CO-OCCURRENCE OF TWO INVASIVE PLANTS IN A TROPICAL SAVANNA ECOSYSTEM: A TOP PRIORITY FOR MANAGEMENT

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ABSTRACT

In this study, we assessed the co-occurrence influence of *Hyptis suaveolens* and *Urena lobata* on native plant species and soil properties in a guinea savanna vegetation in Nigeria. We sampled 120 plots of 10 × 10 m^2 with 30 plots each in sites invaded by *H. suaveolens*, *U. lobata*, mixed site and in sites with none of the species (control). A sparse partial least square discriminant analysis was used to assess the effect of invasive plant treatments on the plant diversity and soil properties, whereas the relationships between the soil properties, plant diversity and invasive species treatments were assessed using the canonical correspondence analysis. The indices of diversity of the control were significantly higher than all the other treatments ($p < 0.001$) with the mixed site having the lowest. There were significant differences in phosphorus, calcium, aluminium, soil alkalinity and diversity indices among the treatments. The results also indicated that the diversity indices and some soil properties were negatively associated with the mixed site. The negative impacts on the native diversity and change in the soil properties caused by the co-invasion of these two plants are more additive than non-additive. Therefore, priority should be placed on the management of co-invaded sites.

Keywords: *Hyptis suaveolens*; invasion; Nasarawa State; species diversity; *Urena lobata*

Introduction

There has been a proliferation of research on biological invasion in the last 20 years (Gurevitch et al. 2011). This is partly due to the realization of the negative impacts of the invasives on ecosystems and economy of nations of the world (Mack et al. 2000; Pyšek and Richardson 2010). History recorded that most of the studies on invasion have emphasized more on single species and factors enhancing their impacts on their invaded ecosystems (Davis 2006; Simberloff 2011a). Advances in plant invasion studies have produced trait-based approaches and mechanistic and probabilistic models in predicting the areas susceptible to such invasive plants (Kuebbing et al. 2013; Ordonez et al. 2010), produced potential environmental factors that drive the invasion (Fridley et al. 2007; Simberloff 2009; Drenovsky et al. 2012), and robust understanding of the mechanisms which produce much invasion impacts (Levine et al. 2003).

Among several effects, invasive plants have been reported to produce the following impacts on the native communities they invaded: they disrupt the plant-pollinator relationship by reducing visitation rates or making the habitats unconducive for pollinators (Brown et al. 2002; McKinney and Goodell 2010); releasing of allelopathic chemicals thereby reducing the growth rates of native plants (Stinson et al. 2006); altering the ecosystem services, such as nutrient cycling by changing the litter quality (Liao et al. 2008; Ehrenfeld 2010) or changing the intensity and timing of natural fire regimes, and modifying the structure of habitats (Simberloff 2011b).

There are relatively fewer studies on the impacts of biological invasions in tropical ecosystems around the world (Hulme et al. 2013; Zenni et al. 2017). Many other types of research in savanna ecosystems have focused on the community-level impact of invasive species rather than the impacts at ecosystem levels (Almeida-Neto et al. 2010; Rossi et al. 2014). Some ecosystems are invaded by multiple alien species. However, researchers don't focus on understanding the ecological combined impacts of co-occurring invasive species (Kuebbing et al. 2013; Lenda et al. 2019). Ecosystems invaded by co-occurring alien species do exhibit different ecological impacts depending on the nature of the species and their patterns of co-habiting (Zenni et al. 2020). This is because individual invasive species has a peculiar impact niche, which is described as the number and magnitude of ecological impacts it produces in the invaded ecosystem (Tekiela and Barney 2017).

Therefore, the interactions and overlap in the impact niches of each invasive species will determine how the impacts of their co-occurrence will be. This may be additive, non-additive, independent, antagonistic or synergistic. Literature has described these terms in clearer forms (Kuebbing et al. 2013). But independent means the impact niche of individual invasive species does not overlap one another.

In the present study, we filled the gap in the invasion ecology of plants by assessing the impacts of two co-occurring invasive plants *Hyptis suaveolens* and *Urena lobata* on soil chemical properties and resident plant communities in a guinea savanna ecosystem of North Central

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Nigeria. We hypothesize that the co-occurring invasive plants have higher impacts on the soil's chemical properties and resident plant communities. Consequently, the following research questions were asked: (1) Are there differences in resident plant communities and soil chemical properties among the treatments (control, *H. suaveolens* invaded, *U. lobata* invaded and two co-occurring species invaded communities)? (2) Does the co-occurrence of these two plants have a higher invasion impact? (3) Do relationships exist among resident plant diversity and soil chemical properties and the invasive species treatments?

