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Soil and plant chemical profiles of invasive *Cyperus aromaticus* (Cyperaceae) and co-occurring pasture species across land-use types: potential implications for invasion and plant–soil feedbacks

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ABSTRACT

Context. Biological invasions diminish the structures of ecosystems and biological functions. In this regard, *Cyperus aromaticus* (Cyperaceae) (Navua sedge), a native of Africa, recently established along the coastal regions of far north Queensland (FN-QLD), Australia, forming extensive monospecific stands and affecting both agricultural and natural landscapes. **Aims.** This study examined the changes in soil physico-chemistry and differences in plant tissue chemical profile of *C. aromaticus* and its co-occurring pasture species in invaded landscapes of varying land-use types. **Methods.** Across many *C. aromaticus* invaded sites in FN-QLD ($N = 14$), we collected above-ground vegetation and soils in invaded and nearby non-invaded patches. We also set up a microcosm trial in which *C. aromaticus* and a desirable pasture grass species (*Urochloa humidicola*) were grown individually in potted soils, and changes in soil chemistry were monitored for 3 years. **Key results.** Neutral effects of *C. aromaticus* invasion were detected in soils of active agricultural lands, but significant differences occurred in other land-use types (roadside, riparian corridor, abandoned agricultural land) and in the microcosm trials. The plant tissues of *C. aromaticus* are higher in many micronutrients (e.g. sulfur, copper, aluminium, iron, zinc) than those of co-occurring pasture species. Significantly higher lignin concentration, but lower forage quality of fibre, cellulose, and hemicellulose were also detected in *C. aromaticus*. **Conclusions.** *C. aromaticus* invasion is associated with changes in soil processes and systems, but its effect can be obscured by land-use (e.g. anthropogenic) practice. In invaded landscapes, the changes in soil chemistry and observed differences in tissue composition between *C. aromaticus* and co-occurring pasture grasses might lead to positive plant–soil feedback, thus promoting the establishment and further spread of the weed. Additionally, the lower forage quality of *C. aromaticus* reinforces the need to manage the weed, especially in grazing landscapes. **Implications.** These findings highlight the capacity of *C. aromaticus* weed to modify soil processes and ecosystem functions, reinforcing its threat to both ecological integrity and agricultural productivity in north-eastern Queensland.

Keywords: above-below ground processes, biological invasion, leaf chemistry and nutrition, Navua-sedge, ordination technique, pasture grasses, soil physico-chemistry, weed impact.

Introduction

Biological invasion, a process increasingly accelerated by anthropogenic activities such as habitat fragmentation and worldwide human movement, imposes severe costs on nature. Biological invasion hinders the provisions of ecological goods and services, including biodiversity reduction and alterations of ecosystem structures and functions (Seebens *et al.* 2018; Hulme *et al.* 2024). Of the new species introduced into novel environments, only ~10% successfully established in their new range, mainly through a sequential process of dispersal, colonisation, extinction, recolonisation, establishment, naturalisation and spread (Kowarik 1995; Coutts *et al.* 2018; Duncan 2021). The spread of these invasive alien species (IAS) could be insidious and slow, taking a long period to manifest or could occur within a short duration (lag time) (Kowarik 1995; Osunkoya *et al.* 2021). In both scenarios, the consequences are grave as ecological systems in natural or agricultural landscapes are changed, often adversely, and are challenging to reverse to their natural states (Gioria *et al.* 2014; Shackleton *et al.* 2020).

Below-ground processes and systems comprise a suite of soil and food-web interactions that are vulnerable to disruption by biological invasions. This is especially critical of IAS (e.g. weed) incursion (Gioria *et al.* 2014; Frouz 2024). Many empirical works have shown that weed incursions, through their dominance, tissue and litter properties, affect all aspects of soil processes and systems, including soil physico-chemistry (Osunkoya and Perrett 2011; Perrett *et al.* 2012; Osunkoya *et al.* 2017; Xie *et al.* 2023), soil biota (Osunkoya *et al.* 2011; Zhang *et al.* 2019), soil seed banks (Gioria *et al.* 2014; Chadha *et al.* 2022*a*), soil litter quality and decomposition process (Castro-Díez *et al.* 2019; Souza-Alonso *et al.* 2024), soil enzyme activities (Elgersma and Ehrenfeld 2011; Corneo *et al.* 2013; Osunkoya *et al.* 2017; Zhou and Staver 2019), soil nutrient cycle and allelopathy (Scharfy *et al.* 2010; Greer *et al.* 2014; Kalisz *et al.* 2021), and soil DNA signature (metabolomic) (Skoneczny *et al.* 2017; Clerissi *et al.* 2023). These changes invoked by IAS ultimately influence soil–plant feedback and its mechanisms (Qu *et al.* 2021; Frouz 2024). The changes, including their directions and magnitudes, may be apparent and easy to recognise, but at times are obscured by the nature of the landscape and types of land use. In this respect, documenting changes in soil processes in the field requires taking samples from paired (adjacent) patches of weed invasion and weed-free areas. However, the signals for the weed impact may be weak or non-existing where there are continuing fertiliser inputs by farmers in grazing and cropping lands and/or by animals (such as cattle) that freely move around, depositing faeces randomly in the paddock. Intensity of the weed impact also might be a function of plant life form, invasion extent and time since invasion (Meisner *et al.* 2014; Xu *et al.* 2022; Gruntman and Segev 2024). To overcome these challenges, several authors have called for microcosm trials where the weed of interest is grown in a controlled environment and the changes in soil property can be documented over time (Elgersma and Ehrenfeld 2011; Corneo *et al.* 2013; van der Putten *et al.* 2013; Niu *et al.* 2023).

In the invaded range, the exotic weed may spread and outcompete co-occurring plants. Among other factors, the presence of a different chemical profile of the tissue of exotic invasive plants compared with that of native/non-invasive exotic species has been implicated in the spread of IAS (Greer *et al.* 2014; Dai *et al.* 2020; Frouz 2024). Where and if some of the IAS plant's chemical signatures are absent (and hence novel) in the new environment, it may allow the invader to escape predation by herbivores such as insects and grazing animals, including cows, thereby offering opportunity for the exotic invasive plant to pre-empt the use of space, proliferating, and/or outcompeting co-occurring plants, perhaps via allelopathy (Kalisz *et al.* 2021; Qu *et al.* 2021). These factors are likely to result in creation of monospecific stands of the invader (Greer *et al.* 2014; Skoneczny *et al.* 2017; Pyšek *et al.* 2019; Dai *et al.* 2020). Plant chemical profile studies provide an additional tool for a deeper understanding of biological invasion and have made contribution to the so-called 'novel weapon/escape/evolution of increased competitive ability' hypotheses (Jogesh *et al.* 2008; Sasu *et al.* 2023; Griffin-Nolan *et al.* 2024).

In this study, we quantified above-ground biomass, cover, abundance, and the chemical profiles of plant tissues and topsoil for an exotic sedge (a monocot) exhibiting invasive behaviour in northern Queensland Australia landscapes. These metrics were compared with those of co-occurring native or non-invasive exotic species. *Cyperus aromaticus* (Ridl.) Mattf. & Kük. (*Cyperaceae*) (common name: Navua sedge) is native to equatorial Africa and has become established (~1970) along the coastal (eastern) part of northern Queensland (QLD), affecting both agricultural and natural landscapes. *C. aromaticus* is now classified as an exotic weed of great concern in the State of QLD (https://www.business.qld.gov.au/industries/farms-fishing-forestry/agriculture/biosecurity/plants/invasive/other/navua-sedge), with a current control cost of A$2300–35,600 per affected farmer (~A$80 per hectare; Osunkoya *et al.* 2025). Although, currently, *C. aromaticus* is not a prohibited nor restricted invasive plant species, property owners have a legal obligation to manage it under the *QLD Biosecurity Act 2014* (https://www.business.qld.gov.au/industries/farms-fishing-forestry/agriculture/biosecurity/plants/invasive).

Focussing on various land-use types (riparian corridors, roadsides, grazing lands and sugarcane plantations) that *C. aromaticus* has established in northern QLD as well as making use of microcosm trials in a control glasshouse environment, our aims are to:

a. document and explore differences in above-ground species cover, abundance and biomass at sites with and without *C. aromaticus* invasion;
b. examine how *C. aromaticus* invasion alters physico-chemical properties of soils in affected areas, including major, minor, and trace elements; these analyses provide insights into changes in soil as a key indicator of ecosystem health and function;
c. compare the tissue profile (plant elemental composition of major- and micronutrients, and complex macromolecules [such as fibre and lignin] as a measure of forage quality) of *C. aromaticus* weed to those of co-occurring, desirable pasture grass species. We embarked on the last aim of this work because *C. aromaticus*, in its invasion of grazing landscapes, often co-occur with palatable pasture grasses, and cattle are known to feed accidentally and/or intentionally on the weed. Thus, plant tissue profile was examined to assess how invasion of *C. aromaticus* might alter forage quality.

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Materials and methods

C. aromaticus invasion history and study site description

C. aromaticus is a monocot weed that is native to equatorial Africa, the Seychelles, Mauritius and Madagascar. *C. aromaticus* is of a relatively recent incursion in the northern part of the State of QLD, Australia (Osunkoya *et al.* 2021; Shi *et al.* 2021). Following its introduction into Cairns, a town in northern region of QLD, in the 1970s (anecdotally via the Pacific Island of Fiji, and hence, where its common name, Navua sedge, is derived from), *C. aromaticus* experienced a relatively short lag time of ~23 years and, by 1990s, became explosive in its spread and abundance (Osunkoya *et al.* 2021). *C. aromaticus* has become an aggressive weed, affecting the beef, dairy and sugarcane industries in both coastal and upland parts of the QLD wet tropics (see Shi *et al.* 2021; Osunkoya *et al.* 2025). The weed is known to spread through both seeds and underground rhizomes into agricultural and natural landscapes, including riparian (waterway) corridors and along roadsides and railway lines, and can form dense monospecific stands, often replacing palatable tropical pasture species of the region (Chadha *et al.* 2022*a*; Shi *et al.* 2023). Parker *et al.* (2007) also ranked *C. aromaticus* in their risk assessments of 250 incoming (horizon) species into the USA as a candidate exotic in the top 25 that is likely to become invasive and cause damages in agriculture or natural systems.

