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The absence of keystone indigenous trees inhibits bird recovery up to a decade after invasive tree removal from riparian habitats

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ABSTRACT

When invasive alien trees are removed, ecosystems are usually left to "self-repair". Little is known about the extent of recovery or whether plant and animal taxa respond in a similar way. In most cases, the absence of a historical condition makes it difficult to measure restoration success and a flexible approach is usually followed using practical target communities. We explored these issues by sampling bird and plant assemblages after the removal of invasive trees, using a chronosequence (space-for-time substitution) approach. We used the Berg River, one of the most invaded riparian systems in the Cape Floristic Region of South Africa, as a case study. Study sites – cleared of *Eucalyptus camaldulensis* in 2005, 2007, 2008 and 2014 – were sampled in 2014 and compared to invaded and near-pristine areas. In total, 27 native plant species (four trees, six shrubs, seven forbs, four graminoids, four geophytes and two vines) and 26 alien plant species (four trees, three shrubs, twelve forbs and seven graminoids) from 50 genera and 31 families were recorded across all sites and years. Cleared sites had significantly more native plant species than invaded sites, but this was similar to near-pristine sites. Cleared sites had the highest plant species richness, driven by significantly more alien species, but canopy cover was significantly lower than in invaded or near-pristine sites. In total, 2049 birds from 52 species were recorded across all sites and years. A decade after clearing, bird species richness, abundance and community composition are different to near-pristine sites. This is due to the lower abundance and diversity of trees in cleared sites, which could be important as habitat or a food source for birds in an agricultural landscape. From a bird perspective, we support the approach of selectively clearing invasive trees over time to allow native trees to recover through succession. We highlight the importance of monitoring fauna to evaluate recovery after invasive alien plant clearing and to guide further management interventions.

1. Introduction

Riparian habitats are important channels for the transportation of propagules and matter from catchment areas to low altitude areas (Naiman and Decamps, 1997). Due to this – and disturbances through natural and man-made processes – riparian zones are highly susceptible to alien plant invasions (Naiman and Decamps, 1997; Esler et al., 2008). Invasive alien tree species are important invaders of riparian systems, altering ecosystem services and functions (Richardson et al., 2007; Esler et al., 2008). Restoring these areas is a complicated and expensive process (Zavaleta et al., 2001; Gaertner et al., 2012). Consequently, restoration is usually a passive process whereby, after invasive plant removal, the ecosystem is left to self-repair from soil-stored seed banks and seed dispersal from adjacent native vegetation (Roberts and Gilliam, 2003; Impson et al., 2013). In contrast, active restoration involves reseeding, replanting and sometimes soil treatment to aid the recovery of native vegetation and consequently ecosystem services and functions (Esler et al., 2008). Passive restoration is therefore far less costly since it relies on unassisted ecosystem recovery (Geldenhuys et al., 2017).

Monitoring and evaluation following invasive alien plant clearing is important to assess the success of restoration programs and to determine the need for further interventions (Zavaleta et al., 2001; Heleno et al., 2010; González et al., 2017b). However, evaluation is usually complicated by the absence of a pristine reference site to measure restoration success against (Prach et al., 2007). Other than largely short-term (but see Ruwanza et al., 2018) and vegetation studies (e.g. Galatowitsch and Richardson, 2005; Blanchard and Holmes, 2008; Ruwanza et al., 2013a; Kerr and Ruwanza, 2016; Ndou and Ruwanza, 2016; Fill et al., 2018), longer term studies and those that quantify the recovery of other taxa become more common (Golet et al., 2008; Heleno et al., 2010; Magoba and Samways, 2010; Samways et al., 2011;

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Shanahan et al., 2011; Atkinson et al., 2015; Maoela et al., 2016a, b; Hale and Swearer, 2017). This is important because of the untested assumption that the recovery of native plants will result in the recovery of other taxa and subsequently ecosystem services and functions (Atkinson et al., 2015; Kaiser-Bunbury et al., 2017). Despite this, the response of animal communities to alien tree removal from riparian areas remains less well understood (Kaiser-Bunbury et al., 2017). Birds are a particularly useful group to use as indicators of ecosystem recovery since they are highly mobile, reliably identified, feed at different trophic levels and respond quickly to habitat changes (Dobson et al., 1997; Burnett et al., 2005; Majer, 2009). For these reasons, the recovery of bird assemblages can act as a reflection of the responses of other faunal communities (Fox and Hockey, 2007).

