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PRIMARY RESEARCH PAPER

Physico-chemical impacts of terrestrial alien vegetation on temporary wetlands in a sclerophyllous Sand fynbos ecosystem

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Abstract Temporary depression wetlands form a characteristic feature of the wet-season landscape in the south-western Cape region of South Africa, yet they remain largely unstudied. We hypothesized that the loss of sclerophyllous Sand fynbos habitat around these temporary wetlands causes in-wetland physico-chemical changes. We expected to observe a decrease in the concentration of humic substances in wetlands and a corresponding rise in surface water pH as fynbos cover decreases around wetlands, in this case owing to alien vegetation invasion. A set of 12 differentially invaded temporary depression wetlands within a Sand fynbos ecosystem in Cape Town were repeatedly sampled during the 2009 wet season. Multivariate gradient analysis techniques revealed associations between fynbos cover bordering wetlands and various physico-chemical and biotope constituents within wetlands. Univariate linear regression models reported strong and temporally consistent negative relationships between terrestrial fynbos vegetation cover and wetland pH and positive relationships with humic content. Results indicate that replacement of Sand fynbos with alien vegetation causes a reduction of humic input to wetlands, which in turn has knock-on effects on other wetland environmental constituents such as pH. These findings are expected to be applicable to any wetland where surrounding humic-rich sclerophyllous vegetation is replaced by a non-sclerophyllous agent.

Keywords Temporary wetlands · Environmental conditions · Habitat transformation · Alien vegetation

Introduction

Pronounced negative effects of human land-use activities on freshwater ecosystem structure and function are well documented for rivers and lakes (Carpenter et al., 1998; Leavitt et al., 2006; Pham et al., 2008). However, information on the effects of habitat transformation on wetland ecosystems is scarce, particularly for small temporary wetlands, which are often the most common wetlands in temperate, semi-arid and arid regions (Semlitsch & Bodie, 1998; Angeler & Moreno, 2007). Temporary wetlands in low-lying areas (e.g. coastal plains) are highly threatened by human transformation of surrounding natural habitats, mainly from agriculture and urban development (Williams et al., 2001; Oertli et al., 2005; Williams, 2006; Zacharias & Zamparas, 2010).

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Their small size and temporary nature has meant that the loss of many of these wetlands has historically not received much attention, although the wide-scale loss of temporary wetlands across the globe is now well recognised (Semlitsch & Bodie, 1998; Williams, 2006; Zacharias & Zamparas, 2010). The effects of human alteration of the landscape on remaining wetlands are still poorly understood. In the south-western Cape mediterranean-climate region of South Africa, temporary wetlands are an abundant and characteristic feature of the wet-season landscape, yet their ecology remains largely unstudied (but see De Roeck et al., 2007; De Roeck, 2008; Mlambo et al., 2011). No attempts have yet been made to link the environmental components of these temporary wetlands to anthropogenic influences in the landscape in South Africa, and very few studies (e.g. Rhazi et al., 2001; Brooks et al., 2002; Carrino-Kyker & Swanson, 2007) have done so worldwide.

The indigenous vegetation of the south-western Cape is characterised by an evergreen, sclerophyllous, shrub-dominated vegetation type known locally as ‘fynbos’ (Rouget et al., 2003; Rebelo et al., 2006). Sand fynbos (sensu Rebelo et al., 2006) is a type of fynbos that was once widespread on the highly leached oligotrophic sands of the south-western Cape coastal lowlands, but it has been reduced to less than 15% of its original extent by human-induced habitat transformation. Terrestrial alien invasive plants pose a particularly serious threat to remaining lowland Sand fynbos habitat in the region (Witkowski, 1991; Musil, 1993; Heijnis et al., 1999; Rouget et al., 2003; Gaertner et al., 2011). Whilst a number of studies have addressed the potential impacts of this invasion on the quantity of water available to aquatic ecosystems in South Africa (e.g. Enright, 2000; Le Maitre et al., 2000; Dye & Jarmain, 2004; Görgens & van Wilgen, 2004; Richardson & van Wilgen, 2004), there have been no assessments of effects on surface water chemistry (Chamier et al., 2012).

This study assesses the environmental characteristics of a set of temporary wetlands differentially impacted by habitat transformation caused primarily by invasion of alien vegetation. Direct and indirect effects of replacing surrounding indigenous Sand fynbos with alien plants on these temporary wetland ecosystems are quantified. It is hypothesized that the loss of Sand fynbos around wetlands alters the characteristic physico-chemical signature imparted to surface waters by fynbos vegetation. The potential knock-on effects of these physico-chemical changes on various biotope characteristics in wetlands (percentage cover of macroalgae, complex-structured vegetation, simple-structured vegetation and open water) are also explored. In terms of the specific constituents driving physico-chemical changes in this study, we expect a decrease in the concentration of humic substances in wetlands and a corresponding rise in surface water pH with an increase in fynbos transformation around wetlands. The characteristic darkly stained waters of the south-western Cape are caused by leaching of humic compounds into these aquatic systems from the surrounding indigenous fynbos flora, which contain high levels of polyphenolic compounds (collectively known as humics or tannins) in their tissues (King et al., 1979; Gardiner, 1988; Raubenheimer & Day, 1991; Midgley & Schafer, 1992). This has evolved as an anti-herbivory adaptation for an evergreen lifestyle (Raubenheimer & Day, 1991; Rebelo et al., 2006). Any loss of fynbos vegetation around wetlands, due to human-induced transformation of habitat, is expected to be associated with a decrease in the allochthonous input of humic compounds to these wetlands. However, it is also important to consider the potential allochthonous input of humics from the invading plant species concerned.

