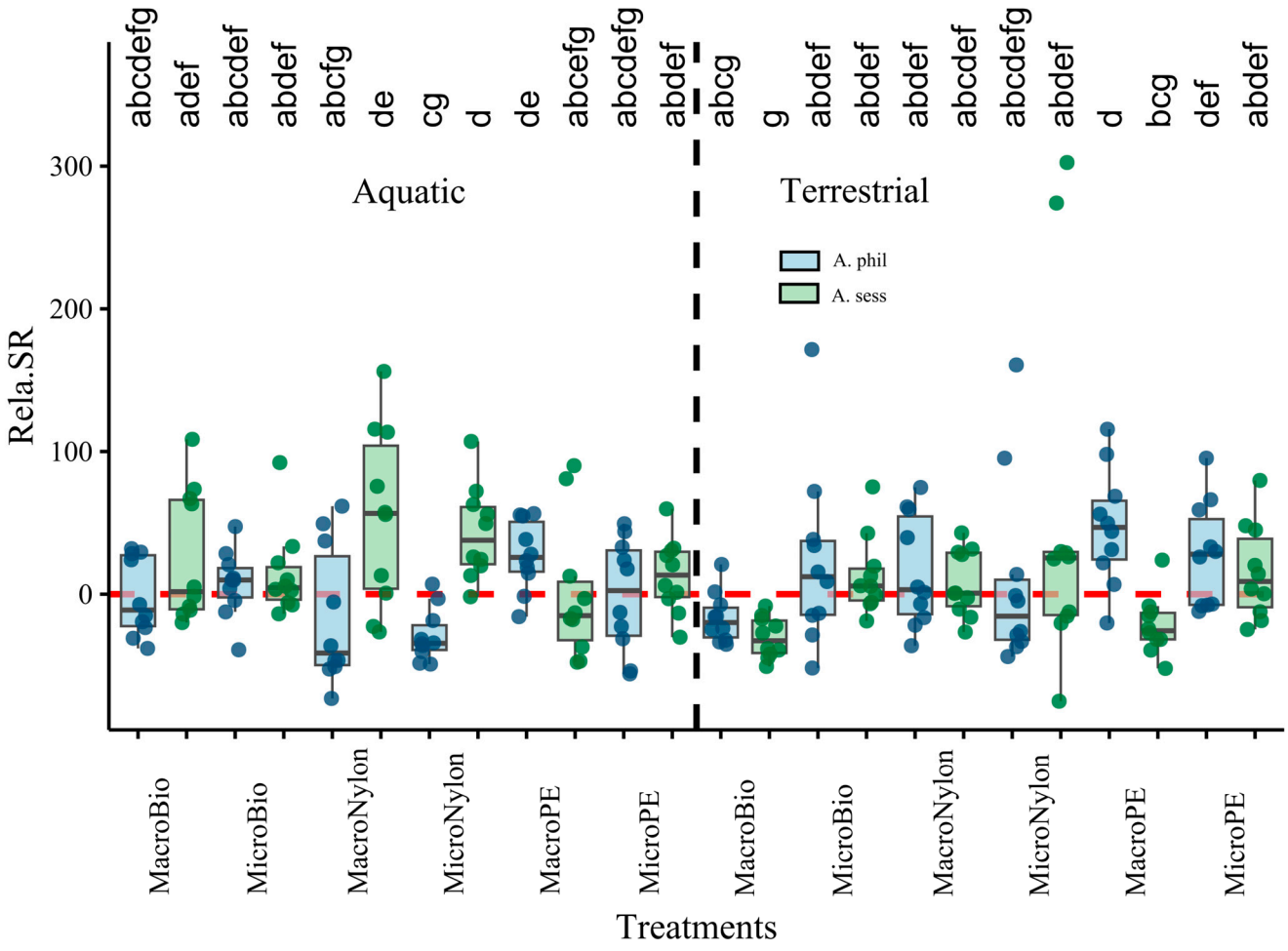

Figure 8. Relative effects of microplastics on shoot:root of *A. philoxeroides* and *A. sessilis*.