Affected grazing and cropping (especially sugarcane) farmers of the QLD wet tropics region are acutely aware of the spread of *C. aromaticus* and have adopted integrated weed management and control measures for the weed (see Osunkoya *et al.* 2025). These include strict on-farm biosecurity measures and the planting of competitive pasture species following herbicide/cultural treatment of invaded, localised patches, including *Urochloa humidicola* (Humidicola), and *Chloris gayana* (Rhodes grass) (Shi *et al.* 2023; Osunkoya *et al.* 2025). Affected stakeholders in the region have also demonstrated the ineffectiveness of the registered herbicide (Sempra; Nufarm Australia; active ingredient: halosulfuron–methyl) on the weed (Chadha *et al.* 2022*b*; Osunkoya *et al.* 2025) and are now requesting for more herbicide trials as well as a speedy development and release of biological control agents to curtail the spread and impact of *C. aromaticus* (see Dhileepan *et al.* 2024).

C. aromaticus invasion dynamics were investigated in 14 selected sites that spanned a distance of ~500 km (long) × 100 km (wide) across the eastern coastal region of far north- QLD (Fig. 1, Supplementary Table S1). The investigated sites varied widely in land-use types, ranging from agricultural farmlands for cattle grazing ($N = 8$) and sugarcane crop production ($N = 2$), to natural landscapes including riparian corridors ($N = 2$) and roadsides ($N = 2$). Ten of these sites were along the coastal strips of the northern QLD wet tropics, stretching from the agricultural township area of Ingham to the dense rainforest area of Daintree and Cape Tribulation in far-northern QLD, whereas four sites were in the upland region of the Atherton Tablelands (Fig. 1). The coastal areas experience higher temperature (min/max: 20–33°C) and rainfall (average: 3500 mm/year) than do the upland areas (temperature, min/max: 17–28°C; and rainfall average: 1800 mm/year) (https://www.bom.gov.au/location/australia/queensland/north-tropical-coast-and-tablelands), resulting in differences in biodiversity and plant growth. For an in-depth description of the vegetation of the wet tropics region of QLD, see https://www.dcceew.gov.au/parks-heritage/heritage/places/world/wet-tropics.

Sampling to quantify above- and below-ground invasion effect

At each of the 14 chosen focal sites, we identified four to eight vegetation patches (each ~30–60 m^2 in size) with visible, heavy invasion of *C. aromaticus* as well as corresponding adjacent areas (~4–8 m from the invaded patches) lacking or having a very low density of the focal weed. These areas were used for survey and collection of above-ground vegetation and below-ground (soil) data. In the centre of each paired-patch (invaded vs non-invaded) area, a 1 × 1 m quadrat was placed on the ground for soil sampling. Also, within each quadrat, a smaller area of 50 × 50 cm dimension in the middle was selected, marked and used for vegetation (mainly pasture) sampling and measurements. Within each smaller quadrat, three independent assessors identified and counted number of plant species (*C. aromaticus*, other monocots and broadleaf [dicots]) and visually estimated the mean percentage of foliar cover per taxonomic group. Thereafter, the entire mass of aboveground vegetation in each of the smaller plot were clipped and placed in labelled paper bags for dry-matter (biomass) estimation later in the laboratory. For soil chemistry profile, from each corner and the middle of the larger size (i.e. 1 × 1 m) quadrat, the litter layer was cleared and soil samples down to a depth of 10 cm were collected using a handheld soil corer (7 cm in diameter, 10 cm deep); the resulting five soil cores per quadrat were then pooled into a single bag to make a composite sample for chemical analyses (see also Osunkoya and Perrett 2011). Because of logistic and time constraints, samplings of above-ground vegetation were conducted in only 6/14 (three each in coastal vs upland region) of our focal sites (see Chadha *et al.* 2022*a* for details), whereas below-ground (soil) samplings were taken in 9/14 sites. The sampling of paired *C. aromaticus* invaded versus weed-free patches occurred simultaneously at each site. Soils in all invaded grazing lands were collected in April 2021, whereas times of collection in other land-use types (riparian, roadside and abandoned farm) varied somewhat but were in the same year of 2021 (see Table S1).

Sampling for plant tissue chemistry

Above-ground tissue (leaf and tiller [stem]) of *C. aromaticus* and of co-occurring pasture plants (grass species) was collected

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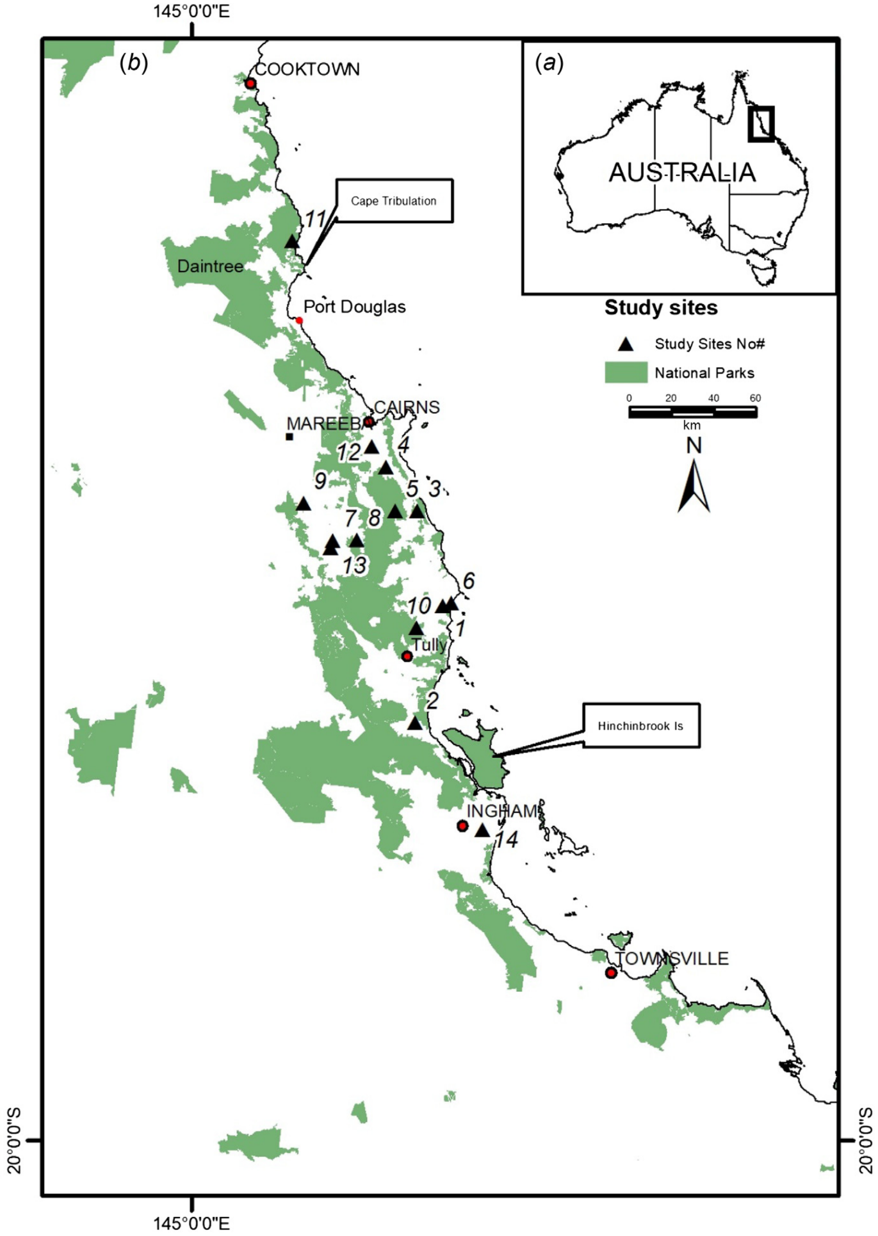

Fig. 1. Map of Australia, showing (*a*) the study locations between Cooktown and Townsville in northern Queensland, Australia, and (*b*) zoomed-in map indicating the 14 study sites. Numbers on the map represent nearest township to the study sites as follows: (1) McCutcheon; (2) Cardwell; (3) Babinda; (4) Aloomba; (5) Babinda II; (6) Cowley; (7) Malanda/Tarzali (upland); (8) Topaz (upland); (9) Atherton (upland); (10) Innisfail; (11) Cape Tribulation; (12) Gordonvale; (13) Malanda (upland); and (14) Ingham.

from the field sites. These pasture species, many of which have been introduced from tropical Africa (see Cook and Dias 2006), are *Setaria sphacelate* (Setaria grass), *Urochloa humidicola* (humidicola), *Urochloa decumbens* (signal grass), *Chloris gayana* (Rhodes grass), and *Megathyrsus maximus* var. *maximus* (Guinea grass). The last co-occurring grass species, *Megathyrsus maximus*, is a coloniser of disturbed sites, including roadsides and is often regarded as an environmental weed in QLD. For each species, plant tissue materials were collected from three to eight clumps per site, each clump being ~5–10 m apart. *C. aromaticus* plant materials were collected in 12 of the 14 sites (Table S1), whereas collection sites for co-occurring pasture grass species varied depending on their availability (see Table S1). In the laboratory, collected materials were washed to remove any surface dirt, and damaged or senescing leaves and tillers were discarded. Samples

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were then dried in oven at 60°C for 48 h prior to chemical analyses.

