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Research Article

Balloon milkweed *Gomphocarpus physocarpus* distribution and drivers in an internationally protected wetland

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Abstract

Invasive species continue to spread and alter ecological function and structure in natural systems. Invasive alien plant species can be particularly ecologically damaging and costly to control, yet their success might be influenced by key habitat characteristics which can be empirically measured. The present study employs field surveys and laboratory analyses to examine whether the abundance and key characteristics (i.e. height and number of stems) of the non-native balloon milkweed *Gomphocarpus physocarpus* E. Mey are influenced by wetland zonation (i.e. permanent, temporary and seasonal zones) and soil characteristics, within a designated Ramsar wetland. Significant site- and zonation-specific differences were observed in a range of soil parameters (e.g. pH, conductivity, Na, Ca, Mg, Cu, Zn, Mn, Fe). Overall, milkweed numbers did not differ significantly according to wetland zonation, but differed significantly among sites. However, in turn, both plant heights and stem numbers related significantly to habitat zonation and sampling sites. Whilst unrelated to most soil properties, milkweed variables were found to relate significantly positively to Mn (abundance), negatively to Cu and positively to P (stem numbers). Furthermore, principal components analyses concerning milkweed abundances indicated clear patterning across sites, finding strong associations with soil variables (i.e. soluble S, Mn, pH, Na, SOM and conductivity). The present study illustrates distributions of a non-native plant species and assesses how its characteristics relate to environmental properties in an internationally recognised protected area. This information could be employed to help predict future distributions and better target management efforts towards sites at high-risk of invasion.

Key words: invasion success, non-native species, plant characteristics, Ramsar wetland, soil chemistry

Introduction

Biological invasions are a serious threat to global biodiversity and have long been recognised as significant causes of ecological impacts within natural systems (Odour et al. 2016; van Wilgen et al. 2020). Recent work has estimated alien species to have contributed to 25% of plant and 33% of animal extinctions worldwide (Blackburn et al. 2019). The rate of alien species accumulation also shows no sign of abatement across taxonomic groups or geographic regions (Seebens et al. 2017). Owing to ongoing biological diversity homogenization (McKinney and Lockwood 1999), it is vital to quantify the impacts invasive species have on the stability and functioning of ecosystems, particularly as their ecological effects can be context-dependent (Dick et al. 2014). This is pertinent as, once established, invasive alien species are often impossible to eradicate (van Wilgen et al. 2020). Developing an understanding of the environmental characteristics that mediate invasion pathways is essential for management efforts. Such knowledge could allow for effective identification and monitoring of high-risk habitats or areas for managers. Accordingly, examinations of habitat characteristics that mediate invasion, alongside the development of effective biosecurity practices (Crane et al. 2019; Bradbeer et al. 2020), are needed to prevent the introduction, establishment and spread of invasive species.

Invasive species enter novel geographic areas using various pathways through natural processes (e.g., animals, river, oceanic and atmospheric currents) or human activities (e.g., ballast water, religious release, angling, pet trade) (Arianoutsou et al. 2010). Birds (and other animals) aid in the distribution of seeds and plants and are one of the most effective vectors in long distance plant dispersals (Green 2016). Humans also play a major role in dispersal of invasive species through their movements and can introduce species intentionally and/or unintentionally (Hulme 2015; Turbelin et al. 2017). Invasions in South Africa alone, including high numbers of invasive plants, are thought to cost US$450 million annually, and might contribute to ongoing water crises (van Wilgen and Wilson 2018).

Milkweeds (Apocynaceae) are plant species that usually grow along roadsides, wetlands, disturbed areas, wet meadows, canyons, wood lands, and agricultural field boarders (Woodson 1954). Atmospheric and water currents can aid dispersal of milkweed species as they can carry plant seeds and introduce them to new areas (Morse and Schmitt 1985; Edwards et al. 1994; van Wilgen et al. 2020). According to Wilbur (1976), the plants get their name from the milky latex sap which they release as a defense mechanism to protect them from herbivores or when harmed, either on their stem, roots and/or leaves. This milky sap makes the plants toxic and unpalatable. Milkweeds are normally self-incompatible and individuals produce flowers that have balloon structures with cotton on the inside (de Casas et al. 2012). According to the South African National Biodiversity Institute (SANBI; http://pza.sanbi.org/gomphocarpus-physocarpus), the perennial milkweed *Gomphocarpus physocarpus* E. Mey (hereafter, milkweed) is considered as an introduced and widespread species in South Africa, being native to tropical Africa. Numerous milkweed species are documented as being invasive in several regions globally (Ward et al. 2012; Bukovinszky et al. 2014), yet information on impact is generally sparse. In most cases, reported impacts are anecdotal and speculative rather than proven (Szitár et al. 2018), but they are known to negatively affect monarch butterflies by providing them with a year-round food source (Faldyn et al. 2018), reducing the propensity to migrate, thereby causing an increased disease prevalence in non-migratory populations (Satterfield et al. 2015).

