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Abstract

Urochloa arrecta, commonly known as African signal grass, is an aquatic plant native to Africa that has become highly invasive in Brazil. This species poses a particular threat in a neotropical coastal river of high conservation value. We conducted a co-occurrence analysis to assess patterns between *U. arrecta* and native macrophytes. We hypothesized positive associations with free-floating species due to potential anchoring effects, and negative associations with other life forms due to competitive interactions. For that, we used classic null-model co-occurrence models and repeated analyses for different sampling periods to evaluate consistency in patterns. Negative associations occurred only among erect emergent and creeping emergent species, possibly due to resource competition. Positive associations were more frequent, mainly with free-floating species, as the dense stands formed by *U. arrecta* may facilitate their persistence. However, some creeping emergent species in some periods were also positively associated, likely because the invader expanded the suitable habitat for these species beyond the margins. Results highlight the complexity of interactions and reinforce that either positive or negative associations can occur, depending on the context.

Keywords: biological invasion; biotic homogenization; community assembly;
non-native macrophyte; species co-occurrence.

Biological invasions can significantly impact native communities, posing threats to biodiversity and ecosystem functioning. A species is considered invasive when it establishes high-density populations that spread beyond its native range and cause ecological disruption (Haubrock *et al.*, 2026). The success of an invasive species in a new ecosystem depends on its ability to overcome both abiotic and biotic filters, which operate across multiple spatial scales (Pulzatto *et al.*, 2019). Moreover, this process is influenced by the species' invasive potential and the vulnerability of the invaded ecosystem (Fleming & Dibble, 2015).

Among the factors that influence invasion success, anthropogenic activities are widely recognized as one of the main drivers of species introductions and establishment. Anthropogenic actions have reduced natural barriers to species dispersal, facilitating introductions into new ecosystems for economic, ornamental, or accidental reasons (Carlton & Schwindt, 2026). Anthropogenic actions have reduced natural barriers to species dispersal, facilitating introductions into new ecosystems for economic, ornamental, or accidental reasons (Huang *et al.*, 2024). Once established, these species can cause severe ecological consequences, including native species extinction and increased biotic homogenization (McKinney & Lockwood, 1999; Padial *et al.*, 2020). Biotic homogenization involves growing ecological similarity across regions, often driven by the dominance of non-native generalist species over endemic specialists. Environmental changes caused by human interventions can intensify this process, as native species frequently exhibit lower tolerance to altered conditions, leading to declines in competitive species (Ricciard & MacIsaac, 2011). Patterns can be evident in aquatic ecosystems, where invasive macrophytes, both non-native and native, often proliferate under favorable conditions created by human-induced disturbances, such as nutrient enrichment (Bora & Padial, 2023; Huang *et al.*, 2024; Skovsholt *et al.*, 2024). These invasion dynamics are shaped not only by environmental conditions but also by the biological characteristics of the species that compose aquatic plant communities.

Aquatic macrophytes can exhibit remarkable adaptive capacity, allowing them to colonize a wide range of environments and display considerable phylogenetic diversity (Santamaría, 2002). They occupy different areas of the water bodies and vary in their life form. The most commonly used life form classification includes erect emergent (EE), creeping emergent (CE), rooted floating-leaved (RF), free-floating (FF), rooted submerged (RS), free submerged (FS), and epiphytic (EP) plants. These life forms differ

in their use of space and resources, which may influence interactions among species and shape patterns of co-occurrence within aquatic plant communities (Lesiv *et al.*, 2020).

Patterns of species co-occurrence are commonly assessed using presence and absence data across sites, allowing the identification of associations among species pairs and providing a basis for investigating the processes that structure community assembly. These patterns are compared against a null model representing the expected co-occurrence in the absence of direct ecological interactions or shared environmental responses. Deviations from this expected pattern may indicate positive or negative associations between species, suggesting nonrandom relationships (Cazelles *et al.*, 2016; Delmas *et al.*, 2019). Such patterns may be influenced by multiple ecological processes, including environmental filtering, competition, facilitation, and habitat segregation (Boschilia *et al.*, 2008; Gayol *et al.*, 2022). Understanding the co-occurrence pattern of these plants, including invasive species, is therefore essential for assessing and preserving aquatic ecosystems (Thomaz & Michelan, 2011).