Here we investigate changes in bird and plant assemblages in response to the clearing of *Eucalyptus* trees from a riparian habitat in South Africa. Riparian areas are the most invaded systems in South Africa and are mainly invaded by tree species of the genera *Acacia*, *Eucalyptus* and *Populus* (Richardson et al., 1997; Le Maitre et al., 2000; Mondlane et al., 2001; Forsyth et al., 2004). These invasive alien trees alter vegetation structure and simplify plant communities (Richardson and van Wilgen, 2004; Holmes et al., 2005; Tererai et al., 2013), which in-turn can affect avifauna directly through the reduction of food resources (Greve et al., 2011; Rogers and Chown, 2013; Moodley et al., 2016) or indirectly through the reduction of breeding and nesting sites (Simberloff et al., 2010; Holland- Clift et al., 2011). Invasive alien trees also significantly deplete the country's already limited water supplies (Le Maitre et al., 2000, 2002; Forsyth et al. 2004; Dzikiti et al. 2016). Consequently, the Working for Water (WfW) programme was established in 1995 as a government sponsored initiative to control alien plant invasions (Esler et al., 2008). WfW employs a passive restoration approach and the removal of alien plants is the final goal (Galatowitsch and Richardson, 2005). Although autogenic recovery can take place in areas where restoration thresholds have not been crossed, the failure of indigenous plants to recover typically results in secondary invasions and a prolonged recovery of associated faunal assemblages (Galatowitsch and Richardson, 2005; Blanchard and Holmes, 2008; Ruwanza et al. 2013a; González et al., 2017a, c). Furthermore, the failure of recovery by keystone mutualist native plant species, which are critical for and support pollinators and seed dispersers (Gilbert, 1980), also affects the recovery of associated ecosystem functions and resilience (Handel, 1997; Geerts and Pauw, 2009; Geerts et al., 2012).

Here we employ a chronosequence (space-for-time substitution) method to evaluate plant and bird assemblage recovery at six sites cleared of *Eucalyptus camaldulensis* (Palmer et al., 2007). We then compare these cleared sites to five invaded and four near-pristine reference sites. We predict that (i) plant communities in recently cleared sites will not have returned to near-pristine diversity and structure, ii) bird communities will have a higher abundance and richness in spring versus winter, (iii) recently cleared sites will have depauperate bird assemblages, due to low plant diversity and simple vegetation structure, and (iv) oldest cleared sites will have regained plant diversity and complex vegetation structure, hence supporting bird communities similar to near-pristine sites.

2. Methods

2.1. Study area

The study was conducted along the Berg River, between the towns of Wellington and Hermon, Western Cape, South Africa (Fig. 1; Table S1). The Berg River is 294 km from source to mouth with a catchment area of 7715 km^2 (de Villiers, 2007). The study area falls within the west coast renosterveld vegetation type (Mucina and Rutherford, 2006). The climate of the area is Mediterranean with average daily temperature ranging from 8 to 30 °C (Mucina and Rutherford, 2006) and minimum and maximum annual temperatures range between 11 °C and 22 °C respectively (Mucina and Rutherford, 2006). Mean annual precipitation is 550 mm, with June being the wettest and February the driest month (Mucina and Rutherford, 2006).