A distinct interspecific divergence was observed in aquatic habitats: *A. philoxeroides* tended to reduce its SR (negative effect size, indicating increased root investment relative to shoot) under MacroNylon, MicroNylon, and MacroBio treatments, whereas *A. sessilis* exhibited positive relative effect sizes for SR under almost all aquatic treatments.

In terrestrial habitats, both species generally exhibited positive effect sizes, indicating a shift toward aboveground allocation; however, specific outcomes varied with polymer type and size (e.g., *A. sessilis* showed negative responses to MacroBio and MacroPE but positive to micro-sized counterparts) (Figure 8).

3. Discussion

3.1. Microplastics as Habitat-Dependent Modulators

Our results demonstrate that microplastics do not act as uniform stressors but rather function as habitat-dependent ecological filters that differentially regulate plant performance based on species identity, polymer type, and environmental context. This finding supports our first hypothesis that microplastic effects are strongly habitat-dependent.

In aquatic habitats, microplastic exposure generally enhanced the growth and biomass accumulation of the invasive *A. philoxeroides*, as evidenced by significant increases in above-ground biomass under macro-PE treatment (Figure 1) and consistently positive relative effect sizes across most polymer types (Figures 5–7). In marked contrast, *A. sessilis* exhibited variable and often negative responses in water, particularly under nylon treatments (Figures 5–7). This pattern was reversed in terrestrial habitats: *A. philoxeroides* showed predominantly negative responses (relative effect sizes < 0), whereas *A. sessilis* maintained neutral or slightly positive performance (Figures 5–7). These contrasting patterns confirm that microplastic impacts cannot be generalized across ecosystems and underscore the need for habitat-specific risk assessments.

This distinct habitat-switch effect challenges the prevailing view that microplastics are universally detrimental to plant health [10]. Instead, our findings align with the "novel weapons" or "environmental matching" hypotheses, suggesting that anthropogenic alterations can create niches that disproportionately benefit species with high phenotypic plasticity [23,32]. The absolute effect sizes (Figures S1–S3) further corroborate this divergence, revealing that *A. philoxeroides* gains a clear performance advantage in aquatic plastic-polluted niches, potentially accelerating its invasion, while terrestrial pollution may inadvertently strengthen biotic resistance by favoring the native congener.

3.2. Trait-Based Responses of the Invasive A. philoxeroides in Aquatic Environments

Our second hypothesis, that the invasive *A. philoxeroides* would exhibit greater tolerance or benefit from microplastic exposure relative to the native *A. sessilis*, was strongly supported in aquatic habitats. Relative to the control, the invader showed significantly greater aboveground and total biomass under several plastic treatments (Figures 1 and 3), with positive relative effect sizes for aboveground, belowground, and total biomass (Figures 5–7). In contrast, its SR did not increase consistently; relative effect sizes for SR were treatment-dependent and negative under some treatments (Figure 4). These responses are consistent with the acquisitive, stress-tolerant strategy characteristic of successful invaders [32,33].

The trait-based responses observed in *A. philoxeroides* are consistent with adaptive phenotypic plasticity, a key predictor of invasion success. In aquatic treatments, the relative effect sizes for SR varied among microplastic treatments, which may indicate opportunistic investment in aboveground light capture when belowground conditions change [34]. This plastic allocation strategy is known to boost biomass accumulation under enriched or flooded conditions [35] and may partially explain why *A. philoxeroides* consistently outperformed *A. sessilis* under identical treatments (Figures 1 and 3).