Aquatic macrophytes play a vital role in ecosystem functioning by oxygenating the water, facilitating nutrient cycling, providing habitat and food for various aquatic organisms, and serving as spawning and attachment sites for mollusks, amphibians, and birds (Thomaz *et al.*, 2023). However, macrophyte communities can be profoundly altered by the presence of invasive species, which often displace native species and modify habitat structure (Thomaz & Michelan, 2011).

One of the main invasive species in Brazil is *Urochloa arrecta* (Hack. ex T.Durand & Schinz) Morrone & Zuloaga, commonly known as African signalgrass or tropical tanner grass. It is a species native to eastern and southern Africa, introduced to Brazil primarily for pasture development in wetland areas (Michelan *et al.*, 2010; Sato *et al.*, 2021). This perennial species has long, floating stems, a creeping emergent growth habit, and thrives in swampy, seasonally flooded, or even well-drained soils in high-rainfall regions (Rojas-Sandoval, 2023). It reproduces both vegetatively through stolons, rhizomes, and stem fragments and demonstrates high resilience and dispersal ability (Fares *et al.*, 2020). Its fast growth, broad environmental tolerance, and evolutionary adaptability (Bora *et al.*, 2020) have enabled African signalgrass to spread across multiple Brazilian biomes, particularly in areas affected by human activity.

The Guaraguaçu River, located along the Paraná coast, is severely invaded by African signalgrass, largely due to increased human occupation in its surroundings and the

discharge of untreated domestic effluents from nearby municipalities, such as Pontal do Paraná and Matinhos (Araújo *et al.*, 2021; Sato *et al.*, 2021; Galvanese *et al.*, 2022). Despite human pressures, the river retains conservation value, forming part of the Lagamar Estuarine Complex, a UNESCO-recognized Natural Heritage of Humanity. This study evaluates the effects of the African signalgrass on native macrophyte occurrence patterns. We hypothesize that floating macrophytes may be positively associated with African signalgrass due to structural facilitation and anchoring opportunities, whereas erect and creeping emergent species are negatively associated due to competitive exclusion for space and light.

The Guaraguaçu River is the largest river along the coast of Paraná, southern Brazil (Figure 1; see also Araújo *et al.* (2021), Sato *et al.* (2021), and Galvanese *et al.* (2022). The river flows through the municipalities of Pontal do Paraná, Paranaguá, and Matinhos. It plays a key ecological and socioeconomic role in the region by supporting biodiversity conservation, maintaining estuarine and mangrove ecosystems, and providing distinct microhabitats along the river, while also supplying water resources, navigation routes, and tourism activities for coastal municipalities. Its headwaters originate in the Serra da Prata, within the Saint-Hilaire Lange National Park, at 766 meters above sea level, and the river discharges into Paranaguá Bay via the Cotinga Channel.

In its upper course (Sector 1), the river supports a unique ecosystem (locally known as *caixetal*), dominated by the amphibious tree *Tabebuia cassinoides* Lam. (DC.) (Bignoniaceae), a species listed by IUCN as threatened with extinction. This upstream section is the most preserved, featuring clear waters and minimal tidal influence. The middle section of the river (Sector 2), however, is the most impacted by anthropogenic pressures, including unplanned urban expansion and untreated sewage discharges. This area shows a high dominance of invasive macrophytes such as the African signalgrass (non-native) and *Pontederia crassipes* Mart. (a species native to the Amazon Basin and other tropical regions of South America, listed as one of the worst invasive species worldwide), reflecting a shift in community composition due to environmental degradation. The African signalgrass forms extensive vegetative mats that hinder navigation and alter aquatic plant communities, posing a growing threat to the river's ecological integrity (Sato *et al.*, 2021). In contrast, the downstream section (Sector 3) is protected by the Guaraguaçu River Ecological Station, extending into mangrove areas

influenced by strong tidal flows, where freshwater macrophytes are sparse. In its lower reaches, the Guaraguaçu forms an estuarine environment with a tidally influenced coastal plain.