Invasion effect on soil properties under microcosm/control condition

To control for anthropogenic influence (e.g. fertiliser addition on grazing lands) on soil chemical profile, and thus, to test the validity of the field results, in May 2018 we grew from seeds our focal weed (*C. aromaticus*) and a co-occurring desirable non-native/non-invasive pasture species (*Urochloa humidicola* [humidicola]) (https://www.selectedseeds.com.au/pasture-grasses). Each species was grown alone (i.e. as monospecific) in pots ($N = 5$ pots per species) in an evaporative cooling glasshouse at the EcoSciences Precinct of QLD Department of Primary Industries in Brisbane, Australia. Pot size was 25 cm in diameter and 30 cm deep, growth condition averaged 28 ± 2°C, and relative humidity was maintained at 65% under natural photoperiod. A commercial potting mix (Centenary Landscaping, Darra, QLD, Australia) was used (see Table S2) and no additional fertiliser was applied during the trial. Pots were watered regularly once a day. Yearly (2019, 2020 and 2021), following hand-clearing of each pot litter layer, we sampled the soil beneath the plants to a depth of 10 cm and assayed the soil for chemical changes (see below) in relation to plant types.

Soil physico-chemistry profile determination

Soil analytical procedures used in this investigation have been fully explained elsewhere (see Osunkoya and Perrett 2011; Perrett *et al.* 2012; Osunkoya *et al.* 2017). In summary, the hydrometer test was employed to determine the amount of clay (<2 μm) and silt (2–20 μm) in the soil, whereas the sieving method was used for the larger-size aggregates of fine (0.02–0.2 mm) and coarse (0.2–2.0 mm) sands. All chemical analyses are based on soil samples that were initially oven dried at 40°C for 48 h and were conducted in a National Association of Testing Authorities (NATA) accredited soil laboratory in Brisbane, Australia. To ensure that the results were accurate and repeatable, a maximum of 10% variation within sample results was required before adding them to the data bank. Full details of the analytical procedures are in Supplementary material Box 1. Air dry moisture content (ADMC), soil electrical conductivity (EC, a measure of soil salinity), pH, chloride (Cl^-), total nitrogen (TN), total carbon (TC), and organic carbon (OC) were determined by the wet-combustion technique of Walkley and Black, described by Piper (1942). Exchangeable cations of calcium (Ca), potassium (K), magnesium (Mg), and sodium (Na) were measured using extraction method of Tucker (1974). Extraction for estimation of micronutrients of copper (Cu), iron (F), manganese (Mn), and zinc (Zn) were as in Lindsay and Norvell (1978). Determination of macronutrient of sulfur (S) was as in Tabatabai (1996). Cation exchange capacity (CEC, which is the sum of all cations) was estimated by measurement of ammonium ion displaced from the treated soil by a potassium nitrate–calcium nitrate solution. Ammonium (NH_4-N) and nitrate (NO_3-N) contents were estimated following the recommendation by Keeney and Nelson (1982). Available phosphorus (P avail.) was determined on the basis of Colwell (1963) method.

Plant chemical profile determination

Plant total organic matter was determined gravimetrically by difference in weight via loss on ignition (LOI) at 600°C. Plant total C and total N contents were analysed using the Dumas combustion technique at 1300°C and flushed with oxygen (Buckee 1994). The process generated gases, which were measured using an infra-red detector for carbon, and thermal conductivity cell for nitrogen. Determination of trace and heavy metals of cadmium (Cd), cobalt (Co), molybdenum (Mo), lead (Pb), and selenium (Se) involved adding hydrogen peroxide and nitric acid mixture to the dry plant sample and heating until completely digested. Digests are then read by inductively coupled plasma mass spectroscopy for concentration of each of the metal element mentioned above (McQuaker *et al.* 1979). Similar digestion methods were used for plant aluminium (Al), boron (B), calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), sulfur (S), and zinc (Zn), but their concentrations were determined by inductively coupled plasma spectroscopy. With this latter method, low detection thresholds can be obtained for several elemental ions simultaneously.

Plant major/macronutrients of fibre, lignin, cellulose and hemicellulose

For a comparative nutritional evaluation of the plant tissue of *C. aromaticus* and co-occurring pasture plants (*Setaria sphacelate*, *Urochloa humidicola*, *Urochloa decumbens*, *Chloris gayana* and *Megathyrsus maximus*), various forage quality indices were measured on the plant samples (leaves and tillers combined) collected. All analyses were performed in triplicate for each sample of the collected plant biomass. Neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin concentrations were measured using reflux methodology (Van Soest *et al.* 1991; Undersander *et al.* 1993). ADF was determined gravimetrically as residue remaining after acid detergent extraction. Lignin was evaluated by subjecting the acid detergent fibre residue to 72% sulfuric acid. Note that NDF and ADF represent the indigestible and digestible part of plant cell walls respectively, and lignin is the total indigestible plant component. Cellulose concentrations were estimated as the difference between lignin and ADF; the hemicellulose fraction was determined by subtracting ADF from NDF (Moore and Jung 2001).

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Data analyses

Data were analysed using IBM–SPSS (ver. 28, IBM Corporation, USA) and PRIMER statistical package (ver. 7.0, PRIMER-E Ltd, Plymouth, UK) software. All data were checked for homogeneity of variance (using Levene's test and histogram plots), and where necessary log *x* transformed to meet the assumption of parametric tests. The following traits were transformed: (i) TC, OC, Zn, K and NO_3-N of field soil data, (ii) Cl, S, Cu of microcosm (glass house) soil data and (iii) all trace ions/micronutrients, except Co and Cu, for plant tissue chemistry. For the soil field data, two-way ANOVA involving site (SI), *C. aromaticus* invasion (I) and their interaction effect (SI × I) was performed on each trait. Because of profound difference in bioclimatic conditions, coastal–upland (regional) trends in invasion effects on soil chemistry and above-ground plant traits were examined at 6 of the 14 surveyed sites, all located within grazing landscapes (three each in upland and lowland regions). We used a three-way ANOVA, testing the main effects of site (SI), invasion (I), region (R), and the interactions of SI × I and I × R (the SI × R interaction could not be tested because not all sites were present in all regions). We also quantified invasion impacts across three distinct land-use categories, namely, riparian zone, roadside verge, and abandoned grazing land, analysing each type (site) both independently and as part of a composite land-use category that are characterised by the absence of continuous or pronounced anthropogenic nutrient enrichment.

The above-ground vegetation biomass was analysed as a three-way ANOVA of site (SI), invasion (I) and region (R); however, for simplicity only the main effects and two-way interaction effects (SI × I, I × R) are reported. For the microcosm trial, a two-way ANOVA was also performed on the soil chemistry, with year (Y) and plant type (the invasive *C. aromaticus* vs desirable pasture grass [*Urochloa humidicola*]) as main effects; their interaction effect (Y × I) was also modelled. For analyses of tissue chemical profile of plants collected in the field, two-way ANOVA of plant type (PT) (the invasive *C. aromaticus* vs all co-occurring pastures [pooled]) and site (SI) was conducted; no interaction effect was included in the model because not all pasture species occurred at each site where *C. aromaticus* has invaded and where materials were collected. In all cases, significant effects were identified at $P < 0.05$. Parametric correlation analyses were also invoked to examine bivariate relationships between soil or plant tissue chemical traits for the invasive *C. aromaticus* or for co-occurring pasture grasses.

Ordination is a powerful exploratory statistical technique to generalise trends in large multivariate datasets, allowing data to be constrained on two or three major axes with minimal loss of information (Clarke and Warwick 2001; Clarke and Gorley 2006). As soil and plant data collected were mainly continuous (interval) data in nature, a series of principal component analyses (PCA) were conducted, involving data transformation ($(\log(x+1))$ or arcsine square root (x)) followed by creation of resemblance matrix of predictor/s of interest (site, invasion status, species type, etc.) by using Euclidean distance, and groupings (if any) were then displayed on two or three major axes as in PRIMER (ver. 7) software. For evidence of significant differences between groupings (in our case, invaded vs non-invaded soil or chemical profile of *C. aromaticus* vs co-occurring pasture plants), we used analysis of similarities (ANOSIM) options within the PRIMER (ver. 7) software. Analogous to ANOVA, ANOSIM compares the mean difference of ranks within and among groups, generating the statistic R (Clarke and Warwick 2001; Clarke and Gorley 2006). Values of R range from −1 to +1, with negative values and values near 0 indicating similarity between groups, and values approaching $R = 1$ indicating a strong dissimilarity between groups.

Results

C. aromaticus appears capable of establishing and thriving in a wide array of landscape and soil types of northern Queensland, from riparian corridors with high fine sand content (up to 54.6%) and slightly acidic/near neutral pH (5.56) to roadsides and agricultural systems of coarse sand (up to 38.17%) and growth medium that are more acidic in nature (pH 4.73). In general, the soil physico-chemical properties differed significantly across sites, land-use and landscape (regional) types, with the pH in many cases, being mostly acidic (pH 5.19–5.27; Tables 1, S3). The above-ground plant dynamics varied more at sites of the coastal region than at the upland sies (Fig. 2). In contrast, the dynamics of the soil physico-chemical properties (irrespective of the invasion status) varied more for upland regions of the Atherton Tablelands than in the coastal regions (Fig. 3).