Understandings of the distribution and characteristics of milkweeds across key environmental gradients are poor, hampering predictions of the potential ecological effects the species might have within communities following arrival. In particular, the tolerance of milkweeds to different hydrological contexts lacks examination, impeding predictions of where the species might colonise in future. The present study thus aims to assess the abundance and factors contributing to the distribution of milkweed along different wetland zonations and sites in the Nylsvley wetland, a Ramsar site of international importance. Whether colonisation success of this species is limited by specific hydrological factors has yet to be assessed. We tested the hypothesis that there will be an increase in abundance of invasive milkweed as one moves from permanent to temporary zones of the wetland, due to variations in water saturation levels and changes in soil chemistry, but no differences across the wetland sites. We also expected that there would be differences in plant characteristics (i.e. height and number of stems) across the hydrological gradient and soil variables would differ among wetland zones and sites where milkweed was present.

Materials and methods

Study area

The Nylsvley Wetland is situated in the Waterberg region, Limpopo Province of South Africa. The area was declared a Ramsar wetland site of international conservation significance in 1997 (Tshimomola 2017). The wetland is made up of extensive reed beds and grass veld, surrounded by open savanna woodlands. The wetland lies between 1080 and 1155 m above sea level. The Nylsvley area receives approximately 620 mm of rainfall per annum, with a dry and rainy season between April and September, and October and March, respectively. It receives most of its rainfall around January and its lowest rainfall amounts in June. Average temperatures during the day range from 20.5 °C in June to 28.9 °C in mid-summer, and temperature tends to drop to below zero in winter, especially during the night, and can reach over 39 °C in summer. The study was carried out from five haphazardly selected sites (i.e. N1, N2, N3, N4, N5) along the Nylsvley Wetland in June 2019 (Figure 1).

At each site, the wetland was divided into permanent, seasonal and temporary zones, based on proximity to the permanent zone (Figure 2). The permanent zone was characterised by perennially water-logged, grey soil.

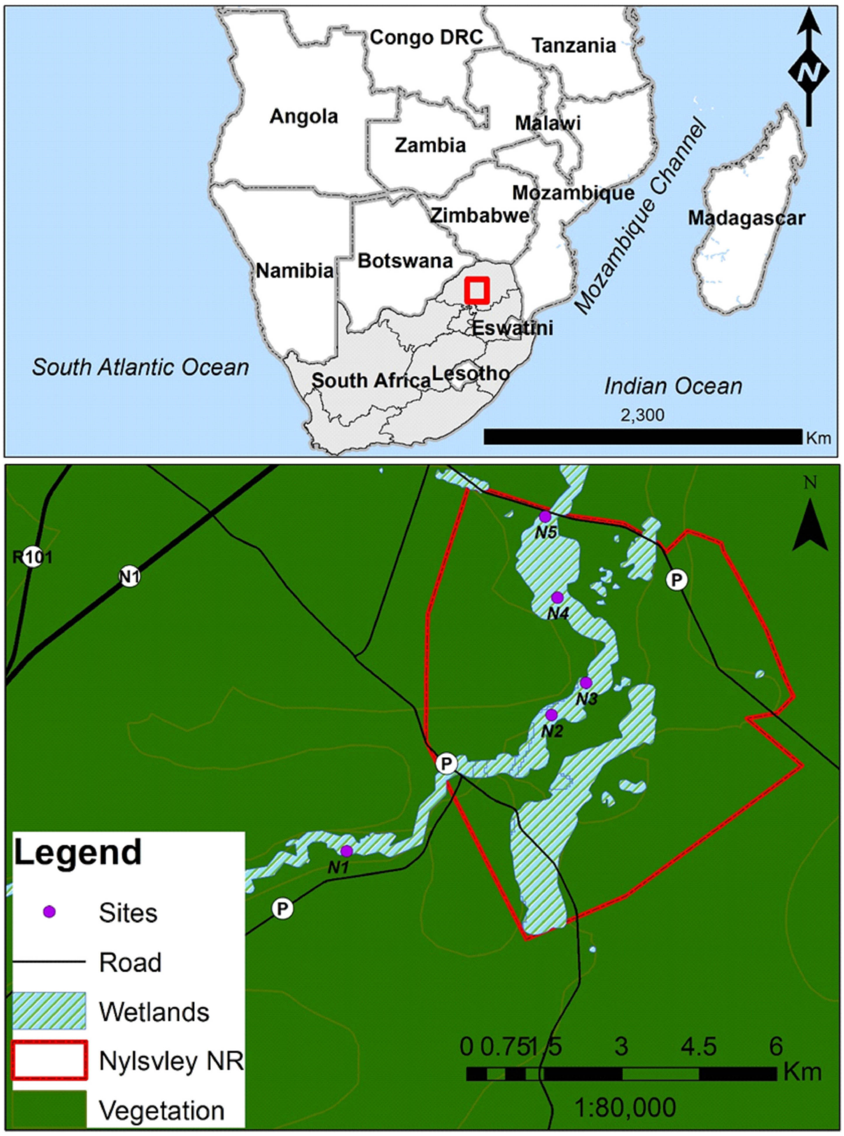

Figure 1. Location of the study sites within the Nylsvley Wetland nature reserve (NR).