Sixteen sampling points were established along the navigable section of the Guaraguaçu River where aquatic plant colonization was observed (Fig. 1), as part of long-term monitoring conducted by the Laboratory of Analysis and Synthesis in Biodiversity (Guaraguaçu Project – <https://lasbufprbio.wixsite.com/home/projeto-guaraguacu>). At each sampling point, a 50 m river transect along the watercourse was delimited following the RAPELD sampling design adapted for river ecosystems. Each segment was surveyed by boat from downstream to upstream, and all aquatic macrophyte species occurring within the segment were recorded. Sampling was carried out during seven campaigns: in April and September of 2016, 2017, and 2018, and an additional campaign in April 2019. The same 16 sampling points were revisited in all campaigns, resulting in a repeated sampling design across time with consistent spatial structure. In each campaign, data were collected on the occurrence (presence–absence) of native aquatic macrophytes and the invasive species African signalgrass, totaling 39 recorded species. All macrophyte species recorded in the study were previously represented by voucher specimens in the UPCB Herbarium (Universidade Federal do Paraná, see Table S9 – Supplementary material), and no additional plant specimens were collected or deposited as part of this study. Sampling points 1 to 5 are located in the most preserved upper section of the river, where African signalgrass was not observed in any of the sampling periods. Similarly, points 15 and 16, located in the mangrove zone, also lacked records of the invasive species, likely due to the high salinity resulting from tidal influence. In contrast, the intermediate section (points 6 to 14) exhibited consistent occurrences of tropical African signalgrass, with most sites dominated by this invasive grass.

Co-occurrence analyses were performed separately for each sampling campaign to maintain temporal independence in the statistical assessment. For each campaign, the 16 sampling points were used as spatial sampling units, generating a presence-absence matrix of native macrophytes and African signalgrass per period. The species were analyzed in pairs (native species and African signalgrass), enabling subsequent interpretation of the results in relation to the life forms of each native species. The

analyses were performed in the R statistical environment (R Core Team, 2023) using the *cooccur* package (Griffith *et al.*, 2016). Co-occurrence patterns were evaluated using the probabilistic model implemented in the package, which estimates the expected frequency of co-occurrence between species pairs based on their occurrence frequencies across sampling sites and compares these values with the observed frequencies. Unlike global co-occurrence indices such as the C-score or T-score, this method assesses each species pair individually by comparing observed and expected co-occurrence frequencies derived from species occurrence probabilities based on their marginal incidences. Significant deviations from expectation indicate positive or negative species associations, whereas non-significant deviations indicate random associations. This approach resulted in a list of species that exhibited co-occurrence either greater or less than expected by chance with the invader, indicating positive or negative associations, respectively.

We found significant positive and negative associations ($p < 0.05$) between native species and the invasive African signalgrass, based on comparisons between expected and observed numbers of co-occurring sampling points. Seven native species exhibited a higher-than-expected co-occurrence with the invader, indicating that the African signalgrass was frequently recorded in the same sampling locations where these species occurred. Among these, *Pistia stratiotes* L. and *Hydrocotyle leucocephala* Cham. & Schltdl. showed consistent positive associations across nearly all sampling periods. The life forms of the positively associated species were diverse, including free-floating, rooted floating-leaved, rooted submerged, and emergent types. In contrast, three native species showed lower co-occurrence than expected with the invader, suggesting negative associations. These patterns were detected only in a single sampling period and involved exclusively emergent species. Notably, *Hymenachne amplexicaulis* (Rudge) Nees and *Ichnanthus cf. tenuis* (J. Presl & C. Presl) Hitchc. & Chase were never recorded in the same plots as *U. arrecta* over the four years of sampling, reinforcing their possible mutually exclusive patterns (See more details in Table S8 – Supplementary material).

Our results are consistent with previous studies indicating that the African signalgrass can simultaneously facilitate and suppress native macrophytes depending on life form (Michelan *et al.*, 2010; Amorim *et al.*, 2015; Bornschein *et al.*, 2022). Our findings further suggest that life form may be an important factor influencing these associations. In our study, CE and EE macrophyte species exhibited negative

associations, while positively associated species showed varied life forms, including FF, RS, RF, and some CE in some periods (Figure 2) (see life forms description above and in Lesiv *et al.*, 2020). It is important to emphasize that, given the nature of co-occurrence-based analyses, these associations should be interpreted as potential relationships rather than evidence of direct ecological interactions.

Positive associations may reflect facilitation via physical anchoring provided by dense vegetative mats, especially benefiting floating species (or some creeping emergent such as *H. leucocephala* that notably use mats to anchor). This mechanism of facilitation has been discussed by Thiébaud & Martinez (2015), who investigated whether invasive species that form dense vegetative mats could support the establishment of other species. Notably, *P. stratiotes*, *P. crassipes*, and *H. leucocephala* have previously been recorded in co-occurrence with the African signalgrass in the Guaraguaçu River (Araújo *et al.*, 2021; Sato *et al.*, 2021), supporting this hypothesis. However, these patterns may also reflect species-specific habitat preferences and spatially structured environmental variation along the river, rather than direct facilitation processes alone (Stefanidis *et al.*, 2023).