Alien vegetation invasion in this study is represented almost entirely by two species, namely the Port Jackson willow *Acacia saligna* (Labill) Wendl. originating from Australia, and the kikuyu grass *Pennisetum clandestinum* Höchst. ex Chiov. of East African origin. *A. saligna* is sclerophyllous and has been reported to have leaves with high condensed tannin content (Makkar et al., 1995; Krebs et al., 2007; Kumara Mahipala et al., 2009), whilst *P. clandestinum* tissue contains negligible concentrations of condensed tannins (Jackson et al., 1996; Marais, 2001). Prior sampling of vegetation cover around wetlands revealed that *P. clandestinum* was the dominant invader in this study, occurring at approximately twice the density in areal cover of *A. saligna* at invaded sites. Therefore, it is expected that humic input to wetlands will be substantially lower for sites where surrounding fynbos vegetation has been largely replaced by *P. clandestinum*. A small amount of humic substances could, however, be leached to these wetlands by stands of sclerophyllous *A. saligna* and this may have an influence on the overall concentration of these substances in wetlands.

The predominant invaders of Sand fynbos are various woody Australian *Acacia* species and various pioneer grasses (Milton, 2004; Musil et al., 2005). Whilst the ecosystem effects of invasive grasses in the region are scarcely documented (but see Gaertner et al., 2011), various studies have documented the ability of invasive acacias to alter terrestrial ecosystem structure and function in the south-western Cape (e.g. Witkowski & Mitchell, 1987; Witkowski, 1991; Musil, 1993; Richardson & van Wilgen, 2004; Yelenik et al., 2004). Nitrogen-fixing acacias have high levels of tissue nitrogen (hereafter N), unlike the fynbos plants they replace. Invading acacias form dense stands which deposit a large amount of high-N leaf litter into the previously nutrient-deficient soils, causing a shift in soil N-cycling from a low to high N-cycling regime, with knock-on effects on other processes and biotic components of the ecosystem (Yelenik et al., 2004). Higher levels of soil N have been found in stands of acacias compared with fynbos soils (e.g. Witkowski, 1991; Musil, 1993; Yelenik et al., 2004; Jovanovic et al., 2009; Gaertner et al., 2011). Furthermore, this may have implications for groundwater quality. For a Sand fynbos system in the south-western Cape (Riverlands Nature Reserve), Jovanovic et al. (2009) documented significantly elevated concentrations of nitrates + nitrites ($NO_3^- + NO_2^-$) in groundwater of *Acacia*-dominated stands compared with the Sand fynbos-dominated control. A logical extension of their findings is that $NO_3^- + NO_2^-$ concentrations may become elevated for small waterbodies surrounded by extensive *Acacia* stands. Thus, we expect that alien vegetation encroachment around these small isolated wetlands has the potential to raise nutrient levels in what are naturally highly oligotrophic systems. Specifically, we expect to observe a positive relationship between the cover of *A. saligna* around wetlands and $NO_3^- + NO_2^-$ levels in wetlands. *A. saligna* cover was, however, sparse in this study relative to that of *P. clandestinum* and as such it is also possible that the N-enriching effects of *A. saligna* may not manifest in these wetlands.

The effects of acacias on soil phosphorus (P) concentrations are poorly understood. Undisturbed Sand fynbos ecosystems are known to have low P levels (Witkowski & Mitchell, 1987; Rebelo et al., 2006), but the impact of invading plants on P levels in these fynbos ecosystems is unclear. Several studies found no difference in leaf litter or soil P loads between undisturbed Sand fynbos sites and those invaded with *A. saligna* (Witkowski, 1991; Musil, 1993; Yelenik et al., 2004). In contrast, another study found greatly elevated soil P levels in areas infested by a mix of *A. saligna* and *Acacia cyclops* A. Cunn. ex G. Donn. and attributed this to the significantly higher levels and turnover of leaf litterfall for acacias relative to fynbos (Witkowski & Mitchell, 1987). In Sandstone fynbos on the Agulhas Plain, no differences in soil P were found between a kikuyu-invaded and a fynbos control site (Gaertner et al., 2011). In this study the relationship between fynbos cover around wetlands and water column phosphate (PO_4^{3-}) concentrations is explored as a hypothesis-generating exercise, given the ambiguous nature of literature findings.

Methods

Study area and site selection

The study took place in and around the Kenilworth Racecourse Conservation Area (KRCA) located in the suburb of Kenilworth in Cape Town, South Africa (Fig. 1). KRCA is situated on a flat sandy coastal plain known as the Cape Flats, which has become extensively transformed by the urban sprawl of Cape Town. The Cape Flats falls within the south-western Cape mediterranean-climate region of South Africa, receiving the majority of its 575 mm of mean annual precipitation during the winter months (Rebelo et al., 2006). KRCA has a total area of approximately 52 ha consisting, first, of a core conservation area with a history of minimal disturbance, and second, a peripheral area that has received moderate levels of disturbance. A third area sampled was an extensively disturbed piece of vacant land (approximately 54 ha in size) at Youngsfield military base, which is separated from KRCA by a highway (Fig. 1). The core conservation area of KRCA occurs inside Kenilworth Racecourse, the oldest horse racing track in South Africa (established in 1882). For most of its existence, the core conservation area was preserved inadvertently from degradation by the South African Turf Club (KRCA was only formally established in 2006), whilst areas surrounding the racecourse have mostly been developed for housing.