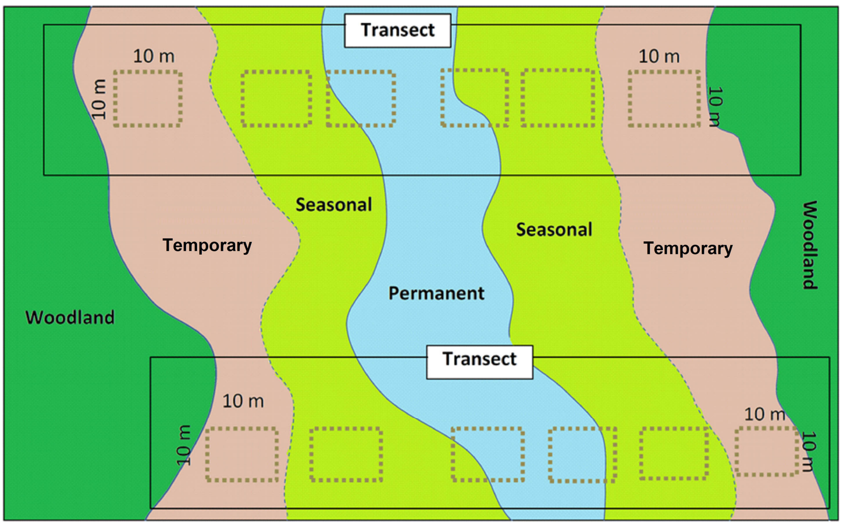

Figure 2. Wetland sampling design conducted to assess invasive milkweed *Gomphocarpus physocarpus* abundances and characteristics in Nylsvley Wetland. The different colours symbolize zonation based on seasonal levels of water saturation in the soil and dotted boxes indicate quadrats.

This zone was dominated by emergent plants, including reeds (*Phragmites australis*), a mixture of sedges and bulrushes (*Typha capensis*), usually > 2 m tall, or floating and submerged plants (DWAF 2005). The seasonal zone was characterized by seasonally water-logged, grey soil and less riparian vegetation than in the permanent zone (Hopcraft et al. 2010). The seasonal zone contained hydrophilic sedge and grass species which were restricted to wetland areas. Next, the temporary zone is characterized by grey-brown soils which are temporarily waterlogged. The temporary zone consisted predominantly of grass species; a mixture of species which occur extensively in non-wetland areas, and hydrophilic woody plant species which were restricted largely to wetland areas.

Soil collection and processing

For each wetland zone and site, soil samples (n = 2) of approximately 1.5 kg were collected where milkweed had been sampled for nutrient and metal analysis, using a hand auger up to a 10 cm maximum depth. Samples were stored in ziplock bags for further processing within 72 hrs in the laboratory. In laboratory, the soils were dried at 60 °C for 48–72 hrs before disaggregation in a porcelain mortar and strained through a sieve (mesh size 0.05 mm) to remove plant roots and other debris.

Soil metal analysis

Soil samples were sent for nutrient and metal analysis at a SANSA approved laboratory, i.e. BEMLAB (Cape Town). Acid digestion utilising a 1:1 mixture of 1N nitric acid (HNO_3) and hydrochloric acid (HCl) under 80 °C for approximately 30 minutes was conducted for cation elements (i.e. Na, B, Ca, Mg, K) using an ICP-OES optimal emission spectrometer. For metal (i.e. Cr, Cu, Fe, Zn, Pb) analyses, extraction was conducted using 5 g of dried soil mixed with 20 mL HNO_3, with 5 mL hydrogen peroxide added prior to filtration on a sand bed that was heated up for 8 hrs. To check for results accuracy, certified reference natural standards (i.e. SL-1(IAEA), SARM-51(MINITEK)) were applied, digested and analysed in triplicate and used for recovery testing, which ranged between 88% and 110%.

Soil total nutrient and organic matter content

Nitrate concentrations were determined using 1N potassium chloride (KCl). Nitrate-N (NO_3^-) concentration in the extract was determined using a SEAL Auto Analyzer 3 via the reduction column, before the nitrate acted in response to the sulphanilamide under acidic conditions using N-1-Naphthylethylenediamine dihydrochloride. Phosphate (PO_4^{3-}) and total phosphorus (TP) concentrations were analysed using the Bray extract (Bray and Kurtz 1945).