Materials and Method

Study area

This study was conducted in Nasarawa State which is predominated by typical guinea savanna vegetation in Nigeria. The guinea savanna vegetation is characterized by abundant grasses and woody shrubs with few trees (Akomolafe et al. 2024). This State has a land area of 27117 km², a population of about 1,826,883 people and 13 local government areas also known as districts (Fig. 1). Nasarawa State occupies the central part of the middle belt region (north-central) of Nigeria. It has a topography ranging from lowland, undulating plain land and hills. This State is typified by a tropical rainy climate with a distinct dry season. It usually experiences up to seven months of rainy period and five months of the dry season. The annual rainfall ranges from 1200–2000 mm while the temperature ranges from 22.5 to 27.5 °C which may be higher during the peak of the dry season (Binbol and Marcus 2010). The indigenous people of the State are mainly farmers who are into the production of food crops such as groundnut, soybeans, melon, sesame, millet, yam and maize (Kwon-Ndung et al. 2016).

Study species

Hyptis suaveolens (L.) Poit. (family Lamiaceae) originated from the Neotropical regions and has now spread across several tropical and sub-tropical regions after its introduction. Its high adaptability to climatic conditions made it easier for this plant to naturalize itself in its introduced ranges (Padalia et al. 2015). The severity of its invasion has been reported in Nigeria, particularly in the savanna ecosystems Nigeria (Akomolafe et al. 2024; David et al. 2021). In the same vein, *Urena lobata* L. (family Malvaceae) has also been found to be a noxious weed in many parts of northern Nigeria (Akomolafe and Nkemdy 2020). Its aggressive invasiveness enabled it to outcompete native species in the invaded ecosystems.