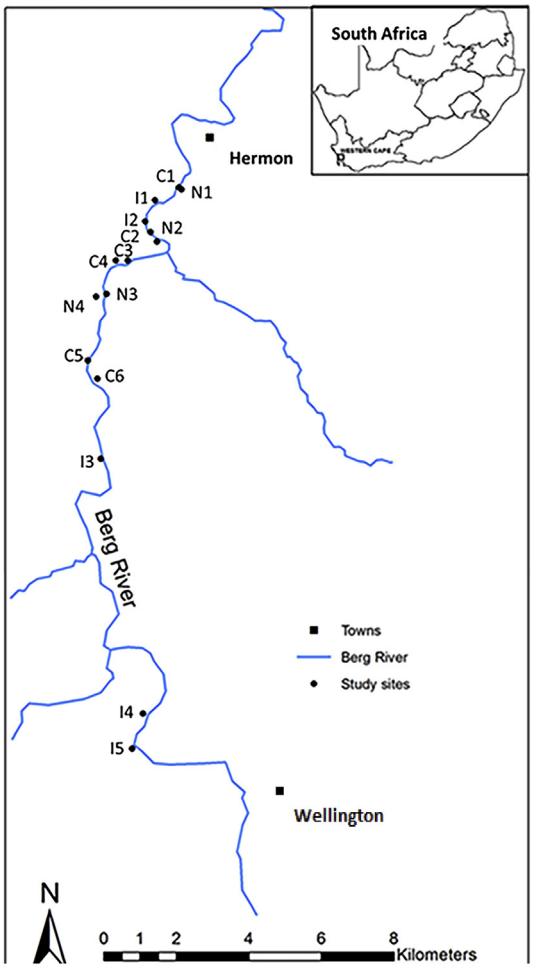

Fig. 1. Locations of invaded (I), cleared (C) and near-pristine (N) sites along the Berg River in the Western Cape of South Africa.

Invasion by alien *Eucalyptus camaldulensis* dates back approximately 60 years ago with no clear historical information about when the species was introduced, although it is now the dominant tree species along long stretches of the Berg River (Geldenhuys and Bezuidenhout, 2008; Ruwanza et al., 2014). The Berg River vegetation is driven by periodic flooding and consists of herbaceous-shrubby vegetation interspersed by scrub forest. The pristine state of the vegetation is unknown but the invasion by *E. camaldulensis* has led to an increase in the species richness of shade-tolerant riparian plants and a decrease in light-demanding plant species (Tererai et al., 2013).

In total, 15 sites spanning ~19 km along the Berg River, were used (Fig. 1). To evaluate the recovery of plant and bird assemblages after *E. camaldulensis*' clearing, a chronosequence approach was followed by sampling sites cleared in 2005 (two sites), 2007 (two sites), 2008 (one site) and 2014 (one site) (Table S1). Clearing was done by Working for Water (WfW) through manual cutting down of trees. No burning was applied.

The five invaded sites ranged in size between 2.4 ha and 12.5 ha (Table S1). The canopy cover of *E. camaldulensis* in these sites exceeded 55%, with the remainder largely made up of the alien invasive *Acacia mearnsii*. Only four isolated pockets of near-pristine riparian vegetation remain in this area and their sizes range from 1.6 ha to 5.6 ha. Although near-pristine sites were dominated by native woody vegetation, they still contained a few isolated *E. camaldulensis* and *A. mearnsii*

individuals (Tererai et al., 2013). This might suggest an expansion of scrub forest along the Berg River. Woody vegetation in near-pristine sites largely consists of *Kiggelaria africana, Olea europaea* subsp. *africana, Podocarpus elongatus, Diospyros glabra* and *Searsia angustifolia* (Tererai et al., 2013). Except for *P. elongatus,* all these species also occur in cleared sites with only *D. glabra* and *K. africana* in invaded sites.

Sites were located within a mosaic of agricultural land. Sites were largely surrounded by a monoculture of a specific crop. We therefore only scored the prevailing land-use at each site. Study sites were a few hectares in size, so the distance from a sampling point to the surrounding land use varied from 50 m to a few hundred meters. Invaded and near-pristine sites served as reference locations.

2.2. Vegetation surveys

Two plant surveys were conducted per site (n = 15) one in winter and one in spring for a total of 30 surveys. A pre-determined fixed-point was selected in all sites from where bird counts were conducted. Line transects extending for 30 m from these preselected points were used (James and Shugart, 1970). The point intercept method was used, dropping a vegetation height pole every 2 m along the 30 m transects. All plants that touched the vegetation pole or had their canopy directly above the pole, were identified and species names recorded (Table S2). When a tree or shrub species was present above a point multiple times, it was still scored as one, but if the same tree was present at multiple points along a transect, it was scored multiple times for percentage cover. Flowers and/or fruits/seeds (Table S2) that could be utilised by birds were recorded together with the following variables which might be important for birds (either for nesting, shelter, hunting or roosting): plant height, percentage canopy cover and growth form. Plant height was measured using a 2 m long vegetation height pole with 10 cm demarcations while height was estimated for plants taller than 2 m. Canopy cover was visually determined every 2 m along the transects and recorded as present or absent. We calculated percentage species cover as the number of times a species occurred in a transect. Plant species cover was considered as a measure of species abundance in subsequent analyses. Vegetation on the river bank and adjoining floodplain were included, but aquatic submerged and emergent plants were excluded.