Total organic carbon was identified using the modified Walkey-Black method in 500 mmol L^{-1} Erlenmeyer flask, where 0.5 g of soil was followed by 10 mL 0.167 $MK_2Cr_2O_7$ and then 20 mL of concentrated sulphuric acid (Chan and Parkin 2001). In order to calculate the amount of dichromate taken up by the soil, post-reaction and excess dichromate was determined by titrating against 1M $FeSO_4$. The procedure was repeated several times, with 5 mL and 10 mL concentrated sulphuric acid being utilised instead of 20 mL, and this resulted in three acid aqueous solutions of 0.5:1.

Milkweed sampling

The abundance and height of milkweed in Nylsvley wetland was estimated using transects positioned perpendicularly across the wetland sites, i.e. spanning all zones (see above). Within each transect per site, the wetland was divided into three wetland zones (i.e. temporary, seasonal, permanent) by assessing the different wetland vegetation type indicators and observing soil cores for mottles. In each wetland zone along the demarcated transect, a 10 m × 10 m quadrat (n = 2) was haphazardly selected and all individual milkweed plants enumerated, measured (i.e. height) and the number of stems per plant counted. For the permanent zone, due to its smaller size, the quadrats overlapped slightly into the seasonal zonations (Figure 2).

Data analysis

All data were assessed for normality and homogeneity of variance and were found to conform to parametric assumptions using the Shapiro-Wilk's W and Levene's tests, respectively. Differences in metal and nutrient concentrations, soil contaminant indices, as well as milkweed plant heights, abundances and numbers of stems among three zones (i.e. temporary, permanent and seasonal) and five sites (i.e. N1–N5) were assessed using a two-way ANOVA with significant variables being further assessed for pairwise differences using Tukey's post-hoc analysis. Additionally, using a Pearson correlation, we tested for relationships among milkweed plant height, abundance and number of stems, metal and nutrient concentrations, and soil organic carbon (SOM) to assess if the environmental variables influenced the milkweed plant characteristics. All correlations, ANOVAs and the testing of data for normality and homogeneity of variance were carried out in SPSS version 25 (SPSS Inc. 2017).

Principal Coordinates Analysis (PCoA) (Legendre and Anderson 1999; McArdle and Anderson 2001) was used to visualise milkweed multivariate structure variation among the three wetland zones (i.e. permanent, seasonal, temporary) and five sites (i.e. N1–N5) using log (x + 1) transformed data for environmental variables and square-root transformed data for milkweed abundances. The PCoA was conducted in PRIMER version 6 (Anderson et al. 2008).

Table 1. Two-way ANOVA results for soil chemistry variables measured from Nylsvley Wetland.

Dependent Variable	Site		Wetland zonation		Site × Wetland zonation	
	F	*p*	F	*p*	F	*p*
pH	**7.304**	**< 0.001**	0.627	0.435	1.287	0.298
EC	**3.156**	**0.029**	1.571	0.220	1.722	0.172
P	0.575	0.683	1.759	0.195	0.638	0.639
Na	**5.814**	**0.001**	0.779	0.385	1.277	0.302
K	2.157	0.099	3.558	0.069	1.760	0.164
Ca	1.140	0.357	**4.242**	**0.049**	**2.790**	**0.045**
Mg	**2.791**	**0.045**	**6.133**	**0.019**	1.944	0.130
Cu	0.793	0.539	**9.215**	**0.005**	1.226	0.322
Zn	0.171	0.951	**10.053**	**0.004**	1.445	0.244
Mn	**5.965**	**0.001**	0.381	0.542	1.657	0.187
B	0.888	0.483	0.079	0.781	0.393	0.812
Soluble S	0.811	0.529	0.274	0.605	0.890	0.482
C	1.253	0.311	3.916	0.057	1.921	0.134
Fe	0.850	0.505	**4.633**	**0.040**	0.518	0.723

Results

Environmental variables

Supplementary material Table S1 highlights means (± standard deviation) of the measured soil chemistry variables from Nylsvley Wetland. Conductivity, pH, Na, Mg and Mn were found to significantly differ ($p < 0.05$) across sites, whereas Ca, Mg, Cu, Zn and Fe were significantly different ($p < 0.05$) among wetland zones (Table 1). An interaction of sites and wetland zones indicated significant differences ($p = 0.045$) for Ca. Post-hoc analysis for sites indicated significant differences for pH [sites 1 *vs* 2 ($p = 0.006$), 1 *vs* 3 ($p < 0.001$), 1 *vs* 4 ($p = 0.005$)], conductivity [sites 2 *vs* 4 (p = 0.042), 4 *vs* 5 ($p < 0.042$)], Na (sites 1 *vs* 5 ($p = 0.024$), 3 *vs* 5 ($p = 0.005$), 4 *vs* 5 ($p = 0.001$)] and Mn [sites 1 *vs* 4 ($p = 0.014$), 1 *vs* 5 ($p = 0.001$)]. While for wetland zonations, significant differences were observed Ca and Mg (all combinations, $p < 0.01$), Cu, Zn and Fe for wetland zonations permanent *vs* seasonal ($p < 0.001$) and permanent *vs* temporary ($p < 0.001$).