Invasion effects on above- and below-ground processes

Invaded plots, irrespective of region (coastal vs upland), had significantly ($P < 0.001$) higher above-ground biomasses of the *C. aromaticus* weed (30.34 g/0.25 m^2) than did the control, mostly weed-free plots (2.47 g/0.25 m^2); *C. aromaticus* cover and biomass in the invaded plots were higher ($P < 0.001$) at sites of the coastal region (cover, 95% CI: 68.29–79.7%; biomass: 90.78 g/0.25 m^2) than at the upland sites (cover, 95% CI: 58.22–69.35%; biomass: 76.82 g/0.25 m^2). Equally, the abundance and biomass of pasture species differed between the two regions, with significantly ($P < 0.001$) higher value in the coastal (90.78 g/0.25 m^2) than in the upland (56.29 g/0.25 m^2) sites. Multivariate analyses (ordination) of the above-ground data indicated that within each of the six cattle grazing sites surveyed, our sampled invaded and non-invaded areas (plots) are indeed not the same, in the sense that invaded plots are visually and statistically different from the weed-free plots (Fig. 2). Across sites and regions, the cover, abundance and biomass of *C. aromaticus* as well as the cover of pasture species are the

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Table 1. Summary two-way ANOVA of soil physico-chemical properties in *C. aromaticus* invaded versus non-invaded habitat patches across three different land-use types (treated as sites) that experienced minimal anthropogenic nutrient inputs in the wet tropics of northern Queensland, Australia.

Soil trait	*F*-ratio (significance)			Group mean				Direction of invasion effect
	Invasion (I) (d.f. = 1, 12)	Site (SI) (d.f. = 2, 12)	Interaction I × SI (d.f. = 2, 12)	Control (non-invaded) soil	s.e.	Invaded soil	s.e.	
Soil chemistry								
pH	2.90 (n.s.)	243.80**	4.55 (**)	5.26	0.02	5.20	0.02	–
Total carbon (TC) (%)	2.89 (n.s.)	8.76 (**)	5.12 (**)	3.34	0.36	4.20	0.36	–
Total nitrogen (TN) (%)	1.28 (n.s.)	9.70 (**)	4.59 (**)	0.26	0.02	0.29	0.02	–
Nitrate-ammonium (NH_4-N) (mg/kg)	112.87 (**)	23.85 (**)	10.01 (**)	47.89	3.54	38.11	3.54	C > I
Nitrate-nitrogen (NO_3-N) (mg/kg)	3.82 (†)	14.49 (**)	15.09 (**)	22.89	2.83	65.33	2.85	C < I
Phosphorus (P) (mg/kg)	0.55 (n.s.)	11.72 (**)	8.99 (*)	38.22	2.43	40.78	2.43	–
Organic carbon (OC) (%)	2.27 (n.s.)	7.84 (**)	4.35 (*)	3.32	0.37	4.11	0.37	–
Chloride ion (Cl) (mg/kg)	1.34 (n.s.)	23.23 (**)	23.70 (***)	34.50	2.57	35.33	2.57	–
Electrical conductivity (EC) (dS/m)	66.61 (***)	4.96 (*)	10.62 (*)	0.096	0.007	0.177	0.007	C < I
Sodium (Na) (cmol/kg)	3.28 (†)	3.03 (†)	2.42 (n.s.)	0.075	0.020	0.125	0.020	C < I
Sulfur (S) (mg/kg)	7.25 (*)	21.11 (**)	11.49 (**)	18.00	0.85	14.78	0.05	C > I
Calcium (Ca) (cmol/kg)	6.06 (*)	17.15 (***)	4.76 (*)	1.812	0.20	2.52	0.20	C < I
Magnesium (Mg) (cmol/kg)	14.76 (*)	18.79 (***)	8.11 (*)	1.42	0.09	1.92	0.09	C < I
Potassium (K) (cmol/kg)	15.56 (*)	5.08 (*)	12.41 (*)	0.52	0.05	0.81	0.05	C < I
Copper (Cu) (mg/kg)	45.12 (***)	97.91 (***)	36.59 (***)	1.30	0.04	1.72	0.05	C < I
Zinc (Zn) (mg/kg)	1.74 (n.s.)	98.77 (***)	1.39 (n.s.)	7.40	0.79	8.88	0.79	–
Iron (Fe) (mg/kg)	4.29 (†)	10.73 (**)	0.91 (n.s.)	164.67	10.66	195.89	10.65	C < I
Manganese (Mn) (mg/kg)	5.37 (*)	39.89 (***)	0.43 (n.s.)	18.21	0.97	21.40	0.97	C < I
Soil physical properties								
Fine sand (%)	22.48 (***)	508.62 (***)	2.94 (†)	41.81	0.46	38.72	0.46	C > I
Coarse sand (%)	35.93 (***)	257.82 (***)	19.96 (***)	19.86	0.91	27.60	0.91	C < I
Silt (%)	13.49 (**)	56.03 (***)	10.84 (**)	21.96	0.62	18.76	0.61	C > I
Clay (%)	6.22 (*)	32.73 (***)	21.34 (***)	17.58	0.38	16.23	0.38	C > I
Air-dry moisture content (%)	1.19 (n.s.)	6.76 (*)	1.15 (n.s.)	1.87	0.20	2.18	0.20	–

Factors were invasion (I) (invaded vs non-invaded [weed-free] patches), site (SI) (riparian corridor, roadside and abandoned grazing land), and their interactions (I × SI). Degrees of freedom (d.f.) refers to that of the factor and associated residual. Where invasion effect is significant ($P < 0.05$), the overall direction of the effect is also given for each soil trait (C, control, i.e. weed-free plot; I, invaded plot). Group data are predicted values (means ± s.e. are given) from the two-way ANOVA in which site effect has been controlled for.

n.s., not significant.

†$P \leq 0.10$ (marginally significant); *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

main drivers of differences between vegetation patches with and without the weed. This difference is especially displayed on Axis I of the PCA ordination, which captured 56% of the total variation in the above-ground dataset (Fig. 2). *C. aromaticus* abundance, cover, and biomass were higher in invaded plots, whereas for pasture species (both grasses and broadleaf plants), these traits were higher in non-invaded plots (Fig. 2).

In the grazing lands, the soil physico-chemical traits differed significantly amongst the six investigated sites (Fig. 3, Table S3). However, within this land-use type we found little or no evidence of invasion impact of the *C. aromaticus* on soil chemistry and physical properties, either within each site or for the pooled (across sites) data sets (Fig. 3, Table S3). In contrast, other land-use types of roadside verge, riparian corridor and abandoned grazing farm showed evidence of strong invasion effects on soil chemistry, both individually and collectively (Table 1, Fig. 4). In the above three land-use types, *C. aromaticus*-invaded soils exhibited elevated concentrations of exchangeable ions and micronutrients (Ca, Mg, K, Cu, Fe and Mn). Ionic exchanges in form of electrical conductivity (EC), exchangeable Na^+ ions, and nitrogen in form of nitrate availability (NO_3-N) were also higher in invaded soils than in adjacent soils lacking the

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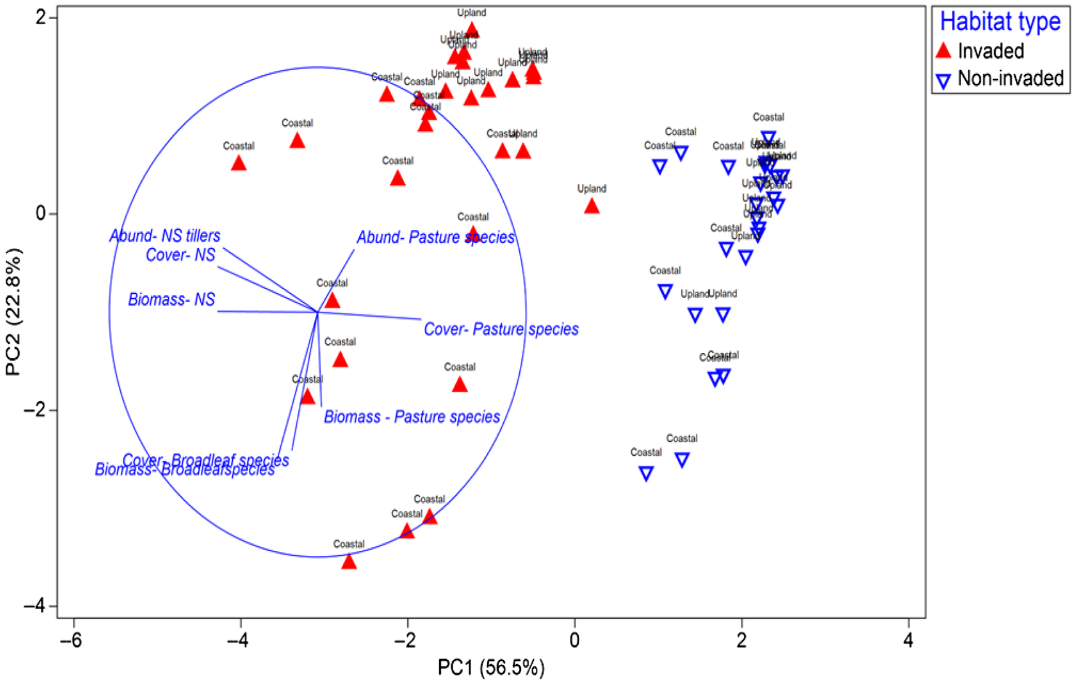

Fig. 2. PCA ordination on Axes I and II of above-ground vegetation of the six cattle grazing sites invaded by *C. aromaticus* (indicated as NS). Arrows radiating from the centres indicate direction and magnitude of above-ground plant traits influencing the ordination pattern. Note the clustering of the upland sites chiefly in the upper-right and middle corner of the plot, whereas the coastal sites are more diffused, irrespective of invasion status. Within each site and for overall pooled data, invasion effect was significant on above-ground vegetation. ANOSIM between invaded and non-invaded pasture patches was 0.806, $P < 0.001$.

weed (Table 1). Major nutrients/ions of total C, organic C, total N, P, Cl, and soil pH were not influenced by invasion status. It is noteworthy, and as expected, that the riparian corridor has the least ionic content of total nitrogen (TN) and total carbon (TC), but highest pH, Cl, Fe and Mg concentrions, and differed significantly from the other two land-use types (roadside and abandoned grazing land) (see Fig. 4, in which site separation was mainly on Axis I of the PCA ordination, with 38% explanatory power).