The specific type of Sand fynbos in and around KRCA is Cape Flats Sand fynbos (sensu Rebelo et al., 2006), which covers those parts of the Cape Flats with acid sandy soils of Tertiary origin (c.f. Cape Flats Dune strandveld occurring on calcareous sands of marine origin, Rebelo et al., 2006). KRCA contains the largest remaining and the best condition fragment of Cape Flats Sand fynbos habitat and harbours 310 indigenous plant species within its 52-ha area (Gehrke et al., 2011). Cape Flats Sand fynbos habitat contains an abundance of depression wetlands that fill during the winter when rising water tables manifest as surface water on the sandy coastal plain. Although these wetlands are still abundant across the Cape Flats, the majority now occur in a transformed urban landscape, primarily as depressions in vacant pieces of land invaded by alien vegetation and surrounded by residential and informal housing. Other than at KRCA, very few wetlands exist within the original fynbos habitat. It is likely that this widespread transformation of the landscape corresponds with a change in the environmental characteristics of these wetlands, but the extent of this change has not been investigated.

During the 2009 wet season, 12 temporary isolated depression wetlands (sensu Ewart-Smith et al., 2006) in and around KRCA were sampled repeatedly for various environmental constituents. The chosen wetlands spanned a gradient of habitat transformation due to alien vegetation invasion and occurred across the three differentially transformed areas at Kenilworth. These three areas have been differentially invaded by alien vegetation because of differences in their land-use histories. Four wetlands (sites 1–4, see Fig. 1) occurred within the core conservation zone of KRCA

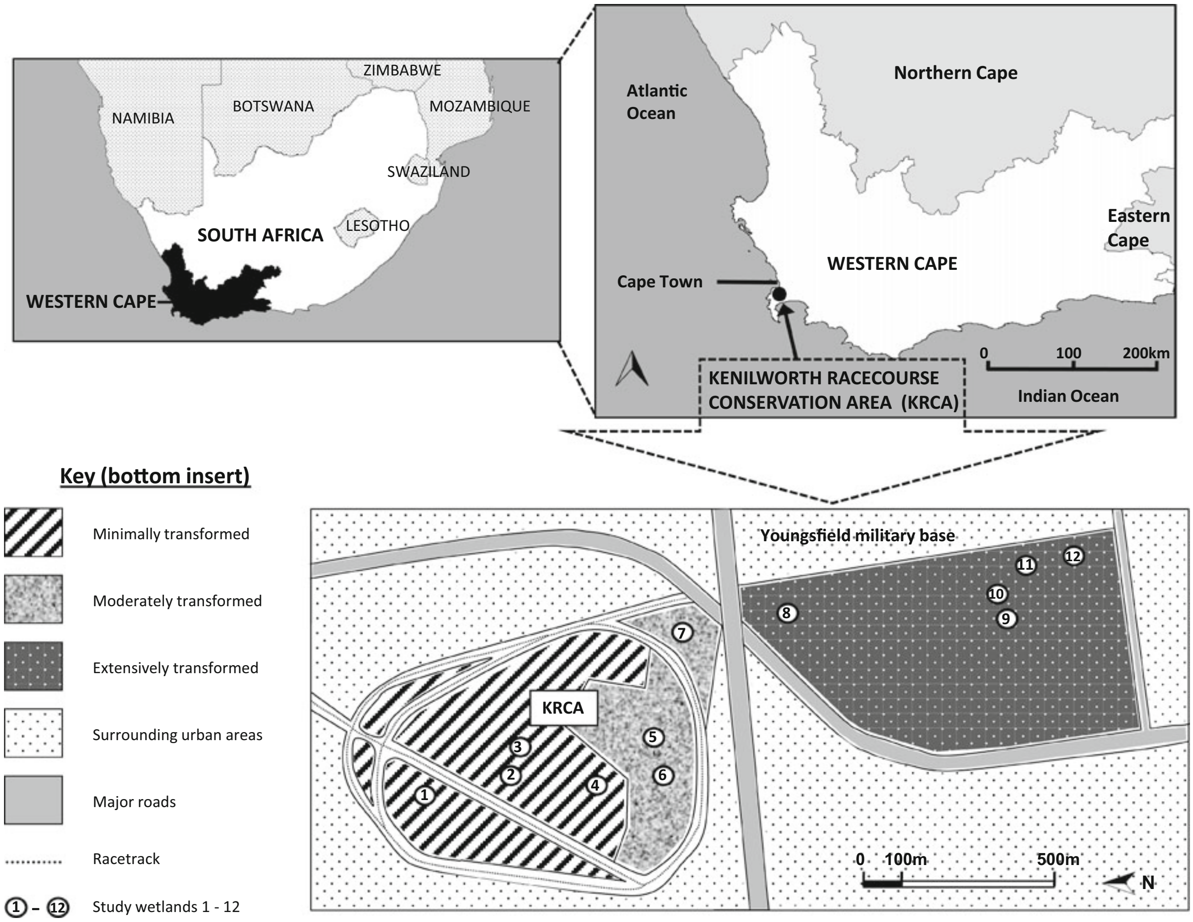

Fig. 1 Position of the Kenilworth Racecourse Conservation Area (KRCA) within the Western Cape Province of South Africa (*top*). The layout of the 12 study wetlands is also depicted (*bottom*)