Several non-exclusive mechanisms, none of which were directly measured in this study, may contribute to the polymer-specific responses observed. First, larger PE fragments could act as physical mulch or structural elements, improving gas exchange and reducing hypoxia at sediment-water interfaces, creating conditions that would favor fast-growing invasives. Second, in contrast, smaller nylon fibers may entangle roots, alter boundary layers, and absorb or release chemicals, potentially disrupting nutrient uptake and allocation [36,37]. Third, recent studies have further shown that microplastic fibers can alter rhizosphere microbial communities and enzyme activities, creating feedbacks

that can differentially affect plant species [38,39]. Fourth, polymer type may also influence performance outcomes through allelopathy. Exposure to PE has been shown to increase plant biomass while enhancing chemical interference via changes in leaf metabolites [24]. These mechanisms are proposed as plausible explanations based on published evidence from other systems; because oxygenation, root entanglement, microbial community composition, and allelochemical production were not quantified here, they should be regarded as hypotheses rather than experimentally demonstrated outcomes.

3.3. Terrestrial Reversal: Species-Specific Responses to Plastic Pollution

In sharp contrast to aquatic results, terrestrial microplastics suppressed the invader while often promoting or having neutral effects on *A. sessilis* (Figures 5–7). This reversal is consistent with the pattern described as "pollutant-enhanced biotic resistance" in other systems [40], in which soil degradation disproportionately constrains fast-growing species while buffering stress-tolerant ones. However, because this study included only one invasive-native congeneric pair and did not measure biotic resistance (e.g., herbivore pressure, pathogen load, or competitive interactions), this interpretation should be treated as a hypothesis rather than a demonstrated mechanism. In addition, species identity and invasion status are completely confounded in a two-species design, so the observed differences cannot be attributed to invasion status per se.

The suppression of *A. philoxeroides* on land likely results from soil biophysical degradation. Microplastics, particularly fibers (nylon) and films (PE), can disrupt soil aggregation, reduce water-holding capacity, and impede root penetration [9,13]. *A. philoxeroides*, the invasive species in this study, typically requires high resource fluxes to maintain rapid growth and may be more sensitive to these physical constraints than the stress-tolerant native *A. sessilis*. The ability of *A. sessilis* to maintain or increase biomass under these conditions may reflect adaptation to resource-poor or physically challenging substrates, although this interpretation is specific to the species examined here and was not tested directly.

Furthermore, particle size played a critical role in modulating these outcomes. We observed that smaller particles often induced different responses than larger ones (e.g., terrestrial *A. sessilis* inhibited by micro-nylon/PE but promoted by macro-nylon/PE, Figures 5–7). This aligns with findings that nanoplastics and microplastics exert distinct toxicity profiles: smaller particles can block root pores and accumulate in tissues [41], whereas larger fragments primarily act as physical barriers or channels [12]. The varying responses of the two species to these size-dependent stressors highlight the complexity of soil–plant-plastic interactions.

Our results are qualitatively consistent with findings from other systems, although these comparisons involve different species and experimental scales. For example, low-density PE fragments increased aboveground biomass and shoot-to-root ratios of the invasive *Solidago canadensis* under moist conditions but had negligible or negative effects on native congeners [31]. Community-level experiments in other systems have similarly demonstrated that fertilization can interact with microplastics to shift biomass gains toward natives rather than aliens [10,42], and that PE residues may strengthen allelopathic suppression by native plants [24]. These studies provide context for our findings but do not constitute evidence for community-level reorganization in the present experiment, which was conducted with two species only.

3.4. Polymer Type and Particle Size: Potential Modulators of Plant Response

Our third hypothesis that polymer type and particle size further modulate microplastic effects was supported by the significant interactions detected in our statistical models (Supplementary Tables S1 and S2). However, the direction of these size effects was

highly context-dependent. In aquatic habitats, polymer type appeared to override particle size: *A. philoxeroides* exhibited consistently positive relative responses across all plastics, whereas *A. sessilis* was inhibited by Nylon but stimulated by PE, regardless of particle size. In contrast, a distinct size-dependent divergence emerged in terrestrial habitats. For *A. sessilis*, micro-sized PE and Nylon induced negative relative effects, while their macro-sized counterparts induced positive effects, aligning with the prediction of our third hypothesis. Strikingly, *A. philoxeroides* showed the opposite pattern, responding positively to micro-sized particles (Bio and Nylon) but negatively to macro-sized ones.