Plant species were classified as indigenous or alien according to Goldblatt and Manning (2000) and Bromilow (2010). Plant species were assigned to the following growth forms based on the classification by Goldblatt and Manning (2000): trees, shrubs, forbs, geophytes (perennial plants that are propagated by buds on underground bulbs, tubers or corms), graminoids (grasses, sedges and restioids – reed-like plants that belong to the *Restionaceae*) and vines (creeping and climbing plants). We used percentage cover to calculate the relative cover of the different plant growth forms for each site condition (invaded, cleared or near-pristine).

2.3. Bird surveys

The fixed-point count method was used to conduct bird surveys (Bibby et al., 2000). Fixed-point counts are essentially conducted in a 360° arc around a fixed survey station (Bibby et al., 2000). Since the near-pristine sites were small, only one bird survey station, situated at least 50 m from the river channel was used per site. All bird survey stations were situated at least 100 m from the site edge. Only birds that actively utilised or perched within a 30 m radius were recorded and birds were identified audio-visually. Brown-throated Martins and Yellow-billed Kites are species that rarely perch and were only recorded when they were actively hunting for prey within sites. Bird species were classified into eight feeding guilds: insectivores, granivores, carnivores, frugivores, herbivores, omnivores, nectarivores and raptors (Hockey et al., 2005). Raptors can also be classified as carnivores, but to assess the influence of invasive alien trees specifically on raptors, we included raptors as a separate feeding guild.

All bird surveys were done on days with no rain, mist, high temperatures or strong winds as these weather conditions affect bird activity and detection (Bibby et al., 2000). Surveys commenced at approximately 30 min after dawn and continued to mid-morning as bird activity declines after this time. Bird counts were conducted for 10 min. This was preceded by a 2-min resting phase after the observer arrived at a survey station (Bibby et al., 2000).

To improve accuracy and reduce variance in the data, we substituted space-for-time by re-sampling the same sites (Bibby et al., 2000). Sites were sampled more than 3 days apart. Six surveys were conducted for each cleared site (n = 6) during winter (19 May to 9 September 2014) and spring (15 September to 13 November 2014). In total, 72 bird surveys were carried out for cleared sites. For each site, we pooled species richness and bird abundance data from all surveys and used these in subsequent analyses. Bird surveys followed the same procedure as in invaded and near-pristine sites (see Mangachena and Geerts, 2017). Bird data for invaded and near-pristine sites could thus be sourced from Mangachena and Geerts (2017).

2.4. Statistical analyses

The effect of native and alien plant species richness on total plant species richness was tested with a one-way ANOVA. To determine the effect of season (winter and spring), plant species richness was compared with a one-way ANOVA. Differences in plant species richness between invaded, near-pristine and cleared sites and between sites cleared in different years (2005, 2007, 2008 and 2014) were analysed with a one-way ANOVA and a posthoc Tukey's HSD test performed for multiple comparisons.

Comparisons of bird richness and abundance between invaded, near-pristine and cleared sites were done with a generalised linear model (GLM) using Poisson error distribution with a log-link function and a chi-squared test for significance. Bird richness and abundance between sites cleared in different years (2005, 2007, 2008 and 2014) were analysed with a one-way ANOVA. We used GLMs to test the multiple effects of the following vegetation characteristics on bird species richness and bird abundance: maximum plant height, percentage canopy cover, plant species richness, total plants with flowers, total plants with fleshy fruits, total plants with seeds. In the same GLMs we also tested for the effect of season (winter and spring) and adjacent land-use (wheat farming, paddocks, fallow land, vineyards and/or pomegranate orchards) on bird species richness and bird abundance. We hypothesised that season will influence birds and therefore tested interactions between variables that might change over seasons, namely plant species richness, canopy cover and adjacent land use. All analyses were done in R (R Core Team, 2016).