(untransformed fynbos habitat) and have a history of minimal disturbance. A form of disturbance in this area is the lack of fire (many elements of Sand fynbos vegetation are serotinous), and whilst a controlled burn of part of the area was performed in 2005, most of the vegetation has not been burned for roughly 100 years (Turner, 2006). This remnant piece of Cape Flats Sand fynbos habitat is otherwise considered to be pristine and ecologically functional (Hitchcock, 2006; Turner, 2006; Hitchcock et al., 2008; Gehrke et al., 2011). Transformation of habitat within 100 m of wetlands within the core area includes the racetrack itself, which encloses the area (unfertilized, mowed kikuyu grass), and several gravel and sand roads. Three wetlands (sites 5–7, see Fig. 1) occurred on the periphery of the core conservation area on a patch of land that has been moderately disturbed in the past for horse jumping activities and dumping of earth for building activities associated with the racetrack and surrounding grounds. Although the peripheral area in which wetlands were sampled has not been physically disturbed by humans for several decades (it was zoned for conservation prior to establishment of KRCA), the once-disturbed patches have been colonised by kikuyu grass and acacias, thus preventing the re-establishment of fynbos in these patches. This has resulted in a mosaic of alien invaded land mixed with fynbos habitat in roughly equal proportions. Five wetlands (sites 8–12, see Fig. 1) occurred immediately outside KRCA at Youngsfield (extensively transformed land). This piece of land was historically a buffer zone around an airfield landing strip (located where the military base now stands), which served aircraft during WWII. This buffer area (consisting of Cape Flats Sand fynbos) was relatively undisturbed during this time, but when the airfield was decommissioned in the 1960s and converted to a military base, much of the land was physically disturbed by dumping activities associated with its construction and much of the fynbos was lost. In the years following this, the area was zoned as a buffer region between the military base and the surrounding urban areas and was not used except for physical training exercises. Since the 1980s the land has remained a buffer zone for the military base and has not been used for human activities. Initial physical disturbance of the Youngsfield landscape allowed for the invasion of alien vegetation. As noted earlier, this came in the form of the Port Jackson willow *A. saligna* and the kikuyu grass *P. clandestinum*. These two species have covered this vacant land for several decades (although the date of their first arrival here is unknown) and taken together constitute almost 100 % areal cover of the land.

Wetlands were sampled on three occasions (late August/early September, October and November). Sampling aimed to assess whether there were patterns of environmental response to the gradient of habitat transformation that were consistent over time and did not aim to test for temporal differences between sampling events. Despite an abundance of isolated depression wetlands in the area, only those of similar overall size and depth were selected. This targeted approach was taken so as to minimise potentially confounding effects of total surface area and hydroperiod on environmental conditions. These hydromorphometrical variables have been shown to have a significant influence on wetland physico-chemistry for temporary wetlands in the south-western Cape (De Roeck, 2008). The sites were selected a priori according to preliminary inspection visits during the wet season of 2007. The chosen sites all had a similar and predictable seasonal inundation regime, filling up with the first heavy rains usually in early May and remaining inundated until late November or early December ('intermittent' sensu Comín & Williams, 1994).

Quantifying habitat transformation

Wetlands across the three adjacent areas described above were surrounded by differing levels of habitat transformation within approximately 500 m of their edges, but beyond this were all similarly surrounded by urban areas. The most pronounced differences in surrounding habitat cover were observed within approximately 100 m of wetlands. This 100-m fringe was selected to quantify the gradient of habitat transformation in this study. Four 100-m transects were assessed at each wetland, radiating north, east, south and west from each wetland edge. The habitat cover type was recorded at 2-m intervals along each transect, producing 50 habitat cover points per transect and 200 per wetland. The categories of habitat cover recorded at each point were: indigenous vegetation (predominantly shrubs, but grasses and herbaceous forms were also recorded); alien shrub (*A. saligna*); alien kikuyu grass (*P. clandestinum*) and other alien vegetation (other annual grasses and herbaceous species were present, although these were very sparsely represented at the site); racetrack (unfertilized kikuyu); mowed field (unfertilized kikuyu) and road (gravel and tar roads were present). Upon completing transects, these variables were expressed in terms of their percentage cover across all four transects. Transects were recorded once before the commencement of sampling and, for analyses, the habitat transformation variables were considered static (Appendix 1 in Supplementary Material).

Sampling environmental variables

Three major biotopes were sampled in this study and were based on habitat structural complexity in accordance with aims of a concurrent study focussing on invertebrate assemblages at Kenilworth. This is because habitat structural complexity has been shown to be an important determinant of invertebrate abundance and assemblage composition in wetlands (Beckett et al., 1992; Cardinale et al., 1998; Batzer et al., 2006; Williams, 2006). The three structural habitat types were complex vegetation (generally submerged), simple vegetation (generally emergent) and open water (no vegetation). Complex vegetation was typically inter-woven and with fine dissected leaves and was dominated by the aquatic macrophyte *Isolepis rubicunda*, endemic to the south-western Cape (van Ginkel et al., 2011). However, various other vegetation species also formed a complex submerged habitat, including flooded semi-aquatic and terrestrial grasses. Simply structured vegetation habitat was further divided into two types: reeded form (consisting of two species in this study, namely *Typha capensis* and *Phragmites australis*) and sedge-like form (consisting mostly of the sedge species *Bulboschoenus maritimus* and the restio *Elegia tectorum*). Vegetation with reeded structure had broad strap-like stems, whereas a sedge-like form entailed finer stems typical of the Cyperacae and Restionacae. Open water habitat was defined as surface water devoid of vegetation, being at least 30 cm in depth above the bottom substrate. At each wetland, two orthogonal transects crossing the centre of the wetland were used to quantify the cover of each aquatic habitat type. Along each transect, ten points were selected at evenly spaced intervals and at each point the habitat type was recorded. The presence of the macroalga *Cladophora* sp. (hereafter referred to as the variable 'macroalgae') was also noted at each point. The twenty habitat points per wetland were used to estimate percentage cover of the three major habitat types and macroalgae per wetland.

The following physico-chemical variables were measured in situ for each of the three major habitat types per wetland: pH was measured using a Crison pH25 meter; dissolved oxygen was recorded using a Crison OXI45 oxygen meter; electrical conductivity was recorded using a Crison CM35 conductivity meter and turbidity was measured using a Hach 2100P turbidimeter. Temperature was also recorded. Physico-chemical readings were taken at a standardised depth of 30 cm across all habitats, with the exception of readings taken in habitats <30 cm deep.