Invasion effect under microcosm condition

The initial physico-chemical profile of soil used in our microcosm experiments are presented in Table S2, with the notable observation of higher pH (6.55, and hence slightly neutral) than that of the natural soil of northern Queensland (pH 5.23, and hence mostly acidic; see Table 1). A year after the pot trial was established, the soil chemical profile was already seen to be diverging (Fig. S1; compare 2018 and subsequent years of 2019, 2020, and 2021). Overall, the chemical profile of microcosm soils under C. *aromaticus* differed significantly from that under the desirable pasture grass (*Urochloa humidicola*) in each of the three years of sampling (2019, 2020, and 2021) and, as seen in the ordination plot of Fig. 5, where Axes I and II captured 50.8% of the variation in the dataset. Notably, the divergence in soil chemistry of pots planted with *Urochloa humidicola* or invasive *C. aromaticus* increased over time, i.e. 2021 ≥ 2020 > 2019. Ionic exchange capacity (CEC, ESP, NH_4-N) and many nutrients (Na, Cl, S, Ca, K, Cu) were noteworthily significantly higher in the *C. aromaticus*-grown soil (Table 2, Fig. 5) than in the soil of the control (pasture) pots. Only 3/20 nutrients (NO_3-N, Mg and Zn) assayed were higher in control (*U. humidicola* pasture) pots (Table 2). Additionally, the microcosm results mirrored that of the roadside, riparian and abandoned grazing field sites where input of artificial fertiliser is negligible/non-existent; also, in both cases (i.e. microcosm trial and in land-use types lacking fertiliser inputs), *C. aromaticus* invasion resulted in elevated concentrations of many micronutrients, whereas macronutrients of TN, TC, and soil pH were generally unaffected (Tables 1, 2).

Plant major/macronutrients of fibre, lignin, cellulose and hemicellulose

Tissue chemistry differed significantly between sites and species groups (Table 3). Once site differences were controlled, ANOVA indicated that plant tissues of *C. aromaticus* are lower than those of co-occurring pasture grasses in macronutrients of NDF, cellulose, and hemicellulose, and loss on ignition (LOI, a measure of total organic matter), but are higher in lignin content (Table 3). Major nutrients of total C and P did not

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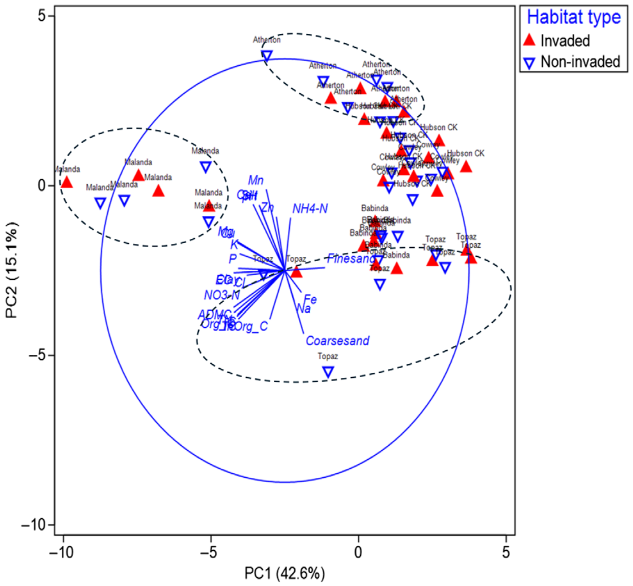

Fig. 3. PCA ordination on Axes I and II of the six cattle grazing sites invaded by *C. aromaticus*. Data are based on their soil physico-chemical profiles. Arrows radiating from the centres indicate the direction and magnitude of soil traits influencing the ordination pattern. In broken circles are each of the three disparate upland sites (Malanda, Atherton and Topaz), whereas the coastal sites (Cowley, Hubson Creek and Babinda) are more homogeneous in soil traits. Within each site and for overall pooled data, *C. aromaticus* invasion effect was neutral on soil chemistry (see also Table S3). ANOSIM between invaded and non-invaded pasture patches was −0.001, $P = 0.77$.

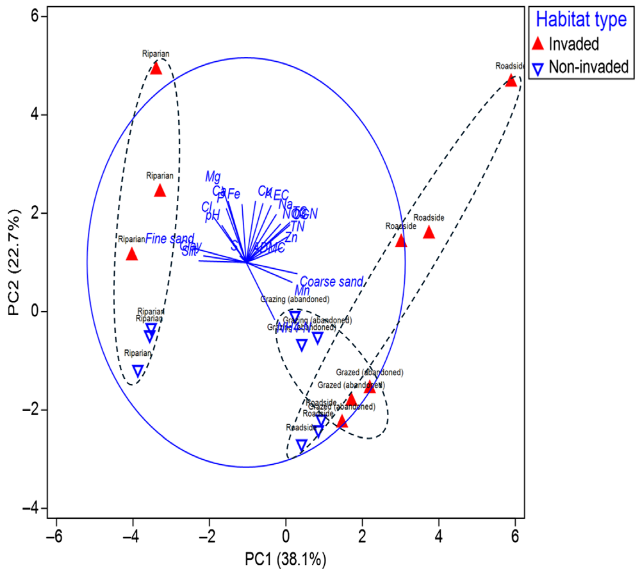

Fig. 4. PCA ordination on Axes I and II of three land-use types invaded by *C. aromaticus* but with no or minimal observable (artificial) chemical input. Data are based on their soil physico-chemical profiles. Arrows radiating from the centre indicate direction and magnitude of soil traits influencing the ordination pattern. In broken circles are each of the three disparate land-use types (site). Within each site and for overall pooled data, *C. aromaticus* invasion effect was significant on soil chemistry. ANOSIM between invaded and non-invaded soil pasture patches was 0.17, $P = 0.05$.

differ significantly between the two plant groups, whereas *C. aromaticus* plant tissue had higher contents of macronutrients of total N, Ca, K, Mg, S and Mn (Table 3). *C. aromaticus* also exhibited a higher capacity for accumulation of micronutrient ions including trace metals (e.g. Cu, B, Fe, Zn, Cd and Mo) as well as heavy and light metals of Cd and Al respectively (Table 3), than did co-occurring pasture plants. Overall, ordination showed that across sites, land-use types and regions where materials were collected, the plant tissue chemical profiles of *C. aromaticus* were substantially different from those of co-occurring pastures (Fig. 6*a*–*c*). These differences, based on ordination and ANOSIM, were magnified more in leaf nutrition (cellulose, hemicellulose, fibre and lignin) than in macronutrients (N, P, K, C, Ca, and P), trace nutrients (Mn and Na), and metal ions (Zn, Fe, Mn, and Co) (compare Fig. 6*a* vs 6*b*). Note that across sites, and as expected, there was substantial variation in the tissue profile for *C. aromaticus*, especially for samples collected in the riparian corridor (two data points at the extreme positive end of Axis I of the ordination plots; Fig. 6*b*). Within the co-occurring pastures, the chemical profile of *Urochloa decumbens* (signal grass) plant tissue stands out as being heterogenous and, at time, matched that of *C. aromaticus* weed (Fig. 6*b*). In terms of macronutrients (N, P, K, Ca, Mg and S), both *C. aromaticus* and co-occurring pastures meet the minimum requirements as forage foliage for livestock, with higher values for *C. aromaticus*. However, the micronutrient/trace metal values in *C. aromaticus* tissue (especially Cu, Fe and Zn; Table 3) were significantly higher than those of co-occurring pastures (~2:1 ratio) and tending towards being excessive beyond the tolerance level for cattle feed.

In both *C. aromaticus* and co-occurring pasture species, we detected a minimal number of significant bivariate correlations between the plant tissue digestibility and their macro- or micronutrient traits (30–37% of the bivariate correlations were significant at $P < 0.05$; Table S4). One exception was with boron (B), in which, for desirable pasture species only, significant negative relationships existed between this trace element and many digestibility traits (Fig. 7*a*, *e*, *g*, *i*); in contrast, these relationships were non-significant for the invasive *C. aromaticus* (Fig. 7). The other exception was zinc (Zn), in which, for the invasive *C. aromaticus*, more positive trends were observed between this trace element and digestibility traits (Fig. 7*b*, *f*); however, these bivariate trends were not significant for pasture plant species (Figs 7*b*, *d*, *f*, *h*, *j*).