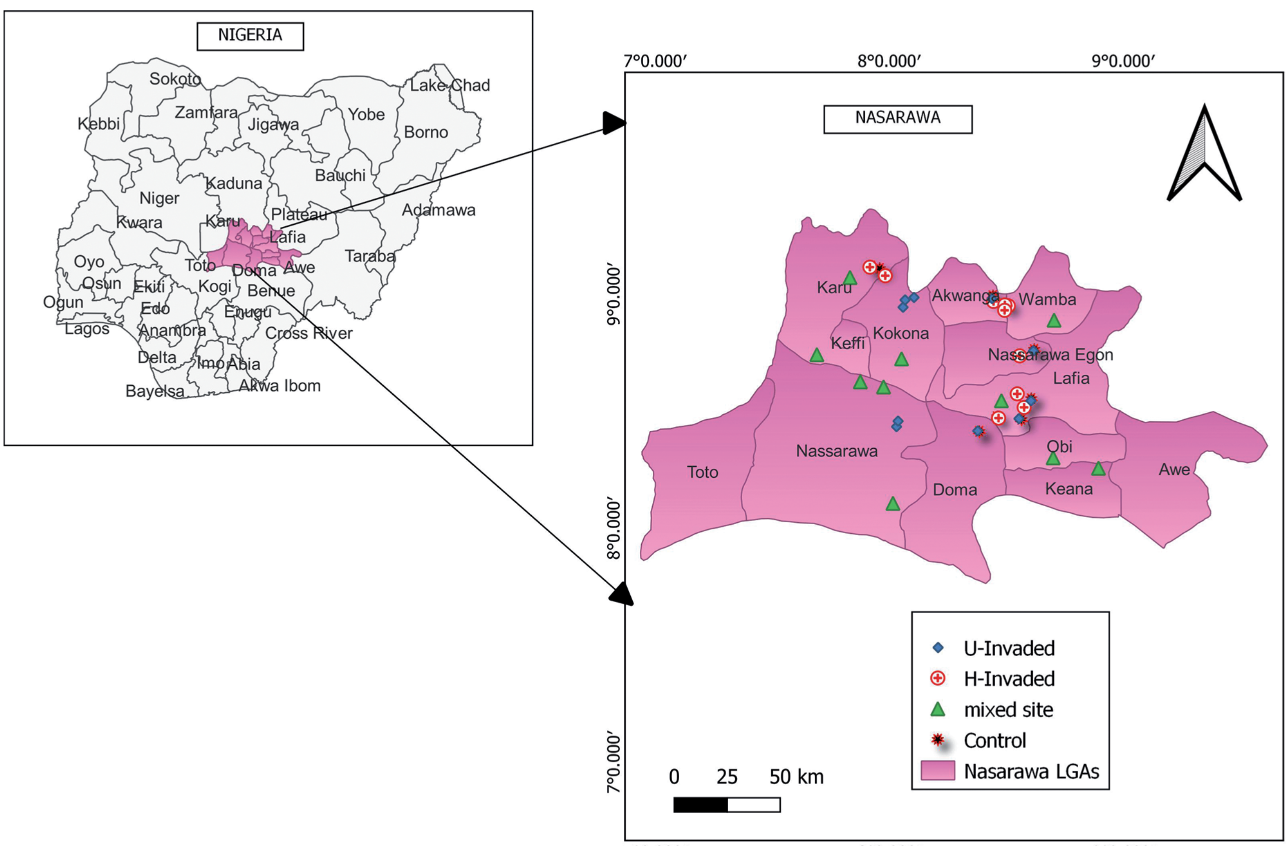

Fig. 1 Study area map showing the sampling sites.