The wetlands studied here were all of similar size and depth, but for descriptive purposes basic hydromorphometry measurements (maximum depth and total surface area) were taken at each wetland on each sampling occasion. Maximum depth (cm) was measured with a calibrated depth stick (approximately 0.5-cm accuracy). Total surface area (m^2) was estimated by mapping the perimeter of each wetland with a Garmin eTrex Vista handheld GPS (point accuracy of 3 m), using a minimum of 10 coordinate points to represent perimeter. Perimeter points were then used to calculate surface area (m^2) in Garmin MapSource v6.11.6 GIS software.

An integrated 5 l surface water sample was collected from various parts of the wetland, from which a 1-l sub-sample was taken for analysis of chlorophyll, nutrients and humics. This sub-sample was stored immediately in the dark at 4°C and filtered in the laboratory within 24 h through a Whatman GF/F 0.7-µm glass fibre filter. The filter and filtrate were stored frozen at −18°C and analysed within 30 days. $NO_3^- + NO_2^-$–N (Lachat QuikChem® Method 31-107-04-1-A) and PO_4^{3+}–P (Lachat QuikChem® Method 31-115-01-1-H) concentrations were estimated with a Lachat Flow Injection Analyser using standard wet chemistry methods. These variables are hereafter referred to in the text as nitrates + nitrites and phosphates, respectively. Chlorophyll *a* was extracted from filter papers using 90% ethanol and concentrations were measured using the spectrophotometric method of Sartory & Grobbelaar (1984), as summarised by Biggs & Kilroy (2000). The relative concentration of humic (polyphenolic) substances among wetlands was proxied using ultraviolet absorbance (UVA) at 254 nm. UVA readings were performed in a 1-cm quartz cuvette using a Beckman DU-64 spectrophotometer. All environmental variables were considered as labile variables and were sampled on each of the three occasions (Appendix 2 in Supplementary Material).

Data analysis

For each wetland, the physico-chemical variables measured in situ were averaged across the three biotopes to produce mean values per wetland. All other environmental variables were measured once in each wetland and these values were used for further analyses. Environmental variables were $\log_{10}$ transformed where appropriate to improve normality. Percentage variables were arcsine square root transformed to improve normality. Principal Components Analysis (PCA) was used as an exploratory technique to visualize multivariate patterns in the transformed, normalized environmental data on a two-dimensional plane (all physico-chemical and biotope variables were included in this matrix), using data across all three sampling visits. The percentage cover of indigenous vegetation was represented on the PCA plot using three broad categories of cover: 'None'; 'Moderate' (33–51%) and 'Extensive' (75–99%). Linear regression models were used to assess relationships between the habitat transformation gradient and environmental conditions in wetlands; analysing each sampling occasion separately (i.e. three separate datasets each consisting of 12 replicate samples). Detrended Correspondence Analysis (DCA) indicated that gradient lengths in the environmental dataset were best suited to linear rather than unimodal analyses (gradients lengths were all <3, Lepš & Šmilauer, 2003). Multivariate linear regressions were used to relate data matrices of physico-chemical and biotope variables to the habitat transformation variables. Multivariate regressions were performed using distance-based Redundancy Analysis (dbRDA, Legendre & Anderson, 1999; McArdle & Anderson, 2001), a non-parametric multivariate regression procedure based on any given dissimilarity measure, in this case Euclidean distance. Univariate linear regression models were used to test for relationships between each of the environmental variables of specific interest in this study (pH, humics, nitrates + nitrites and phosphates) and the gradient of habitat transformation ('% indigenous vegetation cover within 100 m' as a single predictor).

DCA ordinations were performed using CANOCO for Windows v4.5 (Ter Braak & Šmilauer, 2002). All dbRDA models were implemented using the DISTLM routine of the PERMANOVA + software package (Anderson et al., 2008). *P* values for dbRDA models were tested by 9999 permutations of residuals under the reduced model. Univariate linear regressions were performed using STATISTICA v10 software (Statsoft Inc. 2010, Tulsa, Oklahoma, USA). PCA ordinations were performed using PRIMER v6 software (Clarke & Warwick, 2001; Clarke & Gorley, 2006). Due to the small number of observations involved in each of the linear regressions ($n = 12$ for each of the three datasets), we balanced the possible lack of power to detect effects using a significance level of $\alpha = 0.10$. This a priori defined significance level was subsequently adjusted to account for multiple comparisons using Holm's sequential Bonferroni correction (Holm, 1979).

Results

Unconstrained ordination

Environmental conditions were clearly differentiated among those sites with extensive surrounding indigenous vegetation and those with none (i.e. between minimally and extensively transformed sites, respectively, Fig. 2). This pattern of difference between the least and most transformed sites appeared to be consistent over time, as reflected by separation of the two groups in the PCA plot over the three successive sampling occasions in this study (Fig. 2). Environmental conditions in the moderately transformed wetlands shared characteristics of both the least and extensively transformed sites. From the PCA plot it appears that there was considerable environmental variation among individual wetlands, even within each of the three transformation categories. PC1 appears to be associated with the loss of indigenous vegetation. Variables that are positively correlated with PC1 (using $r > |0.3|$ as a threshold) are pH, phosphates, % open water and % macroalgae (Table 1a). Negatively correlated variables are humics and % complex vegetation (Table 1a). The first two axes of the PCA ordination captured a fairly small proportion of the variation in environmental conditions at Kenilworth (50.2%, Table 1b) and thus do not necessarily pre- sent a clear picture of environmental gradients in the dataset.