Discussion

Using an extensive field and microcosm sampling scheme, our study linked the soils of *C. aromaticus* invaded and non-invaded patches with the tissue chemical profile of this focal

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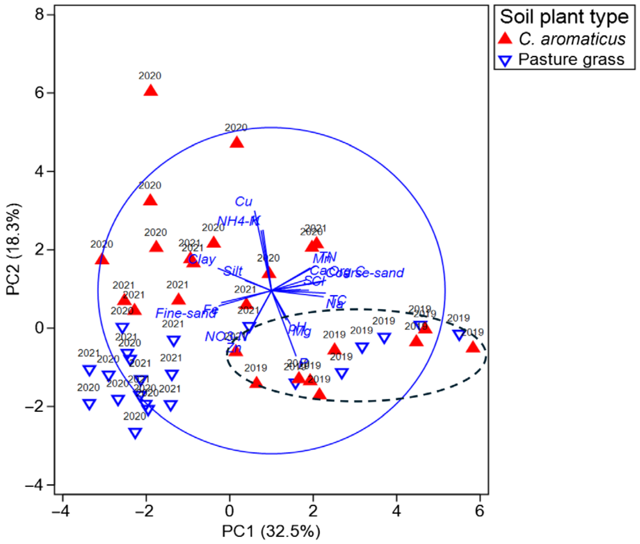

Fig. 5. PCA ordination on Axes I and II of soil physico-chemical profile that resulted from glasshouse (microcosm)-grown plants of either the invasive *C. aromaticus* or co-occurring pasture species over a 3-year period of 2019, 2020 and 2021. Arrows radiating from the centre indicate direction and magnitude of soil traits influencing the ordination pattern. Note the limited/minimal difference between treatments in the early stage of the microcosm experiment (i.e. 2019, indicated with broken circle) compared with later stages of 2020 and 2021 of infestation. See Fig. S1 for the extent of difference between 2018 (when the experiment was initiated) and subsequent years. ANOSIM between invaded (*C. aromaticus*) and pasture (control) soils was 0.19, $P = 0.001$.

weed and its co-occurring pasture species. We demonstrated that *C. aromaticus*, through its greater biomass, abundance, and cover dominance in invaded pastures, can reduce above- and below-ground biodiversity of native and non-invasive exotic pasture plants while altering soil chemistry (see Shi *et al.* 2021, 2023; Chadha *et al.* 2022*a*), although the latter effect (as seen in the present work) may be obscured by anthropogenic land-use practices. The observed lack of significant effects on soil chemistry in the six active grazing lands in the northern QLD wet tropics (Fig. 3) is not because *C. aromaticus* invasion did not invoke changes in the soil process, but we argue that such effect was difficult to demonstrate in view of continuing input of both artificial fertiliser by farmers and manure (faecal deposition) by cattle, because these animals constantly move through and among paddocks. Osunkoya *et al.* (2017) also observed a similar neutral effect of *Parthenium hysterophorus* weed invasion in central QLD cropping lands. We were initially surprised by such neutral results for *C. aromaticus* invasion in grazing landscapes, but our survey of the weed invasion in other land-use types with minimal or no fertiliser inputs (roadside verge, riparian corridor, and abandoned grazing farm) demonstrated that *C. aromaticus* invasion effect on soil properties is real, although site and context (ecosystem) specific. Indeed studies which obtained negative or even neutral invasion results are often under-reported, which decreases the objectivity of the results of any meta-analyses of published data. However, this presumption is changing (see Meisner *et al.* 2014; Čuda *et al.* 2017; Osunkoya *et al.* 2017; Stefanowicz *et al.* 2020). In all, invasive plants such as *C. aromaticus*, through their distinct tissue chemical profiles, can drive changes in root exudate concentrations/diversity and soil microbial communities, which in turn may modulate dry and organic matter decomposition, soil enzyme activity, and other soil processes. These scenarios may thus invoke changes in concentrations of soil total and available nutrients and ion exchange capacities (van der Putten *et al.* 2013; Meisner *et al.* 2014; Frouz 2024).

The tissue chemical profiles of *C. aromaticus* and co-occurring pastures share similarities in several macronutrients, including similarities in major nutrients of TC and P, and ADF content (Table 3). The higher tissue content of TN, Ca, K for invasive *C. aromaticus* is in line with the view of enhanced nutrient uptake of highly invasive plants, especially in disturbed habitats of high nutrient pulses (Osunkoya *et al.* 2010; Xie *et al.* 2023). Significant differences in macromolecules (NDF, cellulose, hemicellulose, and lignin) and trace elements (Fe, B, Cl, Mn, Cu, Cd and Zn) between the plant tissue of the invasive *C. aromaticus* and that of co-occurring pasture grasses were detected in this study. Soil trace elements (where they are not in deficit or in excess) play an important role for the health of the soil, promoting the absorption of nutrients and vitality of the plants (Kaur *et al.* 2023). The higher concentrations of tissue trace elements and lignin in *C. aromaticus* tissue than in pasture species could, through the weed's litter decay, lead to different soil interactions and feedback with associated soil organisms, making the substratum unfavourable for other plants and thus contributing to the invasive potential of the weed (Scharfy *et al.* 2010; Zhang *et al.* 2019). For example, the trace element boron (B) is known as an important precursor for lignin biosynthesis and for cross-linking of plant cell walls (Moore and Jung 2001; Goldbach and Wimmer 2007; Long and Peng 2023), and thus it is interesting to see a significant negative bivariate correlation between tissue lignin and tissue B for co-occurring pasture plants. In contrast, the bivariate trend for the invasive *C. aromaticus* lignin content with its B concentration, although also negative, was non-significant; similarly, for *C. aromaticus*, non-significant trends were observed for its tissue B versus many of the other macromolecules, including cellulose and hemicellulose) (Fig. 7). This could be interpreted as increasing accumulation of the trace elemental ions, such as boron, does not adversely affect (or affects only minimally) the production of macromolecule in *C. aromaticus*, whereas many important dietary components are severely and adversely affected in co-occurring pasture plants under the same increasing tissue B condition, to the extent that at a given boron level, a higher lignin is always produced in *C. aromaticus* than in co-occurring pastures. Also, increasing tissue B concentrations decrease cellulose (hence cell) production significantly in pasture plants. Another notable

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Table 2. Summary two-way ANOVA of changes in microcosm soil physico-chemical properties in which *C. aromaticus* (the weed) and a pasture grass (*Urochloa humidicola*) were grown individually in pots over a 3-year period in a controlled environment of a glass house.

Trait	*F*-ratio (significance)			Group mean				Direction of invasion effect
	Invasion (I) (d.f. = 1, 40)	Year (Y) (d.f. = 2, 40)	Interaction (I × Y) (d.f. = 2, 40)	Control soil (*U. humidicola*)		Invaded soil (*C. aromaticus*)		
				Mean	s.e.	Mean	s.e.	
Soil chemical properties								
pH	1.03 (n.s.)	3.49 (**)	2.86 (n.s.)	8.13	0.05	8.06	0.05	–
Total carbon (TC) (%)	0.31 (n.s.)	32.97 (***)	1.49 (n.s.)	1.61	0.04	1.64	0.03	–
Total nitrogen (TN) (%)	1.95 (n.s.)	8.99 (**)	1.77 (n.s.)	0.03	0.001	0.03	0.001	–
Nitrate-ammonium (NH_4-N) (mg/kg)	4.19 (*)	6.66 (**)	6.35 (**)	1.63	0.46	2.92	0.43	C < I
Nitrate-nitrogen (NO_3-N) (mg/kg)	70.55 (**)	22.72 (***)	22.72 (***)	5.82	0.42	1.00	0.39	C > I
Phosphorus (P) (mg/kg)	18.62 (**)	30.51 (***)	10.42 (***)	66.54	3.67	59.15	3.47	C > I
Organic carbon (OC) (%)	1.12 (n.s.)	30.64 (***)	4.50 (*)	1.23	0.42	1.29	0.42	–
Chloride (Cl) (mg/kg)	4.02 (†)	11.48 (**)	0.33 (n.s.)	48.83	16.34	67.50	15.49	C < I
Electrical conductivity (EC) (dS/m)	1.30 (n.s.)	0.75 (n.s.)	0.13 (n.s.)	0.15	0.02	0.17	0.02	–
Exchangeable sodium percentage (ESP)	2.73 (†)	12.68 (***)	0.36 (n.s.)	1.69	0.24	2.24	0.22	C < I
Cation exchange capacity (CEC) (cmol/kg)	4.49 (*)	4.18 (*)	3.19 (*)	6.26	0.17	6.751	0.16	C < I
Sodium (Na) (cmol/kg)	2.81 (†)	13.29 (***)	0.41 (n.s.)	0.12	0.01	0.15	0.01	C < I
Sulfur (S) (mg/kg)	4.45 (*)	1.76 (n.s.)	0.16 (n.s.)	9.52	2.10	14.00	1.94	C < I
Calcium (Ca) (cmol/kg)	3.18 (†)	3.56 (*)	4.51 (*)	4.81	0.12	5.10	0.11	C < I
Magnesium (Mg) (cmol/kg)	4.92 (*)	0.69 (n.s.)	0.18 (n.s.)	2.49	0.07	2.30	0.06	C > I
Potassium (K) (cmol/kg)	3.46 (†)	6.27 (**)	7.99 (**)	0.09	0.01	0.12	0.01	C < I
Copper (Cu) (mg/kg)	14.45 (***)	18.46 (***)	8.59 (**)	3.62	0.75	8.19	0.69	C < I
Zinc (Zn) (mg/kg)	60.99 (***)	6.15 (**)	8.28 (**)	3.11	0.09	2.19	0.08	C > I
Iron (Fe) (mg/kg)	0.30 (n.s.)	10.25 (**)	1.53 (n.s.)	38.99	1.29	38.01	1.23	–
Manganese (Mn) (mg/kg)	0.01 (n.s.)	5.34 (**)	7.66 (**)	1.89	0.24	1.89	0.23	–
Soil physical properties								
Fine sand (%)	1.42 (n.s.)	8.75 (**)	1.94 (n.s.)	11.08	0.43	10.37	0.41	–
Coarse sand (%)	1.16 (n.s.)	6.82 (**)	2.30 (n.s.)	83.33	0.54	83.63	0.51	–
Silt (%)	6.02 (*)	10.56 (**)	7.09 (*)	3.03	0.17	3.63	0.17	C < I
Clay (%)	3.40 (*)	72.79 (***)	3.47 (*)	5.78	0.12	5.23	0.11	C < I

Factors were invasion (I) (*C. aromaticus* vs pasture grass [weed free]), sampling year (Y) (2019, 2020 and 2021), and their interaction (I × Y). Degrees of freedom (d.f.) refers to that of the factor and associated residual. Where invasion effect was significant ($P < 0.05$), the overall direction of the effect is also given for each soil trait (C, control soil of *U. humidicola;* I, invaded soil of *C. aromaticus*). Group data are values (means ± s.e. are given) from the 2-way ANOVA in which year effect has been controlled for. n.s., not significant.