Milkweed distribution and abundance

Milkweed plants were present in all wetland zonations throughout the study, except for site 1 permanent and seasonal zones, and the site 5 permanent zone (Figure 3a). The milkweed abundances were similar across the different wetland zones (F = 0.342, $p = 0.843$), but were significantly different across study sites (F = 12.731, $p = 0.013$). Milkweed was most abundant in the seasonal and temporary zones, except for the site 2 permanent zone which had the highest abundances ($n = 64$) throughout the study (Figure 3a). Plant height (PH) and number of stems (NS) were found to be significantly different across the different wetland zones (PH: F = 4.337, $p = 0.014$; NS: F = 5.016, $p = 0.007$) and sites (PH: F = 30.371, $p < 0.001$; NS: F = 4.533, $p = 0.002$). Where present, mean height of milkweed plants was generally low for site 2 when different wetland zones were pooled (Figure 3b). Post-hoc analysis revealed significant differences for seasonal

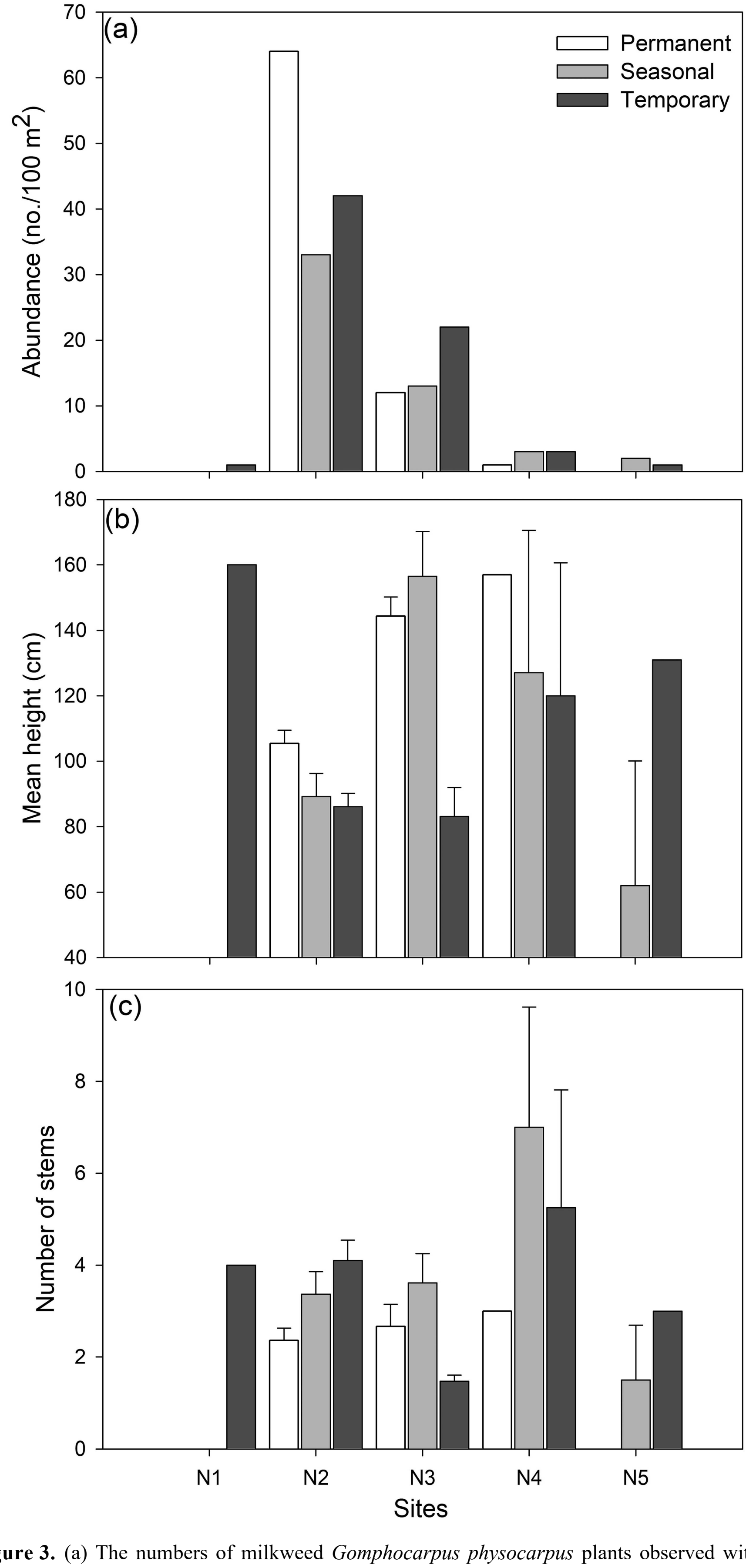

Figure 3. (a) The numbers of milkweed *Gomphocarpus physocarpus* plants observed with a 10 m × 10 m quadrat; (b) mean heights (± standard error) of the plant, and; (c) numbers of stems per milkweed plant (± standard error) for the three wetland zonations and sites.

Table 2. Pearson correlation coefficients between measured environmental variables and milkweed plant variables generated for the Nylsvley Wetland. The values in parentheses are the *p*-values and values in bold are significant ($p < 0.05$).

Variable	Height	Stem	Abundance
pH	−0.26 (0.345)	−0.21 (0.461)	−0.39 (0.148)
EC	0.24 (0.387)	0.32 (0.240)	−0.28 (0.303)
P	0.26 (0.355)	**0.56 (0.029)**	−0.07 (0.803)
Na	−0.04 (0.879)	−0.31 (0.264)	−0.08 (0.777)
K	0.09 (0.756)	0.29 (0.292)	0.30 (0.278)
Ca	0.12 (0.675)	0.40 (0.140)	0.03 (0.915)
Mg	0.08 (0.784)	0.36 (0.188)	0.09 (0.744)
Cu	−0.39 (0.152)	**−0.51 (0.049)**	0.06 (0.842)
Zn	−0.02 (0.930)	−0.32 (0.244)	0.17 (0.544)
Mn	0.12 (0.667)	−0.15 (0.594)	**0.55 (0.033)**
B	−0.31 (0.262)	−0.50 (0.060)	−0.01 (0.963)