Constrained ordination

The multivariate regression results (Table 2) provide quantitative confirmation of the unconstrained gradient patterns observed in the PCA plot (Fig. 2). The two sets of environmental variables (physico-chemical and biotope variables) showed strongly significant (in most cases $P < 0.01$) linear relationships with overall levels of habitat transformation as proxied by the percentage cover of indigenous vegetation around wetlands. The only exception to this was the relationship between percentage cover of indigenous vegetation and biotope variables for the November sampling event, which was deemed non-significant after sequential Bonferroni correction. The amounts of variation in the response matrices explained by overall levels of habitat transformation were not particularly high (ranging between 18.46 and 38.00%), despite being highly significant in most cases. The amounts of variation explained in the physico-chemical and biotope regressions were mostly similar, but the *P* values for the physico-chemical relationships appear to be stronger (Table 2). The percentage of surrounding kikuyu cover was significantly related to physico-chemical conditions in wetlands across all three sampling occasions, but only on one occasion (August/September) kikuyu cover was related to biotope characteristics in wetlands. The percentage cover of *Acacia* was mostly not related to the physico-chemical or biotope response matrices, being significant in only one

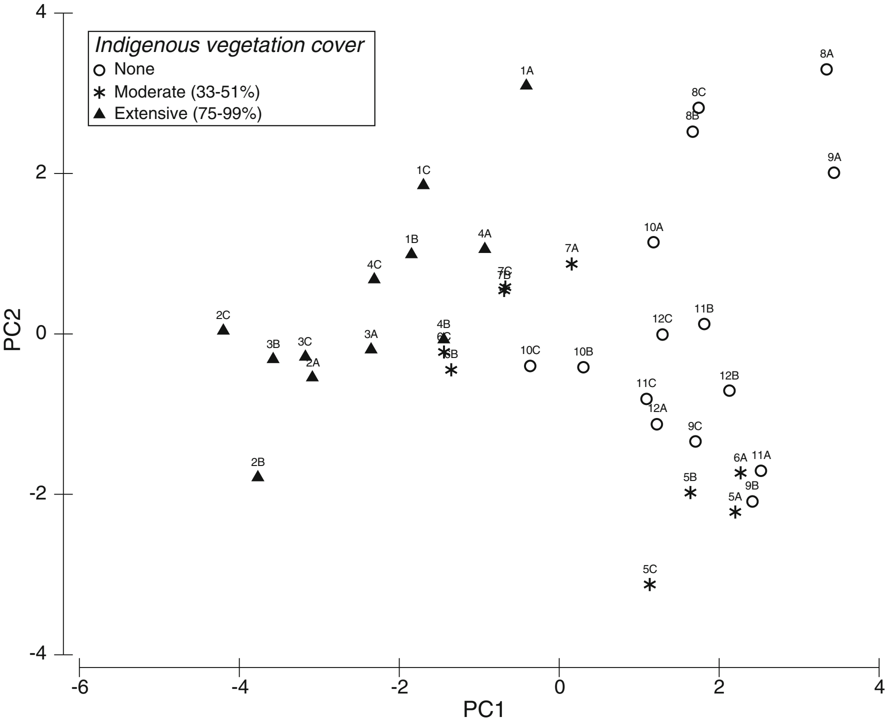

Fig. 2 Principal components analysis (PCA) on the normalized set of environmental variables, showing the ordination of sites sampled at Kenilworth ($n = 36$). The first two principal component axes are displayed, with PC1 and PC2 explaining 32.9 and 17.3% variation in the environmental data, respectively. The level of habitat transformation around wetlands is proxied by the remaining amount of indigenous vegetation within 100 m (coded here according to three broad categories of cover). Sites 1–12 are labelled according to the date of each sampling occasion (A: August/September 2009; B: October 2009; C: November 2009—see Appendix 2 in Supplementary Material for more details on sampling dates)

Table 1 (a) Coefficients in the linear combinations of environmental variables making up principal component axes 1 and 2. Variables with correlation of $r > |0.3|$ with PC1 (associated with loss of indigenous vegetation) are indicated with an *asterisk*. (b) Eigenvalues and corresponding percentage of environmental variation explained by each of the first five principal component axes

(a) Eigenvectors

Variable	PC1	PC2
pH*	0.356	0.294
Conductivity	0.209	−0.019
Turbidity	0.246	−0.353
Oxygen	0.178	0.423
Average temperature	−0.068	0.003
Nitrates + nitrites	−0.062	−0.254
Phosphates*	0.332	−0.212
Chl *a*	−0.105	−0.329
Humics*	−0.341	−0.300
% Simple veg. (sedge)	0.002	0.287
% Simple veg. (reed)	0.292	−0.435
% Open water*	0.375	0.076
% Complex veg.*	−0.374	0.149
% Macroalgae*	0.355	−0.049

(b) Eigenvalues

PC	Eigenvalues	% Variation	Cumulative % variation
1	4.6	32.9	32.9
2	2.43	17.3	50.2
3	1.73	12.4	62.6
4	1.54	11	73.6
5	0.937	6.7	80.3

of the regressions (physico-chemical variables versus % *Acacia* during the October sampling event).

Univariate regression

Table 3 presents the linear relationships between the four environmental response variables of primary interest in this study (pH, humics, nitrates + nitrites and phosphates) and the percentage cover of indigenous vegetation around wetlands. pH and humic concentrations in wetlands were consistently and strongly related to surrounding indigenous vegetation cover across all three sampling events (negative relationship for pH, positive relationship for humics). Phosphate concentrations presented significant negative relationships on two of the three sampling events (October and November), whilst the concentration of nitrates + nitrites presented only one significant positive relationship (October). Reasonably large amounts of the variation in pH and humics were consistently explained by the cover of indigenous vegetation (i.e. habitat transformation), as reflected by the relatively high r^2 values (>0.5) across all three sampling events. The standardised β coefficients for significant relationships in Table 3 were all >|0.5|, indicating reasonably strong linear slopes.