Rather than a universal "smaller-is-worse" rule, these contrasting patterns suggest that macro- and micro-sized plastics likely impose different types of constraints that are strongly filtered by species traits. In terrestrial soils, macroplastics may primarily create physical obstacles to root expansion, whereas the effects of microplastics are highly modulated by species-specific resilience. The ability of the invasive *A. philoxeroides* to maintain positive growth responses under microplastic exposure, particularly where the native species is inhibited, underscores that the ecological impact of microplastics is governed by the interaction among particle size, polymer type, and the inherent adaptability of the target species (Figures 5–7).

The size-dependent effects observed in our study are consistent with emerging evidence that particle dimensions can flip the direction of plant responses. Nanoscale plastics often suppress early growth through cellular uptake and oxidative stress [12,43], while larger fragments may physically modify soil or sediment structure in ways that benefit certain growth strategies. Particle shape also matters: fibrous microplastics (like nylon) have been shown to have stronger negative effects on root development than fragment or spherical forms, likely due to entanglement and altered water flow patterns [44].

The contrasting effects of Bio deserve particular attention. Although Bio is often promoted as an environmentally friendly alternative, our results show that its effects on plant growth are not uniformly benign and can be either positive or negative depending on particle size and habitat (Figures 5–8). This aligns with growing evidence that Bio degradation products, including organic acids and oligomers, may have distinct phytotoxic properties compared to conventional polymers [35,45]. These findings caution against assuming that biodegradable materials pose fewer ecological risks.

It is important to note that our conclusions are based on morphological traits (biomass and allocation), which provide a rapid and integrative measure of plant performance but are non-specific and can be influenced by multiple environmental and experimental variables. Physiological and biochemical indicators (e.g., oxidative stress markers, photosynthetic efficiency, and nutrient stoichiometry) were not measured in this study. Therefore, the underlying mechanisms proposed here—such as altered gas exchange or root entanglement—remain hypothetical. Future studies incorporating a multi-level indicator system (morphological, physiological, and biochemical) are needed to fully elucidate the mechanistic pathways of plant responses to plastic pollution.

3.5. Implications for Ecosystem Management and Future Perspectives

The demonstration that microplastics can fundamentally reverse performance outcomes, shifting from facilitation in aquatic environments to suppression in terrestrial soils, necessitates a more nuanced, habitat-specific approach to ecosystem management. Our findings challenge the "one-size-fits-all" assumption in current ecological risk assessments, suggesting instead that management strategies must be tailored to the hydrological context.

In aquatic ecosystems, riparian zones accumulating microplastics should be reclassified as high-priority sentinel sites for biosecurity. Our data indicate that these sediment sinks, particularly when polluted with polyethylene fragments, effectively act as invasion nurseries. Consequently, managers should target microplastic accumulation zones, such

as slow-flowing river bends or dam reservoirs, as potential "bridgeheads" where plastic pollution and invasive species may generate self-reinforcing cycles of ecosystem degradation [26]. Early removal of plastic debris in these hotspots could deliver a "double dividend" by simultaneously reducing pollutant load and mitigating invasion pressure. Conversely, in terrestrial soils, while microplastics may not directly trigger invasion, they function as a selective filter. Conservation efforts here should focus on the resilience of native communities, as pollution-induced stress could subtly restructure species composition by filtering out sensitive taxa even in the absence of dominant invaders.