Conversely, negative associations may be associated with competitive exclusion driven by shading, space limitation, and reduced oxygen and light availability (Fernandes *et al.*, 2013). Thus, competition is a plausible explanation for negative associations, particularly at fine spatial scales where resource limitations restrict the coexistence of multiple species (Pulzatto *et al.*, 2019). Invasive species often outcompete natives for light, space, and nutrients. In the case of the African signalgrass, dense mats have been associated with reduced dissolved oxygen and lower light availability (Fernandes *et al.*, 2013), creating conditions unfavorable for some native species. Its generalist nature, rapid growth, and adaptability make it a strong competitor, leading to changes in local plant communities (Michelan *et al.*, 2010; Sato *et al.*, 2021). The pattern of negative associations observed here may relate to the "limiting similarity" hypothesis, which states that species with similar ecological niches are less likely to coexist. This is particularly relevant in the case of *H. amplexicaulis*, a native creeping emergent macrophyte that shares morphological and ecological traits with the African signalgrass (Araújo *et al.*, 2021) and also possesses invasive potential (Wearne *et al.*, 2013). Such similarity may further restrict co-occurrence through potential competitive processes. These dynamics likely exhibit a strong scale dependency, with competitive interactions

being more evident at finer spatial grains, where physical proximity intensifies resource overlap and direct interference (Thomaz & Michelan, 2011). At broader spatial scales, other ecological processes: dispersal, environmental filtering, or even facilitation may override the effects of competition, potentially allowing coexistence between native and invasive species. Therefore, assessing patterns of co-occurrence across multiple spatial resolutions is essential to disentangle the relative influence of biotic interactions and environmental constraints.

The positive association between two creeping emergent species, *P. aquaticum* and *P. repens*, deviated from the general pattern, possibly because the spatial arrangement of the African signalgrass indirectly expanded habitat availability along river margins (Bornschein *et al.*, 2022). This highlights that invasion effects are not uniform and may vary with ecological context. It is important to note that the exclusion of native macrophytes may occur primarily under conditions of high biomass of the invasive species, when strong reductions in resource availability are observed (Sato *et al.*, 2021).

The distribution of macrophytes along the Guaraguaçu River is influenced by several factors, including natural environmental variation. Also, the river exhibits a gradient of anthropogenic impacts, with sectors 2 and 3 being the most affected (Santos, 2024; Melo *et al.*, 2024), being the probable cause for macrophyte species turnover (Galvanese *et al.*, 2022). Our results add to this knowledge, by indicating that life form stands out as a key factor shaping the distribution patterns of species along the river. This reinforces the importance of continuous, long-term monitoring, which is essential for improving our understanding of the processes involved in the invasion and for guiding more effective management strategies.

We advocate that the African signalgrass, together with environmental variation, likely influences the distribution and abundance of native macrophytes in the Guaraguaçu River, potentially altering ecosystem dynamics. Patterns observed suggest that species life form plays a key role in shaping these interactions, with floating species potentially benefiting from physical support provided by the invader, while emergent species (particularly erect emergent) may be excluded due to competition. Assessing individual species responses is crucial to understanding the mechanisms of invasion and their ecological consequences. Moreover, enhancing our knowledge of both native and invasive macrophyte distributions contributes to the conservation of aquatic ecosystems. Given the ecological importance of the Guaraguaçu River and the Lagamar

region, a recognized biodiversity hotspot and UNESCO Natural Heritage Site, efforts to mitigate the impacts of invasive species are essential given growing anthropogenic pressures.

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Author's Contributions

Giovanna Tie Curiaki Graciola: Writing - Original Draft, Formal analysis, Visualization; Lucas Abbadi Ebling: Writing - Review & Editing; Hugo Andrade Gonçalves dos Santos: Writing - Review & Editing; Andre Andrian Padial: Writing - Review & Editing, Conceptualization, Methodology, Validation, Supervision, Funding acquisition.

Conflict of Interest

The authors declare that there are no conflicts of interest.

Data Availability Statement

All data supporting the findings of this study are included in the article.

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Supplementary Material

The following online material is available for this article:

Table S1. Macrophyte abundance matrix by sampling site used in the analyses of April 2016.

Table S2. Macrophyte abundance matrix by sampling site used in the analyses of September 2016.