Discussion

This study presents preliminary evidence that transforming Sand fynbos habitat around small temporary wetlands significantly impacts the environmental conditions within these wetlands, both in terms of physico-chemistry and biotope characteristics. Sites in the extensively invaded landscape at Youngsfield showed clear and consistent environmental separation from uninvaded sites in the core conservation area at KRCA. Moderate invasions presented more ambiguous results. Some of the moderately invaded sites possessed a similar environmental make-up as those that were extensively invaded, whilst in contrast to this there were several moderately invaded sites that were similar to uninvaded sites in terms of their environmental constituents (Fig. 2). Thus, it appears that even moderate invasions around temporary wetlands have the potential to cause pronounced environmental changes in these wetlands, but this trend was not consistent in our study and further work is required to establish in which circumstances a moderate invasion will indeed cause pronounced alteration of wetland environmental characteristics. Our findings do suggest that the characteristic environmental signature of temporary wetlands occurring within lowland Sand fynbos is strongly altered in cases where invasion

Table 2 dbRDA regressions of the environmental response matrices on variables representing the habitat transformation gradient (predictors)

Predictors	Environmental response matrices					
	Physico-chemical variables			Biotope variables		
	F	*P*	% Var	*F*	*P*	% Var
August/September						
% Indigenous vegetation	3.295	0.0007*	24.79	5.217	0.0095*	34.28
% Kikuyu	3.328	0.0015*	24.97	6.128	0.0046*	38.00
% *Acacia*	2.264	0.0328	18.46	2.981	0.0537	22.97
October						
% Indigenous vegetation	5.021	0.0002*	33.43	5.053	0.0082*	33.57
% Kikuyu	4.413	0.0007*	30.62	3.430	0.0297	25.54
% *Acacia*	3.661	0.0045*	26.80	2.960	0.0513	22.84
November						
% Indigenous vegetation	4.844	0.0003*	32.63	4.266	0.0199	29.90
% Kikuyu	5.925	0.0004*	37.21	2.474	0.0812	19.83
% *Acacia*	2.769	0.0305	21.69	2.920	0.0607	22.60

Response matrices were constructed using Euclidean distance (after first normalizing the variables). % Indigenous vegetation is used as a proxy for overall amount of habitat loss, whereas the remaining two predictor variables represent the different agents of habitat transformation at Kenilworth. *% Var* the percentage of variation in each response matrix that is explained by the respective predictor variable in each model. Data from the three sampling visits in 2009 were analysed separately. All models had 10 residual degrees of freedom. Significant *P* values (after sequential Bonferroni correction) are indicated by an *asterisk*

Table 3 Linear regressions of environmental response variables regressed against the amount of indigenous vegetation cover within 100 m of wetlands (universal predictor variable)

	Response variables	β	SE	r^2	*t*(10)	*P*
August/September	pH	−0.783	0.197	0.6131	−3.981	0.0026*
	Humics	0.736	0.214	0.5423	3.442	0.0063*
	Nitrates + nitrites	−0.255	0.306	0.0648	−0.832	0.4247
	Phosphates	−0.467	0.280	0.2182	−1.671	0.1257
October	pH	−0.811	0.185	0.6574	−4.381	0.0014*
	Humics	0.805	0.187	0.6485	4.296	0.0016*
	Nitrates + nitrites	0.727	0.217	0.5289	3.351	0.0074*
	Phosphates	−0.685	0.230	0.4694	−2.974	0.0139*
November	pH	−0.743	0.212	0.5518	−3.509	0.0056*
	Humics	0.749	0.209	0.5616	3.579	0.0050*
	Nitrates + nitrites	0.239	0.239	0.0569	0.777	0.4552
	Phosphates	−0.847	0.168	0.7176	−5.041	0.0005*

β standardised regression coefficient, *SE* standard error of regression coefficient, r^2 coefficient of determination. Data from the three sampling visits in 2009 were analysed separately. Significant *P* values (after sequential Bonferroni correction) are indicated by an *asterisk*

within 100 m of wetlands is extensive. Partial clearance of alien plants around wetlands may not induce effective restoration towards natural environmental conditions and it is recommended that aliens are completely eradicated within at least 100 m of the wetland edge.

An interesting finding in this study was that the cover of kikuyu grass was better related to physico-chemical and biotope characteristics in wetlands than was the cover of *Acacia* shrubs (see Table 2). We argue that changes to pH and humics that are associated with alien vegetation invasion are most likely caused by the loss of sclerophyllous fynbos vegetation around wetlands rather than the invading plant species per se. This is because it is the loss of humic-rich tannins to the system associated with losing sclerophyllous vegetation that is likely to be driving further physico-chemical and biotope changes in wetlands, rather than the physico-chemical properties of the invading plants themselves (unless of course they are themselves sclerophyllous). The stronger relationships between kikuyu cover and physico-chemical characteristics relative to those between *Acacia* cover and physico-chemistry may thus be an artefact of the greater proportional cover of kikuyu as an invading agent in this study (occurring at approximately twice the areal density of *Acacia*). This is considered as the most likely scenario, but further manipulative experimental work would be invaluable in disentangling the relative influence of kikuyu versus *Acacia* invasions around wetlands.

Our results further indicate a large amount of environmental variation between individual wetlands independent of the habitat transformation gradient. Temporary depression wetlands appear to display high levels of environmental heterogeneity even at small spatial scales, irrespective of human disturbance in the landscape. Surprisingly few studies have addressed the spatial variation of environmental characteristics in temporary wetlands. Two studies in Canada and the USA, respectively, support the results of this study, reporting high variation in temporary wetland physico-chemistry over small spatial scales (Magnusson & Williams, 2006; Carrino-Kyker & Swanson, 2007).