While this study establishes a clear baseline using pristine polymers to isolate specific physical and chemical mechanisms, real-world scenarios involve complex interactions with weathered particles and environmental vectors. Moving forward, extending this framework to include aged microplastics and broader trophic dynamics, such as herbivory and pollination, will be essential to fully predict community trajectories in the field. Such integrative research will further refine our ability to forecast how the pervasive footprint of plastic pollution intersects with biological invasions to shape future ecosystems.

4. Materials and Method

4.1. Study Species and Propagation

Two congeneric amphibious plant species were used in this study: *A. philoxeroides* and *A. sessilis*. *A. philoxeroides* is a stoloniferous perennial herb native to South America that has become a globally invasive species in aquatic and riparian habitats [27]. In contrast, *A. sessilis* is widespread in tropical and subtropical Asia as a native species, typically inhabiting seasonally flooded wetlands and agricultural margins [29]. Both species are capable of rapid clonal propagation and tolerate fluctuating water regimes.

Plant materials were collected from a rice field in Lanxi Town (30°18′15.76″ N, 115°8′55.48″ E, 25.6 m elevation), Xishui County, Hubei Province, China, in August 2022. To minimize maternal effects and ensure genetic uniformity, clonal seedlings were propagated from stem cuttings of mature plants. Cuttings, each containing two nodes with lower leaves removed, were cultivated in large containers with 0–6 mm Pindstrup peat moss (Pindstrup Mosebrug A/S) under high humidity for one week to promote rooting. Only cuttings that had produced roots of comparable size were retained, and seedlings of similar height (approximately 10 cm) were selected for transplantation. Seedlings with visibly divergent vigor were excluded before random assignment to treatments.

4.2. Experimental Design

The experiment employed a fully crossed factorial design: 2 habitats (aquatic, terrestrial) × 2 species (*A. philoxeroides*, *A. sessilis*) × 3 plastic types × 2 particle sizes (macro, micro), with 10 replicates per treatment. Additionally, a plastic-free control(CK) was established for each habitat-species combination with 10 replicates. The factorial component comprised 2 × 2 × 3 × 2 × 10 = 240 containers, and the CK comprised 2 × 2 × 10 = 40 containers, resulting in 280 experimental units (280 containers and 280 seedlings) in total. Thus, the seven treatments (six plastic treatments plus CK) were arranged across the two habitats, with 20 containers per habitat × treatment group (10 containers per species). Within each habitat × treatment group, the 20 containers were randomly assigned to the two species (10 containers each), and one seedling was transplanted into each container. Each container was labeled with a unique numeric ID.

The substrate was a mixture (1:1:1 by volume) of surface soil (0–20 cm depth, yellow-brown soil collected from a local vegetable field at Huanggang Normal University), river sand, and 0–6 mm Pindstrup peat moss (Pindstrup Mosebrug A/S, Ry, Denmark). The field soil was air-dried, cleared of debris, and sieved (5 mm) prior to mixing.

Three polymer types were used: polyethylene (PE), derived from agricultural mulch film (Lanzhou Jintudi Plastic Products Co., Ltd., Lanzhou, China); nylon (PA6), derived from nylon rope (Binzhou Shengteng Rope Network Co., Ltd., Binzhou, China); and a biodegradable plastic composed of PBAT (65%, *w*/*w*) and PLA (35%, *w*/*w*), derived from biodegradable plastic bags (Henan Longdu Torise Biomaterials Co., Ltd., Puyang, China). The polymer composition was taken from the manufacturer's product specification and is consistent with published compositions of commercial biodegradable shopping bags. In the treatment designations, Macro and Micro denote macro- and micro-sized particles, respectively, and PE, Nylon, and Bio denote polyethylene, nylon, and the biodegradable plastic, respectively. Accordingly, seven treatments were established: MacroPE, MicroPE, MacroNylon, MicroNylon, MacroBio, MicroBio, and an unamended control (CK), with CK receiving no plastic addition. These seven groups are hereafter referred to collectively as the treatments. Plastic particles were prepared in two size classes:

Macroplastics (>5 mm): PE mulch film, nylon rope, and Bio bags were cut into strips or fragments (approx. 5–10 cm length).