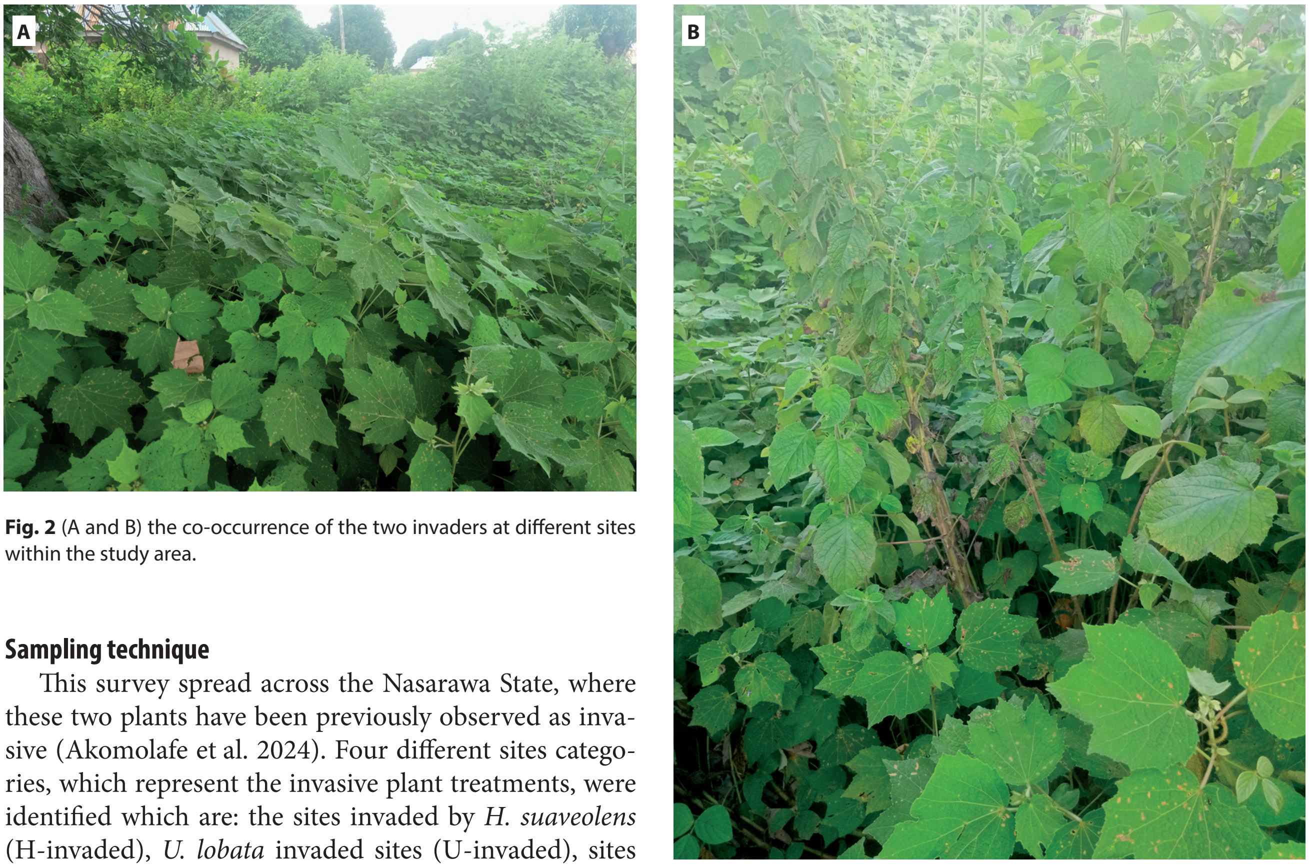

Fig. 2 (A and B) the co-occurrence of the two invaders at different sites within the study area.

Sampling technique

This survey spread across the Nasarawa State, where these two plants have been previously observed as invasive (Akomolafe et al. 2024). Four different sites categories, which represent the invasive plant treatments, were identified which are: the sites invaded by *H. suaveolens* (H-invaded), *U. lobata* invaded sites (U-invaded), sites where both plants co-invaded (mixed, Fig. 2), and uninvaded sites (control). We sampled 120 plots of 10×10 m^2 with 30 plots each in the invasive plant treatments mentioned earlier (i.e., H-invaded, U-invaded, mixed and control). In each plot, the abundance and frequency of all the plants found there were documented. Further precaution was taken to ensure that the selected plots have the same land use history, elevation range and soil type, so that the observed differences can be attributed only to species invasion (Coppi et al. 2022).

Soil sampling and chemical analysis

Ten soil samples were taken at ten different plots in each invasive plant treatment site using a soil core of 2.5 cm in diameter to a depth of 0–10 cm. This gave rise to a total of 40 soil samples. The samples were thereafter conveyed to the laboratory for drying at room temperature and sieving using a 2 mm sieve. The chemical contents of the soil such as the pH, phosphorus, nitrogen, calcium, potassium, magnesium, aluminium, soil organic matter and soil alkalinity were analysed using standard methods. The soil pH was determined using the glass electrode method in water suspension. Available phosphorus and potassium in the soil were determined using ammonium lactate extraction (Egnér et al. 1960). Other elements such as Al, Ca, and Mag were analysed after the digestion of the soil samples using concentrated acids (HNO_3 and H_2O_2) by following the methods described by Vujanovic et al. (2022).

Statistical analyses

We addressed the first question by determining the differences in resident plant communities and soil chemical properties among the treatments (i.e.: control, *H. suaveolens* invaded, *U. lobata* invaded and two co-occurring species invaded communities). The plant community structure was measured as alpha diversity (i.e.: species evenness, species richness, Simpson, and Shannon indices). The differences in the diversity indices among the treatments were determined using the Monte-Carlo permutation test. After this, generalized linear models with normal distribution for soil parameters and Poisson distribution for plant diversity indices were employed. In each of the univariate models, we chose soil chemical properties and plant diversity indices as the dependent variables, while the treatments were selected as the independent (categorical) variables. The significant difference among the treatments in each model was determined using the 95% confidence interval (CI). We also ran separate models using the invasive species treatments as numerical linear variables, and the results obtained were the same qualitatively as those of the previous models (Supplementary Table 1). All these analyses were performed in palaeontological statistics (PAST 3.0) software.

To determine the effect of invasive plant treatments on the resident plant diversity and soil chemical parameters, we performed a sparse partial least square discriminant analysis (sPLS-DA) using the XLSTAT package. In this analysis, we used the already identified significant plant diversity indices (Simpson, Shannon, and evenness indices) and soil chemical parameters (i.e.: phosphorus, calcium, aluminium, and soil alkalinity). Out of these variables, the analysis still removed some variables of lesser influence. Thereafter, we extracted the loadings and did a linear regression model using the treatments as the predictor and loadings as the dependent variable (Legendre and Legendre 2012).