To assess variations in bird composition among invaded, cleared and near-pristine sites, we used non-metric multidimensional scaling ordinations (nMDS) in Primer version 6 (Clarke and Gorley, 2006). Before running the nMDS analyses, data was square root transformed and similarities in bird composition between sites were then calculated using the Bray-Curtis index (Clarke, 1993). The nMDS was performed running 50 restarts on two dimensions. A one-way permutational analysis of variance (PERMANOVA) with 999 randomised tests was used to compare among-group similarity and assess significance by permutation. We investigated relative contribution of individual bird species to the overall dissimilarity using the similarity percentages routine (SIMPER). SIMPER calculates the average dissimilarity between all pairs of invaded, near-pristine and cleared sites (Clarke and Gorley, 2006). Independent variables were placed into two classes namely; plant variables (plant species richness, total plants with seeds, maximum plant height, total plants with flowers, total plants with fleshy fruits and percentage canopy cover) and environmental variables (adjacent land-use such as wheat farming, paddocks and/or fallow land, vineyards and/or pomegranate orchards). Plant and environmental variables were fitted to the nMDS to identify how individual variables

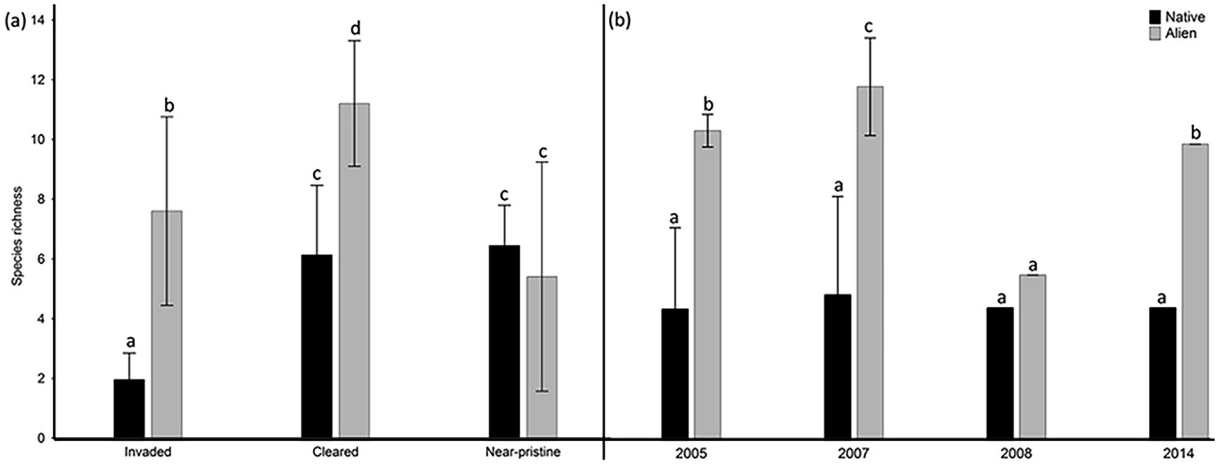

Fig. 2. Comparison of (a) native and alien plant species richness between invaded, cleared and near pristine sites and (b) native and alien plant species richness in sites with different post clearing ages. Bars show means ± SD. Different letters indicate significant differences. α level of significance = 0.05 (one-way ANOVA).

influenced patterns in bird communities.

3. Results

3.1. Plant assemblages' response to the removal of Eucalyptus camaldulensis

A total of 53 plant species (27 native) from 50 genera and 31 families were recorded. Thirty-one species (11 native), were recorded in invaded sites, 27 species (14 native) in near-pristine sites and 37 (16 native) in cleared sites (Fig. 2a; Table S2). There is a significant difference in plant species richness between invaded, near-pristine and cleared sites ($F_{2, 909} = 203.8$, $df = 2$, $P < 0.01$), with cleared and near-pristine sites being similar ($P = 0.56$; Fig. 2a). The difference in species richness is driven, in part, by significantly more native plant species in cleared and near-pristine sites compared to invaded sites ($F_{2, 909} = 681.3$, $df = 2$, $P < 0.01$). This pattern is also influenced by significantly more alien plant species in cleared sites, fewer alien species in invaded sites, and the lowest number of alien species in near-pristine sites ($F_{2, 906} = 26.51$, $df = 2$, $P < 0.01$; Fig. 2a). Spring had significantly more plant species than winter in invaded, near-pristine and cleared sites (Invaded: $F_{1, 295} = 248.6$, $df = 1$, $p < 0.01$; near-pristine: $F_{1, 253} = 38.6$, $df = 1$, $p < 0.01$, cleared: $F_{1, 358} = 33.72$, $df = 1$, $p < 0.01$).