Microplastics (<5 mm): PE and Bio were ground using a cryogenic milling machine and sieved through a 5 mm mesh; film thickness was not separately determined. Nylon microfibers were produced by cutting nylon strands to lengths <5 mm; fiber diameter was not measured.

Because quantitative particle size distributions, fiber diameters, and film thicknesses were not measured, the size classes should be regarded as operational categories rather than fully characterized size distributions.

Plastics were amended into the substrate at a concentration of 1% (*w*/*w*). This concentration is within the upper range of "environmentally relevant" concentrations used in soil microplastic literature (≤1% *w*/*w*) and is not intended to represent current field contamination levels, which are typically orders of magnitude lower. CK groups received no plastic addition.

The experiment was conducted from September to November 2022 in a greenhouse at Huanggang Normal University. Plants were grown in transparent plastic containers (top radius 10 cm, bottom radius 9 cm, height 27 cm) filled with 1.5 kg of substrate.

Aquatic habitat: Maintained with approximately 5 cm of water layer above the soil surface. The aquatic habitat was created by maintaining approximately 5 cm of standing water above the substrate surface. This design represents a flooded soil/sediment condition rather than the full range of aquatic ecosystems (e.g., flowing water, deep-water, or water-column exposures), and the results should be interpreted accordingly.

Terrestrial habitat: Maintained at field capacity (moist soil) without standing water. All terrestrial containers received the same watering volume at the same interval. Soil moisture was not continuously monitored; this is acknowledged as a limitation because small differences in evapotranspiration among treatments could have generated subtle moisture differences.

Watering was performed every three days, and the water level in the aquatic habitat was replenished as needed to maintain approximately 5 cm above the soil surface. During the experiment, containers were randomly repositioned weekly to minimize the influence of environmental heterogeneity. The greenhouse was operated under ambient light and without supplemental heating or lighting; conditions during the experimental period (September–November) were within the ranges typical for unheated greenhouse plant-growth experiments in the region. Irrigation water was tap water; its electrical conductivity and pH were not measured. Containers were closed at the bottom and had no drainage holes, so drainage losses were negligible and did not differ among treatments. No fertilizer was applied during the experiment, so nutrient inputs were identical across all treatments and controls.

Plants were harvested after 80 days of growth. Plants were separated into aboveground (stems and leaves) and belowground (roots) fractions, carefully washed, oven-dried at 80 °C for 72 h, and weighed. We calculated aboveground biomass (AG), belowground biomass (BG), total biomass, and shoot-to-root ratio (SR).

4.3. Data Analysis

All statistical analyses were conducted in R version 4.3.3 (R Foundation for Statistical Computing, Vienna, Austria).

Two complementary analyses were performed: (i) an analysis of plant growth responses using the raw data, and (ii) an analysis of effect sizes. The two analyses differ in how the control (CK) is handled and in the factors included, as specified below.

4.3.1. Plant Growth Response (Raw Data)

Growth responses like aboveground biomass (AG), belowground biomass (BG), total biomass, and shoot-to-root ratio (SR) were analysed with a three-way fixed-effects model including Habitat (2 levels), Species (2 levels), and Treatment (7 levels: the six plastic treatments plus CK), together with all their interactions. CK was included as a treatment level in this model. Polymer type and particle size were not decomposed here because CK has neither attribute, and including CK in a polymer type × particle size decomposition would be logically invalid.

To account for non-normality and heteroscedasticity, all growth variables were analyzed using a Generalized Linear Model (GLM) framework. Candidate distributions (Gamma, lognormal, and Weibull) were fitted using the fitdistrplus package (version 1.2.6) and evaluated based on AIC, BIC, and goodness-of-fit statistics (Kolmogorov–Smirnov, Cramér-von Mises, and Anderson–Darling), and these criteria were used to guide distribution selection..