$^{\dagger}P \leq 0.10$ (marginally significant); $^{*}P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$.

trend is plant tissue Zn (an activator of several enzyme activities) relationship with plant macromolecules studied; for *C. aromaticus*, significant positive trends exist between plant Zn and ADF and plant Zn and cellulose, whereas these trends are neutral for co-occurring pastures (Fig. 7*b*,*f*). Overall, these trends and observations point to the ability of *C. aromaticus* to uptake and store such metals without incurring autotoxicity or cost in production of macromolecules, especially of complex carbohydrate.

In the same vein, in landscapes with limited external nutrient (such as fertiliser) inputs, we found higher trace element loads in *C. aromaticus* invaded soils of riparian corridors, roadsides and abandoned grazing farms. As in our study, some past studies have reported increased trace elements in soil and/or plant tissue in response to plant invasion (e.g. Penuelas *et al.* 2010; Dai *et al.* 2020), whereas others have reported the opposite trend (e.g. McGrath and Binkley 2009; Osunkoya and Perrett 2011; Perrett *et al.* 2012), and some have not been able to detect any effect at all (Čuda *et al.* 2017; Osunkoya *et al.* 2017). No doubt, the magnitude and direction (or lack of it) appear to be species and context specific. In respect of our finding, it could be argued that

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Table 3. Summary two-way ANOVA of differences in chemical profile and forage quality of above-ground tissue (leaves and tillers combined) of *C. aromaticus* weed versus co-occurring pasture grass species (*Setaria sphacelate*, *Urochloa humidicola*, *Urochloa decumbens*, *Chloris gayana*, and *Megathyrsus maximus* var. *maximus*).

Plant trait	*F*-ratio (significance)		Group mean				Direction of difference
	Plant type (PT) (*C. aromaticus* vs pasture grass species)	Site	*C. aromaticus*	s.e.	Pasture grass species	s.e.	
Forage quality/digestibility	(d.f. = 1, 11)	(d.f. = 5, 11)					
Acid-digestible fibre (ADF) (%)	1.23 (n.s.)	1.43 (n.s.)	47.27	1.21	45.34	1.25	–
Neutral-digestible fibre (NDF) (%)	19.59 (**)	28.55 (***)	74.65	0.34	76.80	0.35	*C. aromaticus* < Pasture
Cellulose (%)	3.97 (†)	1.77 (n.s.)	37.99	0.98	39.38	1.01	*C. aromaticus* < Pasture
Lignin (%)	43.10 (***)	2.18 (n.s.)	9.28	0.35	5.92	0.36	*C. aromaticus* > Pasture
Hemicellulose (%)	4.60 (†)	0.32 (n.s.)	27.38	1.32	31.46	1.37	*C. aromaticus* < Pasture
Loss on ignition (LOI) resid. (%)	3.89 (†)	5.68 (**)	89.48	0.49	90.70	0.52	*C. aromaticus* < Pasture
Plant Macronutrient	(df = *1, 26*)	(df = *8, 26*)					
Total carbon (TC) (%)	0.54 (n.s.)	3.83 (*)	42.44	0.52	42.69	0.23	–
Total nitrogen (TN) (%)	5.87 (**)	8.90 (***)	1.24	0.04	1.07	0.05	*C. aromaticus* > Pasture
Calcium (Ca) (%)	7.72 (**)	2.39 (†)	0.45	0.02	0.37	0.19	*C. aromaticus* > Pasture
Potassium (K) (%)	5.63 (*)	2.75 (†)	3.26	0.17	2.68	0.08	*C. aromaticus* > Pasture
Magnesium (Mg) (%)	5.14 (*)	(1.74) n.s.	0.30	0.01	0.25	0.01	*C. aromaticus* > Pasture
Manganese (Mn) (mg/kg)	121.73 (***)	4.94 (**)	574.46	24.54	194.32	24.19	*C. aromaticus* > Pasture
Phosphorus (P) (%)	0.66 (n.s.)	46.26 (***)	0.23	0.007	0.21	0.007	–
C:N ratio	415.92 (***)	396.58 (***)	36.460	1.12	43.34	1.12	*C. aromaticus* < Pasture
Plant trace element/micronutrient							
Sulfur (S) (%)	6.18 (*)	4.46 (**)	0.20	0.01	0.17	0.01	*C. aromaticus* > Pasture
Cobalt (Co) (mg/kg)	1.21 (n.s.)	14.69 (**)	0.54	0.04	0.48	0.04	–
Copper (Cu) (mg/kg)	142.90 (***)	14.29 (**)	11.08	0.31	5.65	0.32	*C. aromaticus* > Pasture
Aluminium (Al) (mg/kg)	4.11 (*)	5.14 (**)	374.87	96.95	112.09	95.55	*C. aromaticus* > Pasture
Boron (B) (mg/kg)	13.47 (***)	7.78 (**)	10.69	0.63	8.81	0.63	*C. aromaticus* > Pasture
Iron (Fe) (mg/kg)	4.52 (*)	6.83 (**)	285.54	56.37	117.29	55.56	C. aromaticus > Pasture
Sodium (Na) (%)	3.30 (†)	13.68 (***)	0.11	0.02	0.18	0.02	*C. aromaticus* < Pasture
Zinc (Zn) (mg/kg)	252.61 (***)	40.85 (***)	76.57	1.56	48.45	1.54	*C. aromaticus* > Pasture
Cadmium (Cd) (mg/kg)	536.15 (***)	8.16 (**)	0.68	0.05	0.04	0.04	*C. aromaticus* > Pasture
Molybdenum (Mo) (mg/kg)	8.46 (**)	8.99 (**)	0.52	0.04	0.45	0.04	*C. aromaticus* > Pasture
Lead (Pb) (mg/kg)	0.01 (n.s.)	8.16 (**)	0.25	0.04	0.29	0.04	–
Selenium (se) (mg/kg)	0.02 (n.s.)	6.21 (**)	0.086	0.012	0.089	0.01	–

Factors were plant type (PT) (i.e.the invasive *C. aromaticus* vs pasture grass species pooled) and site (SI), but no SI × PT interaction effect was modelled because not all pasture species were present at all sites where the weed invaded/were collected. Degrees of freedom (d.f.) refers to that of the factor and associated residual. Where there are significant ($P < 0.05$) plant-type effects, the overall direction of the effect is also given for each plant tissue trait. Group data are predicted values (means ± s.e. are given) from the two-way ANOVA in which site effect has been controlled.

n.s., not significant.

$^{\dagger}P \leq 0.10$ (marginally significant); $^{*}P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$.

C. aromaticus weed prefers microsites of high trace element concentration; however, an alternative explanation is that *C. aromaticus* presence, such as in many invasive plants, alters (i.e. increases) the soil trace elemental environment perhaps through its unique litter production and decomposition as well as via its root exudates of organic acid, sugars and phenolics (Weidenhamer and Callaway 2010; Zhang *et al.* 2019). Additionally, larger loads of soil and tissue micronutrients (as seen in this study for *C. aromaticus*) often boost the synthesis of secondary metabolites, leading to introduction of novel chemical antagonists (allelochemicals) and/or suppression of native species (Zhang *et al.* 2019; Xie *et al.* 2023). For example, higher concentrations of the mineral ions of Fe, Cu, Mn, and S, as seen in invaded plots, often lead to decreases in

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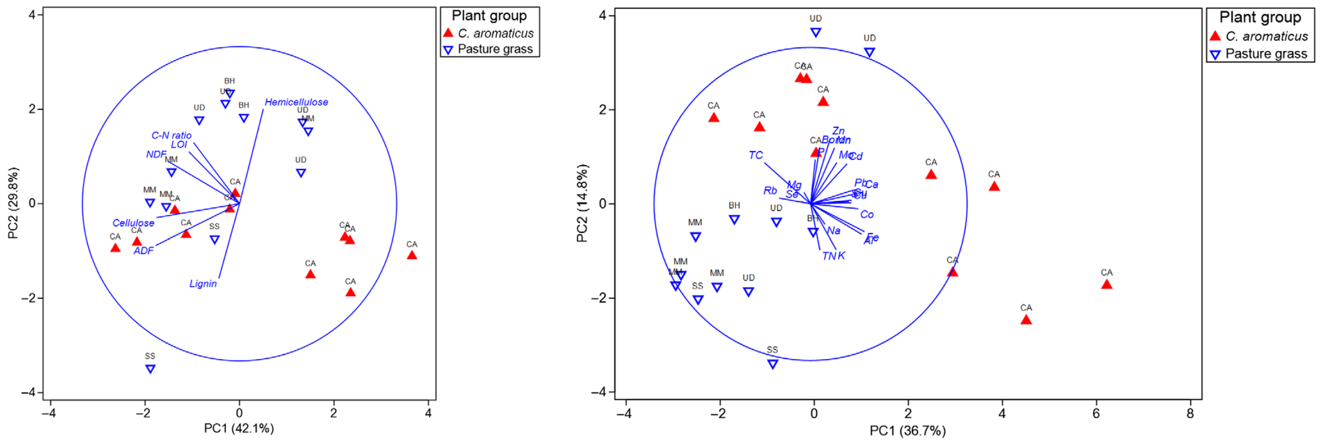
(*a*) Forage quality only