Table S3. Macrophyte abundance matrix by sampling site used in the analyses of April 2017.

Table S4. Macrophyte abundance matrix by sampling site used in the analyses of September 2017.

Table S5. Macrophyte abundance matrix by sampling site used in the analyses of April 2018.

Table S6. Macrophyte abundance matrix by sampling site used in the analyses of September 2018.

Table S7. Macrophyte abundance matrix by sampling site used in the analyses of April 2019.

Table S8. Native macrophyte species that showed a significant association with the invasive species.

Table S9. Species recorded and their respective voucher numbers deposited at the UPCB Herbarium (UFPR) and the Herbarium of the Municipal Botanical Museum of Curitiba (MBM).

AI Usage Statement

The artificial intelligence tool ChatGPT was used to assist with the grammatical review only.

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Table and Figure Captions

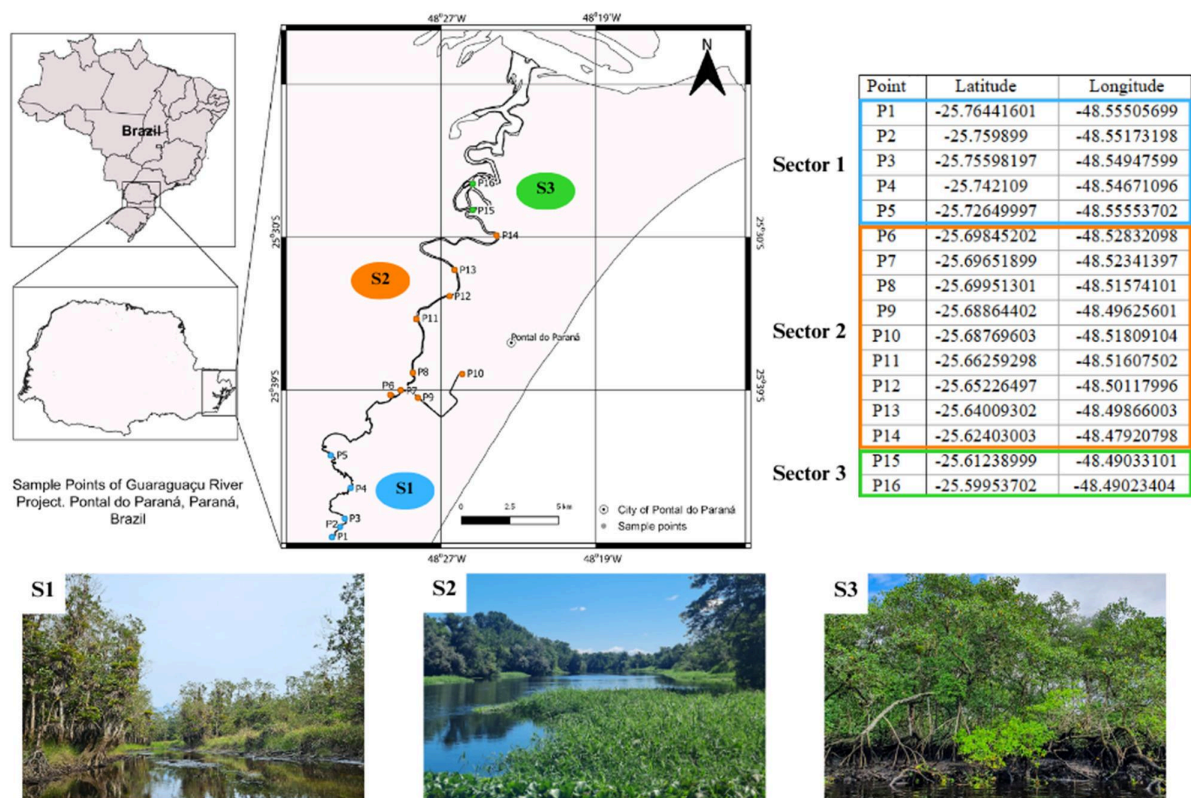


Fig. 1. Geographical location of macrophyte beds sampled in the Guaraguaçu River, Paraná, Brazil. A) Sector 1; B) Sector 2; C) Sector 3.