Specifically, AG and total biomass were modeled using Gamma GLMs with a log link, while BG and SR were analyzed using lognormal GLMs (implemented as Gaussian GLMs on log-transformed data). A sensitivity analysis using a Weibull distribution was additionally performed for total biomass to ensure robustness. Estimated marginal means (EMMs) and pairwise comparisons were calculated using the 'emmeans' package (version 2.0.1), with *p*-values adjusted using the Tukey method for main effects and the Šidák method for habitat-specific analyses (α= 0.05).

4.3.2. Analysis of Effect Sizes

To quantify the magnitude of plasticity and facilitate interspecific comparisons independent of baseline size differences, we calculated both the relative effect size and the absolute effect size for each replicate of the six plastic treatments:

$$\text{Rela} = [(\text{Treatment} - \text{Control})/\text{Control}] \times 100$$

$$\text{Abs} = \text{Treatment} - \text{Control}$$

where "Control" is the mean of the corresponding habitat × species CK. CK therefore served as the baseline for effect-size calculation and was not included as a treatment level in this analysis. Because CK was excluded, the six plastic treatments could be decomposed into two crossed factors—polymer type (3 levels: PE, Nylon, and Bio) and particle size (2 levels: macro and micro)—which were analysed together with Habitat, Species, and all interactions. Because all six plastic treatments within a habitat × species combination were expressed relative to the same CK mean (n = 10), the resulting Rela values are not fully independent and share, to some degree, the error associated with estimating the control mean. The effect-size analysis is therefore used for descriptive among-treatment comparisons and for displaying proportional responses, whereas formal comparisons against CK are based on the raw-data model in which CK is included as a treatment level.

Trends in Abs largely mirrored the raw data; therefore, Abs results are presented in the Supplementary Material, whereas Rela is used in the main text to highlight proportional responses.

Because the relative effect size data contained negative values and did not meet parametric assumptions, they were analyzed using the nonparametric aligned rank transform ANOVA (ART-ANOVA) via the ARTool package (version 0.11.2). Post hoc comparisons were performed using Dunn's test implemented in the FSA package (version 0.10.1), with Benjamini–Hochberg (BH) correction. Significance was set at adjusted $p < 0.05$. Dunn's test was used as a conservative global comparison among treatment combinations; because it does not exploit the factorial structure of the design, interaction effects were interpreted from the ART-ANOVA model terms rather than from Dunn's test, and the post hoc results should be regarded as conservative relative to factorial-specific contrasts.

5. Conclusions

In summary, microplastics are not merely passive contaminants but active drivers of plant community reorganization. By integrating raw growth data with absolute and relative effect sizes, we demonstrated that microplastics facilitate the invasive *A. philoxeroides* in aquatic environments, likely through habitat structural modification and nutrient interactions, while impeding it in terrestrial soils. These findings highlight the urgent need to incorporate habitat heterogeneity and species identity into the global assessment of microplastic impacts, moving beyond simple toxicity tests to understand how plastic pollution reshapes the invasion dynamics of our changing ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/plants15233661/s1, Figure S1: Absolute effects of microplastics on aboveground biomass of *Alternanthera philoxeroides* and *A. sessilis;* Figure S2: Absolute effects of microplastics on belowground biomass of *A. philoxeroides* and *A. sessilis*; Figure S3: Absolute effects of microplastics on total biomass of *A. philoxeroides* and *A. sessilis*; Figure S4: Absolute effects of microplastics on shoot:root of *A. philoxeroides* and *A. sessilis*. Table S1: Effects of plastic on biomass allocation in *Alternanthera philoxeroides* and *A. sessilis*; Table S2: Effects of plastic on absolute and relative biomass allocation in *Alternanthera philoxeroides* and *A. sessilis* (ANOVA).

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Conflicts of Interest: The authors declare no conflict of interest.

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