Soluble S	−0.23 (0.404)	−0.21 (0.458)	0.35 (0.199)
SOM	−0.08 (0.788)	0.01 (0.979)	−0.04 (0.877)
Fe	−0.24 (0.387)	−0.45 (0.092)	0.20 (0.474)

vs temporary ($p = 0.028$), permanent *vs* temporary ($p = 0.019$), sites 1 *vs* 2 ($p < 0.001$), sites 1 *vs* 3 ($p < 0.001$), sites 1 *vs* 4 ($p < 0.001$), sites 2 *vs* 3 ($p = 0.002$), sites 2 *vs* 5 ($p < 0.001$), sites 3 *vs* 5 ($p < 0.001$) and sites 4 *vs* 5 ($p = 0.001$) for milkweed plant height. Number of stems per milkweed plant was highest for the site 4 seasonal and temporary wetland zonations (Figure 3c). Whereas for the number of stems per milkweed plant, post-hoc analysis revealed significant differences for permanent *vs* seasonal ($p = 0.027$), permanent *vs* temporary ($p = 0.026$), sites 1 *vs* 4 ($p = 0.033$) and sites 4 *vs* 5 ($p = 0.010$).

Most of the environmental variables were not significantly correlated ($p > 0.05$) with milkweed plant variables (Table 2). The number of stems per plant were significantly correlated positively with P ($r = 0.56$, $p = 0.029$) and negatively with Cu ($r = -0.51$, $p = 0.049$), whereas, the number of plants per quadrat was positively correlated with Mn ($r = 0.55$, $p = 0.034$).

Principal Coordinates Analysis (PCoA) results are presented in Figure 4, with the first two axes of the selected exploratory variables accounting for 94.7 % of the total milkweed abundance variance. Soluble S and Mn were positively associated with the 1st axis, while pH, Na, SOM and conductivity were negatively associated with the 1st axis (Figure 4). Soluble S and pH levels were positively associated with the 2nd axis, while conductivity, SOM (represented by C), Na and Mn were negatively associated with the 2nd axis. Strong overlaps in the polygons for the three wetland zonations suggest that milkweed populations were similar, but were also different among sites, with three groups identifiable: *group 1* (site 1 permanent and seasonal zonations with no milkweed), *group 2* (sites 2 and 3 with high milkweed abundances) and *group 3* (sites 1 temporary, 4 and 5 with low milkweed abundances).