(*b*) Elemental composition only

(*c*) Forage quality and elemental composition combined

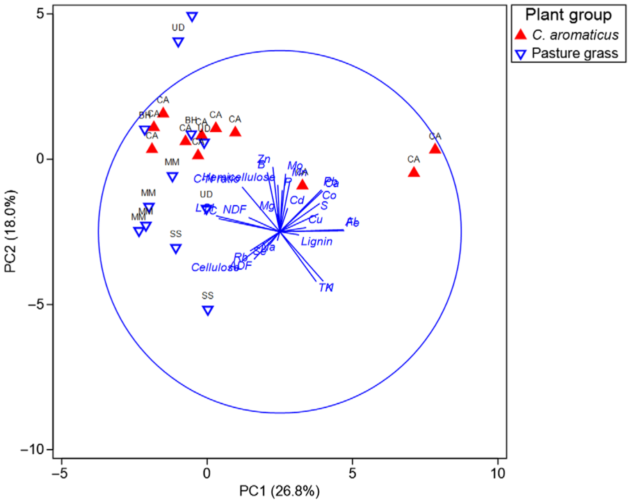

Fig. 6. PCA ordinations of above-ground tissue chemical profile of *C. aromaticus* and co-occurring pasture grass species on the basis of (*a*) forage quality (ANOSIM = 0.284, *P* = 0.002), (*b*) macro- and micronutrients (ANOSIM = 0.217, *P* = 0.001), and (*c*) all chemical traits combined (ANOSIM = 0.306, *P* = 0.001). ANOSIM is analysis of similarity in tissue profile between *C. aromaticus* weed and pasture grass species. Abbreviations on data/symbol points refer to species name: CA, *Cyperus aromaticus* (Navua sedge); SS, *Setaria sphacelate* (Setaria grass); UD, *Urochloa decumbens* (signal grass); BH, *Bracharia humidicola* (Humidicola), and MM, *Megathyrsus maximus* (Guinea grass). Arrows radiating from the centre indicate direction and magnitude of plant tissue traits influencing the ordination pattern.

microbial activity and species richness (Zhang *et al.* 2019; Stefanowicz *et al.* 2020; Xie *et al.* 2023). Elevated electrical conductivity (EC) detected in the field data for the invasive *Heracleum laciniatum* has been associated with phytotoxic effects on other plants (Myrås and Junttila 1981; Jandová *et al.* 2014), and it is surmised that the same phenomenon may apply to *C. aromaticus* weed invasion.

The amount and quality of nutrients of fodder available to animals are important in the determination of animals' productivity and growth (Bonin and Tracy 2011; Knowles and Grace 2014; Sasu *et al.* 2023). Our analyses of plant tissue macronutrients will suggest that aside from digestibility (i.e. ADF), concentrations of most assayed complex macromolecules (NDF, cellulose and hemicellulose) were lower in *C. aromaticus* tissues than in co-occurring pastures, whereas the undigestible plant cell-wall component (lignin) was higher in *C. aromaticus* plant. Some studies suggest that sedges can increase fodder value and, therefore, they should be considered in grazing management as a valuable component of economically important grazing communities (Al-Rowaily *et al.* 2019; Iqbal *et al.* 2020; Janyszek-Sołtysiak *et al.* 2021). Our results suggest otherwise for the northern QLD grazing industry in that *C. aromaticus* has lower forage quality for ruminants, especially cattle. We suggest that this finding lends support to why its management/eradication in grazing lands is critical. The significantly higher concentration of lignin in *C. aromaticus* (almost two folds, Table 3) makes the weed unattractive as fodder for cattle. The higher tissue lignin

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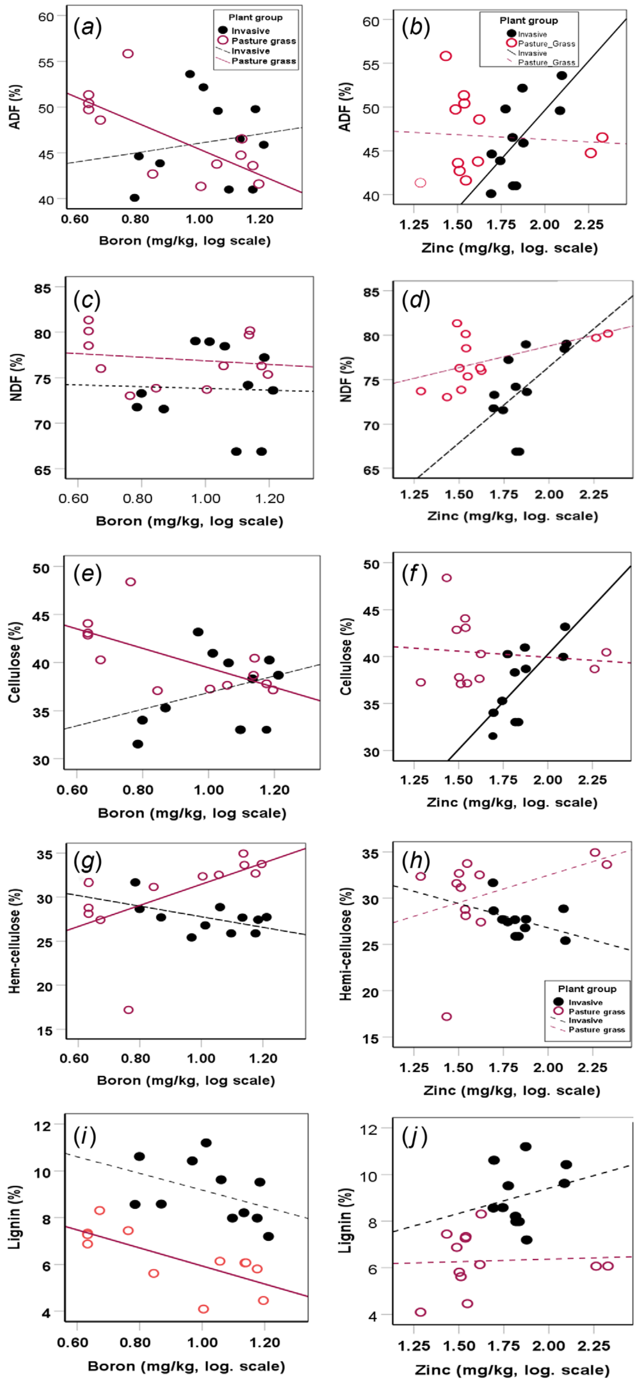

Fig. 7. Bivariate correlation analyses and trends for plant tissue trace elements of boron (B) and zinc (Zn) versus tissue digestibility traits (*a–j*) for the invasive (i.e. *C. aromaticus*) and co-occurring pasture grass species. Significant ($P < 0.05$) trends are indicated by continuous lines. ADF, acid detergent fibre; and NDF, neutral detergent fibre. See Table S4 for strengths of the correlations.

concentation in *C. aromaticus* may also increase the resistance of this species to herbivore damage such as insects, a process lignin assists by limiting the entry of pathogens, thus blocking them physically or by increasing leaf toughness, which in turn reduces the opportunity of feeding by herbivores (Jogesh *et al.* 2008; Huang *et al.* 2020). Thus, it is no surprise that Dhileepan *et al.* (2022) did not find any insect herbivores on *C. aromaticus* plants in the native range of Africa, while prospecting for its biocontrol agents. Higher lignin concentration in its plant tissue might even reduce herbicide efficacy (see Hoagland 1996; Krähmer *et al.* 2021). Additionally, whereas concentrations of macronutrients (N, P, K, C, Ca, Mg and S) in *C. aromaticus* bracketed those of its co-occurring pasture plants, the elevated concentration of micronutrients in the weed (especially Fe, Mn, Cu, Bo, Zn and Cd) are often above cattle tolerance levels (Bonin and Tracy 2011; Knowles and Grace 2014; Squadrone *et al.* 2021). Fodder species that have low Cu and lower to moderate Zn concentrations are usually considered best for the dietary needs of livestock.

Conclusions

Although some aspects of our research may appear to have essentially replicate standard invasion study, the findings remain valuable because of inclusion of diverse soil types, varying landscapes and land-use types. Field surveys and glasshouse microcosm trials showed consistent directional shifts in soil chemical profiles across both settings post-*C. aromaticus* invasion, demonstrating that, without external fertiliser inputs, this species alters soil chemistry. This is particularly true for trace and micronutrients, whereas major macronutrients (N, P, K) and OC often remain unaffected. However, note that we surveyed a limited number of sites for the riparian, roadside and abandoned grazing lands, and as such the changes in soil chemistry reported at these sites (land-use types) might have low statistical power, and thus the findings might be deemed tentative. Additionally, the ecological processes and mechanisms driving such soil changes were not addressed in this study, including the weed litter decomposition pattern, enzyme activities and/or allelopathic exudates, and are thus worthy of future exploration. Our microcosm experiment, whose findings are similar to that obtained in *C. aromaticus*-invaded land-use types lacking direct nutrient input, also suggests that the impact of *C. aromaticus* on soil process will increase with time, buttressing the assertion by Strayer's *et al.* (2006) and Osunkoya *et al.* (2025) that the full effects of an invader might not be seen for a considerable time after the initial invasion and their calls for longer-time monitoring during which some neutral effect seen in macronutrients might change in direction and/or magnitude. Our study showed a significant lower nutritional quality (e.g. fibre and cellulose) and higher lignin content in *C. aromaticus* than in co-occurring pasture plants, providing an additional compelling reason why control of *C. aromaticus* is important, especially in grazing landscapes.

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Supplementary material

Supplementary material can be accessed from the article page online.

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