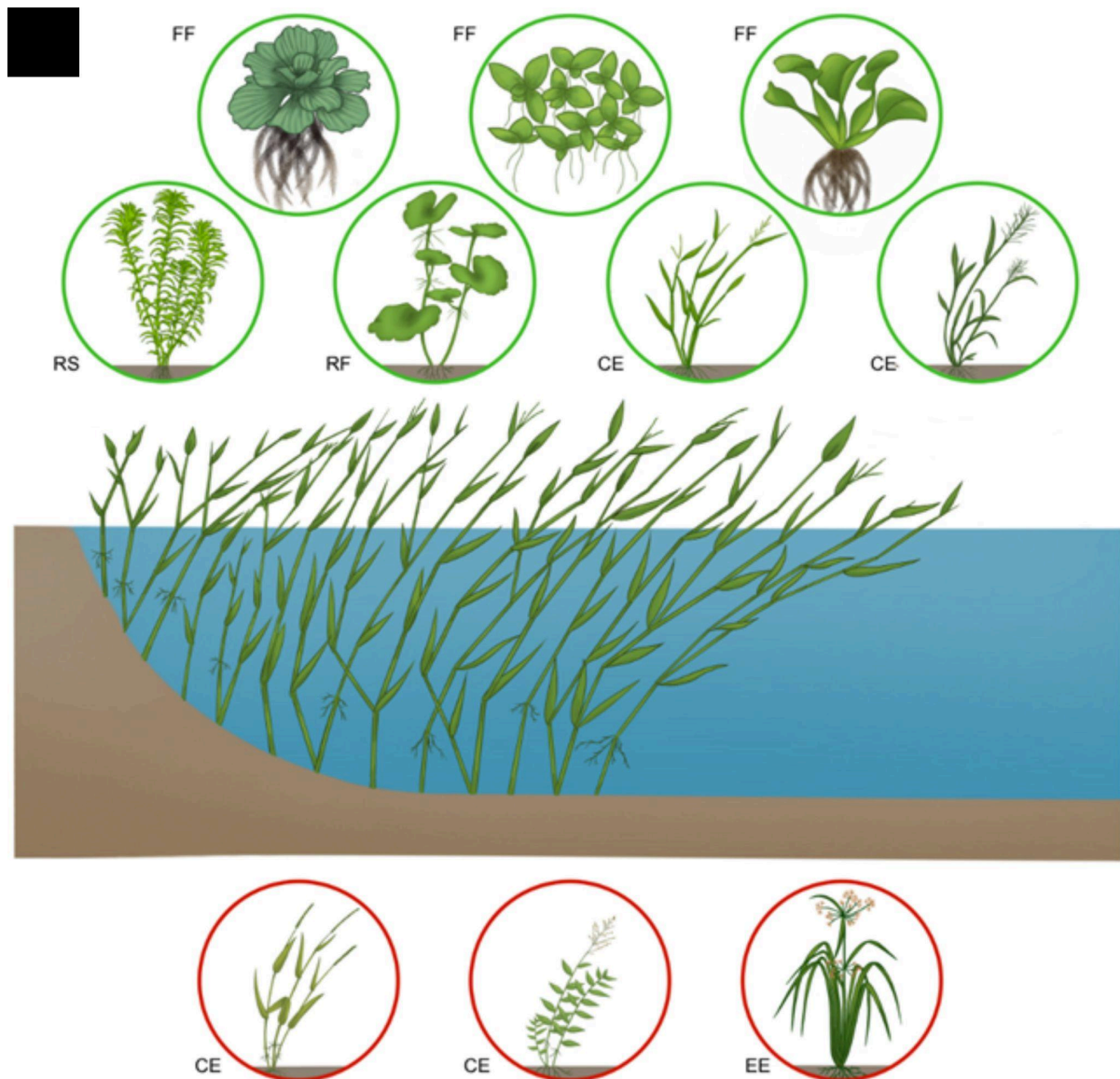


Fig. 2. Schematic representation of the associations between aquatic macrophytes and the african signalgrass *Urochloa arrecta*. Green circles indicate species positively associated with the african signalgrass, while red circles indicate species negatively associated. From left to right, the positively associated species are *Elodea densa*, *Pistia stratiotes*, *Hydrocotyle leucocephala*, *Lemna* cf. *minor*, *Panicum aquaticum*, *Pontederia crassipes*, *Paspalum repens*. The negatively associated species, from left to right, are: *Hymenachne amplexicaulis*, *Ichnanthus* cf. *tenuis*, *Rhynchospora corymbosa*. Life forms: creeping emergent (CE), erect emergent (EE), free-floating (FF), rooted submerged (RS), and rooted floating-leaved (RF).

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