Discussion

Understanding how distributions of non-native species relate to key environmental characteristics is a critical component of predictive efforts and

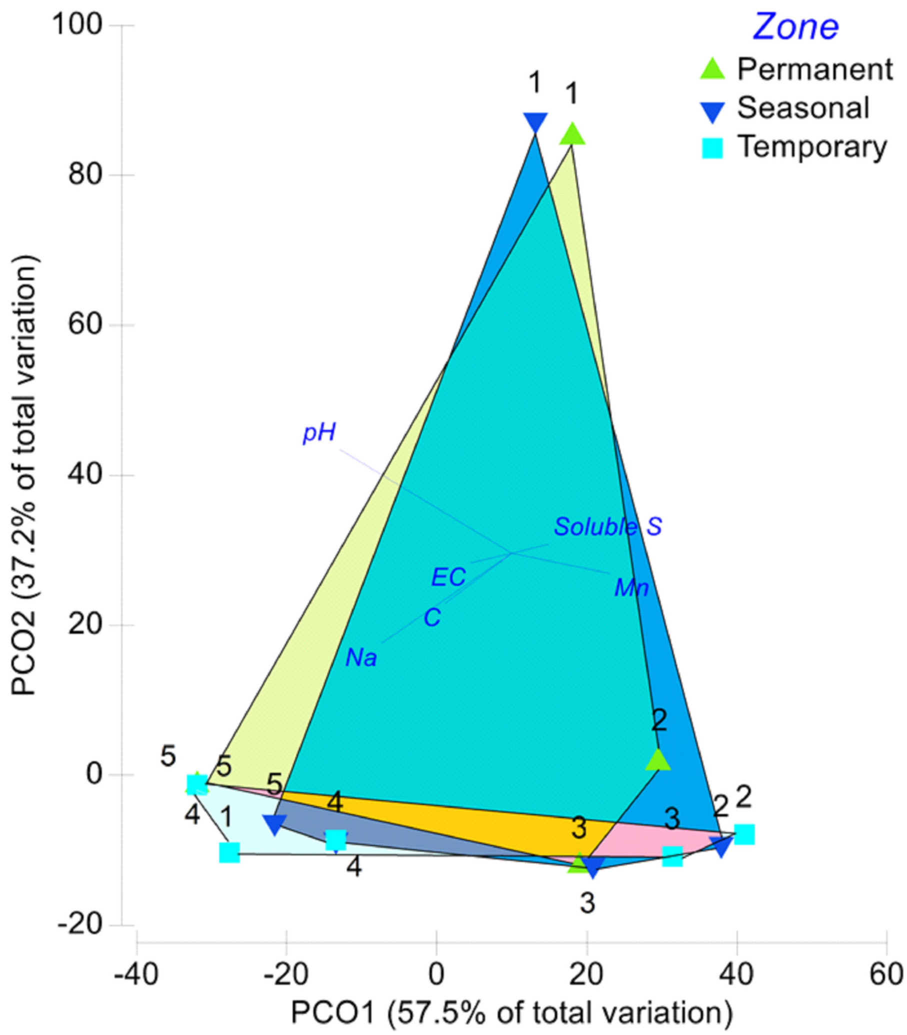

Figure 4. Principal Coordinates Analysis (PCoA) for milkweed species recorded in the Nylsvley Wetland. The PCoA was based on extended dissimilarities and abundances which were square-root transformed. The wetland zonations (i.e. indicated by shapes and colours) for the 5 sites (i.e. indicated by numbers) are outlined by polygons

management responses. The present study examined how the distribution of a non-native milkweed differed across discrete wetland zones and sites, and whether plant numbers and characteristics related to multiple abiotic soil properties. Significant differences in a range of soil properties were deduced among wetland zones and sites. However, the abundance of milkweed was not significantly affected by wetland zones alone; the non-native plant was able to colonise a range of sites with differing hydrological characteristics. Nevertheless, we found significant abundance differences across sites, indicating that underlying soil property differences among sites could be a key driver that modulates distributions of this non-native plant. Indeed, plant abundances were found to relate significantly to Mn in particular across study sites. Certain plant properties (i.e. number of stems) were, however, found to differ significantly across both zones and sites, with stem numbers relating significantly negatively to Cu, and positively to P. Conversely, plant heights did not significantly differ across soil variables from sites. In turn, our study presented key principal components that explained the abundance of milkweed (i.e. soluble S, Mn, pH, Na, SOM and conductivity), illustrating further patterning across habitat zones and wetland sites, as well as key soil properties that might drive distributions.