The relationships between the soil chemical properties, plant diversity indices and invasive species treatments were assessed using the canonical correspondence analysis (CCA). In this CCA, the treatments were chosen as the response variables (the number of each plant species was the entry for each treatment), while the significant soil chemical properties (i.e.: phosphorus, calcium, aluminium, and soil alkalinity) and plant diversity indices (Simpson, Shannon, and evenness indices) were selected as constraining variables. The significance of the model was assessed using a permutation test (ANOVA-like) with 1000 bootstrap replicates. The CCA model loading was used to estimate the relationship between the plant species, soil chemical properties and treatments.

Results

Differences in plant diversity and soil chemical properties among the treatments

The different diversity indices of the invasive plant treatments are presented in Table 1. The indices of species richness and diversity of the control treatment are significantly higher than in all the other treatments ($p < 0.001$, Table 2). In comparing the mixed site with the U-invaded and H-invaded treatments, the mixed site had the significantly (at different p-values) lowest species richness and diversity, as revealed by several indices (Taxa_S, Shannon_H, Margalef and Fisher_ alpha). However, between U-invaded and H-invaded treatments, there were no significant differences in their diversity indices.

Our results showed general significant differences in phosphorus, calcium, aluminium, soil alkalinity, Simpson index, Shannon index, and evenness index among the invasive species treatments (Table 3), whereas the other soil chemical properties and species richness exhibited little variation across the treatments (Table 4). Phosphorus significantly increased in mixed site and control as compared to U-invaded and H-invaded, which were not significantly different from each other (Fig. 3A). Soil calcium and alkalinity in U-invaded, H-invaded, and mixed sites were significantly higher than in the control treatment (Fig. 3B and 3D). Also, aluminium content was significantly higher in the control than in the other treatments (Fig. 3C). The mixed site was observed to have the highest nitrogen and soil organic matter, though not significantly different from the single-species treatments. Simpson and Shannon indices in the control were significantly higher than in the other treatments (Fig. 3E and 3F). The evenness index in the control and mixed site were significantly higher than in the U-invaded and H-invaded treatments (Fig. 3G).

Effect of invasive plant treatments on plant diversity and soil chemical parameters

The results of the PLS–DA revealed that the first and second components explained 92.17% and 7.26% of the variance among the variables. Aluminium, phosphorus, Shannon index, Simpson index, and evenness index were positively correlated (each having correlation values of 0.43, 0.11, 0.43, 0.38, 0.29 respectively), while calcium and soil alkalinity were negatively correlated (each having correlation values of −0.44 and −0.45 respectively) with component 1. The regression analysis revealed that mixed treatment correlated most negatively and

Table 1 Diversity indices of the invasive plants invaded site treatments.

Diversity indices	U-invaded	H-invaded	Mixed site	Control
Taxa_S	16	15	4	68
Dominance_D	0.6286	0.5279	0.4496	0.02049
Simpson_1-D	0.3714	0.4721	0.5504	0.9795
Shannon_H	1.037	1.175	0.885	4.042
Evenness_e^H/S	0.1762	0.2158	0.6058	0.837
Brillouin	0.9635	1.07	0.8553	3.858
Menhinick	0.8889	1.115	0.2843	2.527
Margalef	2.595	2.693	0.5673	10.17
Equitability_J	0.3739	0.4337	0.6384	0.9578
Fisher_alpha	3.532	3.883	0.7099	18.39
Berger-Parker	0.7901	0.7127	0.4949	0.04696
Chao-1	16	17.5	4	68

Table 2 Significant differences in the diversity indices between the invasive plant treatments.

Diversity indices	U-invaded & H-invaded	U-invaded & Mixed site	U-invaded & Control	H-invaded & Mixed site	H-invaded & Control	Mixed site & Control
Taxa_S	0.9486	0.0001	0.0001	0.0003	0.0001	0.0001
Dominance_D	0.0067	0.0001	0.0001	0.0689	0.0001	0.0001
Simpson_1-D	0.3402	0.2824	0.0001	0.0305	0.0001	0.0001
Shannon_H	0.5324	0.0001	0.0001	0.0001	0.0001	0.0001
Evenness_e^H/S	0.0067	0.0001	0.0001	0.0689	0.0001	0.0001
Brillouin	0.3232	0.0002	0.0001	0.0001	0.9314	0.0001
Menhinick	0.8987	0.0001	0.0001	0.0001	0.0001	0.0001
Margalef	0.179	0.0001	0.0001	0.0001	0.0001	0.0001
Equitability_J	0.7481	0.0001	0.0001	0.0002	0.055	0.0001
Fisher_alpha	0.0928	0.0001	0.0001	0.0001	0.0001	0.0001
Berger-Parker	0.9486	0.0001	0.0001	0.0003	0.0001	0.0001
Chao-1	0	0	0	0	0	0

NB: The values represent p-values of the ANOVA-live permutation test.