Impacts of invasion on pH and humics

Of the four physico-chemical variables of particular interest in this study (see Table 3), pH and the concentration of humic substances displayed the strongest and most consistent response to the habitat transformation gradient. pH was generally low for wetlands in the core conservation area and increased steadily as indigenous vegetation around wetlands was replaced by alien species. Two sites surrounded by >90% indigenous vegetation, with pH values between 4 and 5 (Appendix 2 in Supplementary Material), were perhaps the strongest drivers of this trend. As expected, the trend of relative concentration of humic compounds in wetlands was inverse to that of pH, displaying a strong positive correlation with the percentage of indigenous vegetation around wetlands. The evidence gathered in this study strongly suggests that the transformation of sclerophyllous Sand fynbos to alien vegetation around wetlands results in decreased input of humic substances, due to decreased leaching of tannins, which in turn drives an elevation in pH levels. Although this is not a novel concept for aquatic ecosystems of the fynbos biome (see King et al., 1979; Gardiner, 1988, Raubenheimer & Day, 1991; Midgley & Schafer, 1992), the relationship has never been quantified across a gradient of habitat transformation by alien invasion (nor for other agents of habitat transformation such as urban development). Other forms of habitat transformation that result in the replacement of sclerophyllous fynbos habitat around wetlands could equally be expected to alter the humic character and pH of wetlands, due to a differential release of humics or other acidic compounds to the system. The fundamental changes in aquatic physico-chemical conditions described above have not received any comment in the conservation literature, but are expected to result in cascading ecosystem impacts when considering the important ecological role of humic compounds and closely related pH levels in aquatic environments (Harrison, 1962; Gardiner, 1988; Thomas, 1997). These biotic impacts require further investigation.

Impacts of invasion on nutrient cycling

Alien invasion did not appear to cause higher concentrations of nitrates + nitrites in wetland surface water, as was expected following the findings of Jovanovic et al. (2009). Instead, there was a significant positive relationship between nitrates + nitrites and indigenous vegetation cover on one of the sampling occasions (October), while on the two other occasions results were non-significant and very weak (as reflected by the very low r^2 values). These inconsistent results for nitrates + nitrites could possibly be explained by the low density of *Acacia* invasion in this study. Gaertner et al. (2011) found no elevation of nutrient levels in the soil of a kikuyu-dominated landscape compared with an adjacent Sand fynbos landscape, suggesting that kikuyu does not alter ecosystem nutrient levels. For instance, whilst acacias are N_2-fixers and export N to the ecosystem, kikuyu is a nitrophilous opportunistic species, which makes use of the increased soil N made available by acacias, thereby reducing soil N levels (Gaertner et al., 2011).

The negative relationships between water column phosphate concentrations in wetlands and percentage of surrounding indigenous vegetation (significant for two of the three sampling occasions, Table 3) were difficult to interpret. Our results differ from most reports in the literature, but are in line with those of Witkowski & Mitchell (1987) and indicate the possibility that water column phosphate levels in wetlands draining soils partly invaded by *A. saligna* are higher than for those draining oligotrophic fynbos soils. However, there is the possibility of confounding external sources of nutrients in an urban area such as this one, although this is considered to be unlikely given that all sites occurred on vacant land with no apparent sources of nutrients nearby. The entire study area was equally surrounded by urban area at the broader scale (>500 m), and sites surrounded by fynbos tended to occur closer to the urban area boundary than moderately and extensively disturbed sites. Thus, there was no reason to expect elevated groundwater nutrient input from external urban sources for sites that were invaded by alien vegetation.

Impact of alien invasion on wetland biotopes

Another environmental association with the habitat transformation gradient at Kenilworth was the positive relationship with the percentage cover of macroalgae in wetlands (Table 1a). Although macroalgae may be treated as a biotic variable in ecological studies, it is treated as an environmental variable here, describing biotope cover in wetlands. In this study, macroalgae was represented solely by the mat forming *Cladophora* sp. Although capable of surviving slightly acidic waters (pH 6–7), members of the genus *Cladophora* are generally regarded as indicator organisms for alkaline conditions (Prescott, 1951; Whitton, 1970; Dodds & Gudder, 1992). *Cladophora* species are also well known as indicators of elevated nutrient levels, particularly P, but they can also be abundant in habitats where N supply limits primary production (see for review Dodds & Gudder, 1992). The alga was observed to be absent from all sites in this study that were surrounded extensively by indigenous fynbos and proliferated in most wetlands at Youngsfield that had no surrounding fynbos. This algal proliferation in the extensively invaded area was mostly likely caused by a rise in wetland pH levels and phosphate concentrations associated with indigenous vegetation loss around transformed wetlands.

The decrease in the percentage of complex vegetation habitat in wetlands with increasing levels of habitat transformation, and corresponding increase in open water habitat (Table 1a), suggests a general simplification of in-wetland habitat structure with increased levels of habitat transformation. This seemed to be linked to the predominance of the aquatic macrophyte *Isolepis rubicunda* in the least and moderately transformed sites, where it was observed to form the bulk of the complex vegetation habitat, yet was absent from the extensively transformed sites at Youngsfield. Complex submerged vegetation was present in the transformed sites, but mostly in the form of submerged terrestrial vegetation, particularly in shallow areas. Conversely, all the minimally transformed sites in the core conservation area of KRCA possessed extensive cover of *I. rubicunda* beds and two of the three moderately transformed sites had extensive cover of these beds. This pattern is probably linked to the natural distribution of this species, being endemic to sandy temporary depression wetlands of the south-western Cape (Muasya & Simpson, 2002; van Ginkel et al., 2011). It is thus adapted to the typically oligotrophic, humic-rich conditions characteristic of these wetlands. The changes in physicochemical conditions associated with habitat transformation at Kenilworth are a likely cause for the loss of this species. The increase in the percentage of open water habitat associated with increasing habitat transformation appears to be mainly due to the loss of *I. rubicunda*.

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