The presence of non-native milkweeds across all surveyed habitat zones in this study indicates that the focal species is tolerant to a range of hydrological conditions. This is a cause for concern given the international conservation designation of the surveyed site, and its importance for a range of ecologically important taxa. Our results suggest that the examined milkweed could potentially expand its range into other suitable sites in future, to an extent irrespective of hydrology. However, the non-native plant was missing entirely from certain zones at some sites (i.e., 1 and 5), indicating the presence of more complex interactions or other processes not formally examined in this study. Whilst milkweeds were shown to be tolerant to different wetland zones in the present study, we found site-specific differences which likely are linked to other environmental characteristics, such as underlying soil properties. In general, site 2 was found to have the highest milkweed abundances, and particularly in the permanent wetland zonation where there were highest levels of Mn, with Mn overall significantly related to abundances. The fact that this site had the highest abundances but shorter overall plant heights also suggests that the plants might have invested more energy into root growth to find water compared to other sites since the site was particularly dry (TD and FD, *personal observation*). Overall, in contrast to our hypothesis, no clear patterning in the abundance of milkweeds was found across the permanent to temporary wetland zones. Long et al. (2009) found that soil type has a significant effect on seed persistence and seedling vigour of milkweed and they also found that warmer and wetter soils favoured shorter seed persistence, similar to the permanent zone which had less milkweed species. Therefore, soil and moisture conditions have the ability to influence recruitment together with habitat complexities which may shield other effects from being expressed. It may be possible that the differences in soils between our wetland zones was not large enough for differences in seed recruitment to manifest. However, according to principal components analyses, milkweed abundances were mostly structured based on soluble S, Mn, pH, Na, SOM and conductivity. Further, stem numbers were found to be significantly positively related to P levels, owing to its importance as a resource, yet negatively related to Cu.

Accordingly, soil properties were identified as the main factor contributing to distribution and abundance of milkweed species in this study, similar to studies conducted on cereal crops (Rogers and Benfey 2015). Plants prefer to grow where pH values are generally in the range of 5.5 to 6.5 as plant nutrients leach out of soils at pH below 5 much more rapidly than from soils with values between 5 and 7.5 (NeSmith and

McElwee 1974; Gentili et al. 2018). In addition, low pH values could result in reduction of seed germination, destruction of the root cell structure, and change in the nutrient availability and disrupt nutrient uptake, and thus resulting in a significant negative effect on growth in milkweed plants (Peng et al. 2008; Gao et al. 2014). Indeed, pH was found to differ significantly among sites in our study, yet not habitat zones, and so it may thus be one important driver of milkweed growth. However, the pH range recorded in the present study was not particularly broad, with much broader pH ranges having been commonly recorded in soils of South African wetlands (Cilliers et al. 1998; Bird and Day 2014). Asmarlaili et al. (2018) highlighted that increased soil moisture content could also increase soil sulphate acid causing increased crown crop growth. Similarly, the high milkweed plant growth observed in the permanent zonation could be explained by the varying soluble S loads in the soils. Manganese plays an important role as a cofactor in various enzymatic reactions for plant growth. Soils with pH values lower than 5.5 contain large concentrations of water-soluble or exchangeable manganese; this might explain the high concentrations of measured Mn in the soils as the pH values were below 5.5. Accordingly, Mn concentrations increase at pH values < 7, as has been observed in studies such as Adeoye and Agboola (1985) and Zhang et al. (2012). As with pH, Mn also differed significantly among sites in the present study, but not among hydrological zones.

Soil organic matter was another important factor affecting milkweed distribution mostly due to its ability to cause high water retention thereby leading to improved soil structure and water-holding capacity resulting in better milkweed growth and health, and improved movement of mobile nutrients to the plant roots (Parthasarathy and Nandakishore 2016; Hatfield et al. 2018). Sodium may also help many plants grow better including milkweed, but it is not considered essential to plant growth and reproduction as it can cause inhibition of plant water uptake and lock up key soil nutrients, such as phosphates, leading to reduced growth (El-Mohdy 2017).

Conclusions

The present study found milkweed abundance to differ significantly among sites but not across wetland hydrological zones, indicating a capacity of this species to tolerate ranging hydrological conditions. Milkweed height and stem numbers did, however, differ among wetland zones. We also identified key soil properties that can determine distributions of milkweed. Nevertheless, factors other than soil characteristics likely mediate milkweed distributions. In regions such as Australia, the success of milkweeds has been attributed to an absence of intraspecific competition for pollinators in low-density founding plant stands compared to stands with higher plant densities (Ward et al. 2012). Insect-plant interactions can also differ among native and invaded regions regarding milkweeds (Bukovinszky et al. 2014), which could further mediate invasion success, for example, owing to release from specialist natural enemies. Milkweeds are also highly specialized plants with regards to their pollination procedure, however, their invasion success has been facilitated in non-native regions by the availability of alternatively suitable wasp pollinators. Accordingly, pollinator availability within regions is likely a key factor influencing success, yet appears to be readily overcome. Future work should further examine environmental mediators of invasion success in milkweeds, and in particular, the effects of interactions between milkweeds and native plant assemblages. This will contribute to a better understanding of ecological impacts of milkweed invasions and potential biotic resistance processes.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Means of the measured soil chemistry variables from Nylsvley Wetland across sites and zones in the wetland.

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2020/Supplements/BIR_2020_Dalu_etal_SupplementaryMaterial.xlsx