Table 3 The soil chemical properties across the invasive plant treatments.

Soil properties	U-invaded	H-invaded	Mixed site	Control
pH (water)	5.7 ± 0.3	6.9 ± 0.2	6.2 ± 0.2	4.9 ± 0.3
pH (CaCl2)	5.3 ± 0.1	5.8 ± 0.2	5.4 ± 0.1	4.2 ± 0.2
Phosphorus (dag/kg)	0.5 ± 0.1	0.3 ± 0.1	1.5 ± 0.5	1.2 ± 0.1
Nitrogen (dag/kg)	0.32 ± 0.02	0.51 ± 0.02	1.62 ± 0.3	0.82 ± 0.1
Potassium (dag/kg)	34.1 ± 6.7	54.3 ± 12.3	96.71 ± 15.4	19.74 ± 6.5
Magnessium (cmol/dm^3)	1.2 ± 0.4	1.7 ± 0.2	1.6 ± 0.1	0.8 ± 0.1
Calcium (cmol/dm^3)	10.3 ± 1.2	10.8 ± 1.2	11.1 ± 1.4	4.5 ± 1.2
Aluminium (cmol/dm^3)	nd	nd	0.02 ± 0	0.84 ± 0.1
Soil organic matter (dag/kg)	12.1 ± 2.2	12.6 ± 2.2	16.6 ± 2.4	5.6 ± 1.5
soil alkalinity (sum of bases)	11.6 ± 2.0	12.7 ± 3.1	12.7 ± 3.2	5.4 ± 1.3

Nd means not detected.

Table 4 Summary of the regression model with invasive species treatments as predictor.

Response variable	Chi-square	P-value	R2
pH (water)	1.94	0.45	0.23
pH (CaCl2)	1.28	0.17	0.49
Phosphorus	1.09	0.03	0.86
Nitrogen	1.64	0.3	0.35
Potassium	2.5	0.99	0.02
Magnesium	2.08	0.53	0.17
Calcium	1.26	0.04	0.79
Aluminium	0.95	0.05	0.72
Soil organic matter	2.02	0.49	0.19
soil alkalinity	1.33	0.01	0.87
Species richness	1	0.41	0.43
Shannon index	1	0.02	0.56
Simpson index	1	0.05	0.85
Species evenness	1	0.05	0.93

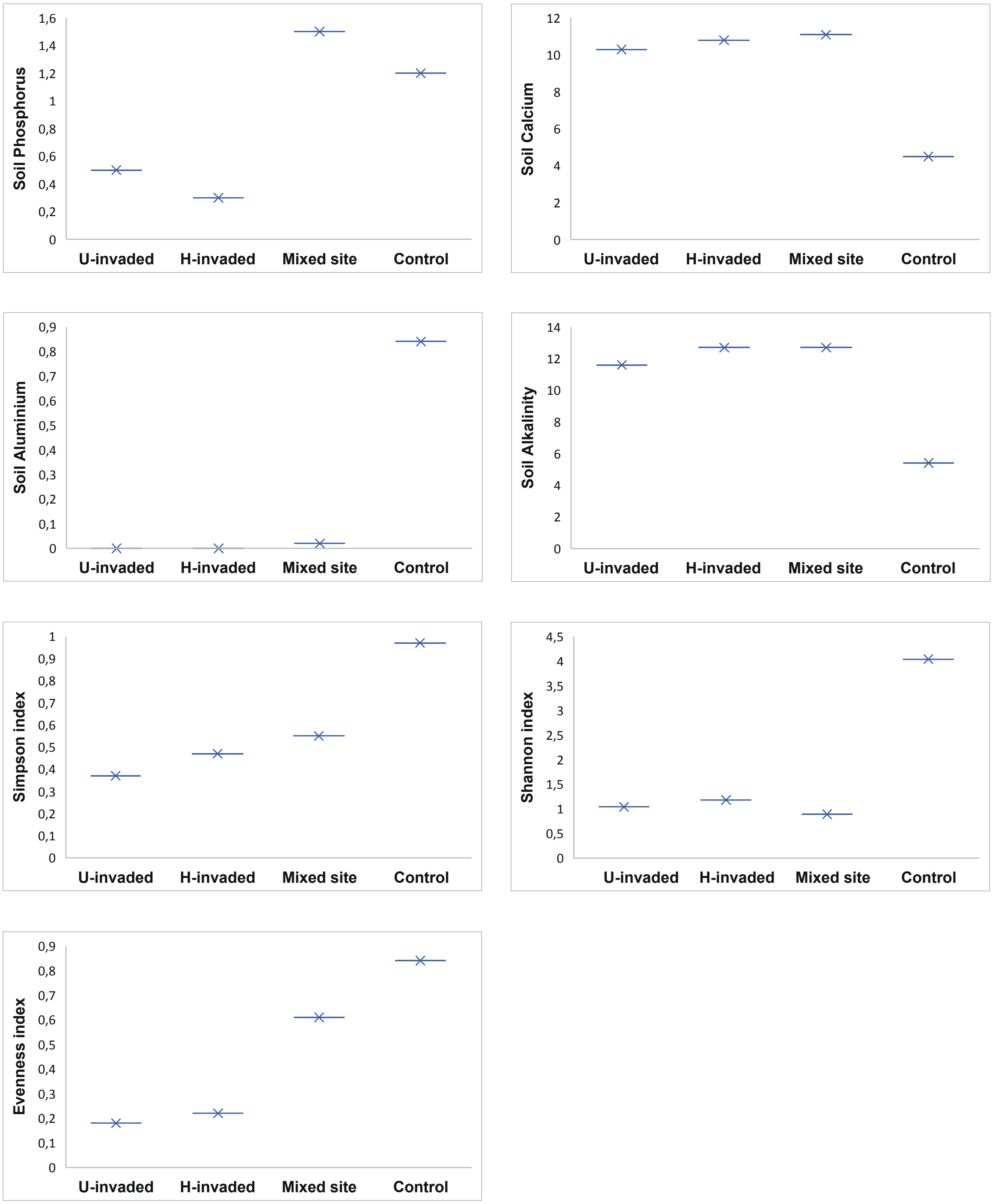

Fig. 3 Effects of invasive species treatments (U-invaded, H-invaded, Mixed site, and control) on different soil chemical properties phosphorus; calcium; aluminium; soil alkalinity and Plant community diversity indices Simpson index; Shannon index; evenness index.

significantly with the first axis ($\beta = -2.47 \pm 0.56$, $P = 0.02$), while control was most positively correlated with the first axis ($\beta = 0.12 \pm 0.05$, $P > 0.05$). The H-invaded ($\beta = -0.84 \pm 0.16$, $P > 0.05$) and U-invaded ($\beta = -0.04 \pm 0.03$, $P > 0.05$) which are single-species treatments were also negatively correlated with axis 1, though not significantly so.

Relationship among plant diversity, soil properties and the invasive species treatments

The multivariate canonical correspondence analysis revealed that the first two axes represent 100% of the total variance in the plant species distribution across the invasive species treatments (Fig. 4). The first axis represents 79.74% of the total variance. The mixed site was on the first axis ($x_{mixed} = 5.38$), while the other single-species treatments and control were distributed along the second axis ($x_{U\text{-}invaded} = 1.41$, $x_{H\text{-}invaded} = 1.57$ and $x_{control} = -0.69$). Calcium and soil alkalinity were positively correlated with the first axis (0.93 and 0.91 respectively), while phosphorus (−0.11), aluminium (−0.93), Simpson index (−0.89), Shannon index (−0.96), and evenness index (−0.61) were negatively correlated with it.

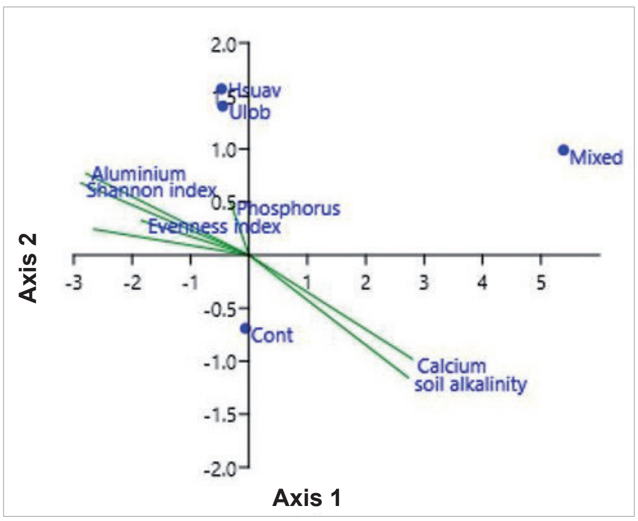

Fig. 4 CCA biplot showing the relationship among plant diversity, soil properties and the invasive species treatments.

Discussion

It is a well-known fact that invasive species are co-occurring in several ecosystems worldwide. However, studies exploring the impacts of the co-occurrence of these invaders (on both soil and native plant diversity) in West African ecosystems are very rare. Our study has revealed the differences in the impacts of the single-species invasion and co-occurrence in the study area. The greater impact of these co-occurring invasive species was observed in the lower plant species richness and diversity of the mixed site in comparison with the control and all the other single-species invaded treatments. The rate of dominance and colonization of invasive plants is normally expressed in the impacts they made on the native plant communities (Chmura et al. 2015; Czarniecka-Wiera et al. 2019). Our observation at the mixed sites where the two species co-occurred shows that both *H. suaveolens* and *U. lobata* contributed almost equally to the total plant cover. This could be a strong reason to deduce that the lower species richness and diversity observed at the mixed site were due to the harmonious impacts of these two invasive plants.

The cumulative allelopathic effects of the invaders could also be partly responsible for the reduction in the native species diversity of the mixed site since most invasive plants are known for exhibiting allelopathy (Coppi et al. 2022). It has not been clearly reported that *U. lobata* exhibits strong allelopathy in literature. However, several studies have reported the strong allelopathic effects of *H. suaveolens* on other plant species (Islam et al. 2013; Maiti et al. 2015; Poornima et al. 2015; Suntia and Singh 2015). At the mixed site, the reduction of the native species diversity affected both annual and perennial herbaceous and woody plants. This further proves the strong effects of the synergistic influence of the two invaders. Specifically, it was only two species *Hyptis lanceolata* and *Heteropogon contortus* that were found together with *H. suaveolens* and *U. lobata* at the mixed sites.

Our observations showed that there were variations in the soil's chemical properties among the invasive plant treatments. As revealed by the PLS-DA and regression analyses, the co-occurring species at the mixed site exerted a more significant negative influence on the soil properties and diversity indices, such as aluminium, phosphorus, Shannon index, Simpson index, and evenness index than when occurring singly at U-invaded and H-invaded sites. This further indicates the joint effects of these two invaders on the soil properties, when co-occurring. Soils invaded by co-occurring invasive plants have been described as normally having a high amount of nitrogen, carbon, and organic matter (Coppi et al. 2022). This was not totally true in our study, where the mixed site had a higher amount of nitrogen and organic matter, but not significantly different from the other treatments. A large amount of nitrogen and organic matter was said to have been due to the higher amount of litter produced by the co-occurring high-impact invasive plants, which decomposed at a more rapid rate than in other treatments (Krevš et al. 2013; Jo et al. 2016; Incerti et al. 2018).

Although our study did not involve the determination of the soil microbial communities of these invasive plant treatments, past studies have related the increase in soil organic carbon and nitrogen directly to the increased activities of soil microbes (Jo et al. 2017; Coppi et al. 2022). The results of the CCA also indicate that the mixed site had a strong negative relationship with the diversity indices. This further suggests that the influence of the joint invasion of the two plants reduces the plant diversity and richness of the areas affected.

Conclusion

From our observations in this study, we conclude that the joint invasion by *U. lobata* and *H. suaveolens* in the study area could promote their persistence in the ecosystem through the strong negative impacts on the native species diversity and change in the soil properties. The impacts of these two co-occurring invaders in the study area tend to be more additive than non-additive. By implication, restoration efforts on these co-invaded sites might be more difficult in the future if neglected or not prioritized now. Therefore, it is recommended that more priority be placed on the application of integrative control and management methods on these two invasive plants in the study area and any other part of the world, where co-occurring invasive species have threatened the natural ecosystems. This will help in reducing the negative effects of these plants on the native plant species.

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