Although there is no clear pattern, there was a significant difference in plant species richness between cleared sites ($F_{5, 910} = 154.4$, $df = 5$, $P < 0.01$) due to more alien species in some sites (Fig. 2b). Expectedly there was a lower relative cover of trees immediately after clearing, whilst the relative cover of shrubs, forbs and graminoids was greater (Fig. 3a). This pattern persisted a decade after clearing (Fig. 3b). The abundance of the following plant species that produce abundant fruits and seeds and are important food sources for birds (Hockey et al., 2005), increased in cleared sites: shrubs: *Diospyros glabra* (native) and *Ricinus communis* var. *communis* (alien); graminoids: *Bromus diandrus* (alien), *Avena fatua* (alien), *Lolium multiflorum* (alien), *Bromus catharticus* (alien); geophytes: *Zantedeschia aethiopica* (native) and forbs: *Picris echioides* (alien), *Rumex crispus* (alien), *Sisymbrium capense* (alien) and *Solanum nigrum* (alien) (Table S2).

3.2. Differences in plant compositions between sites

Based on variations in plant species composition, all cleared sites grouped with two near-pristine sites, while the remaining near-pristine sites grouped on their own (Fig. 4; Stress = 0.1). All invaded sites grouped together on their own. There was a significant difference in plant composition between invaded, cleared and near-pristine sites (PERMANOVA; $P < 0.05$). Pairwise tests show that there is no significant difference in plant composition between cleared sites and near-pristine sites ($P = 0.47$) while there is a significant difference between cleared and invaded sites ($P < 0.05$) as well as between invaded sites and near-pristine sites ($P < 0.05$). SIMPER shows that *Eucalyptus camaldulensis* contributed the most to differences between invasion conditions (20.6%). *Podocarpus elongatus*, *Kiggelaria africana*, *Acacia mearnsii*, *Pennisetum clandestinum* and *Ricinus communis* var. *communis*

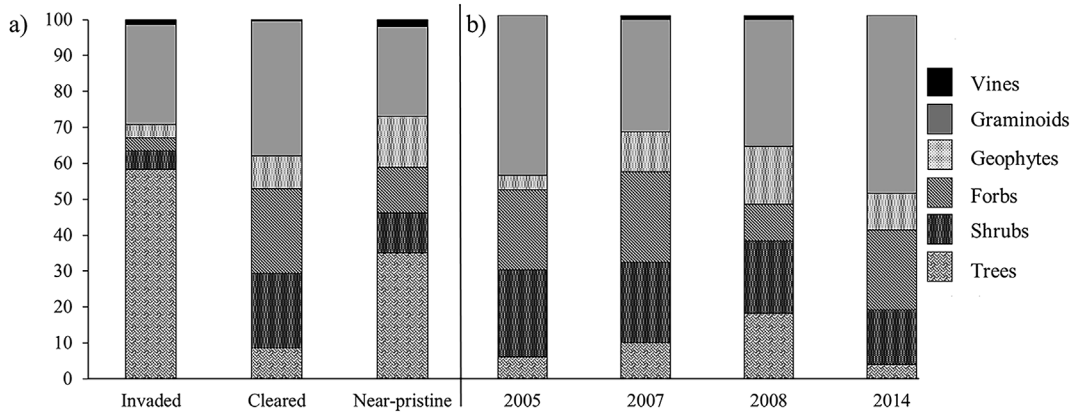

Fig. 3. A comparison of plant growth form composition – including alien and native species – between (a) near-pristine, invaded and cleared sites and (b) sites with different post clearing ages (sampled in 2014).

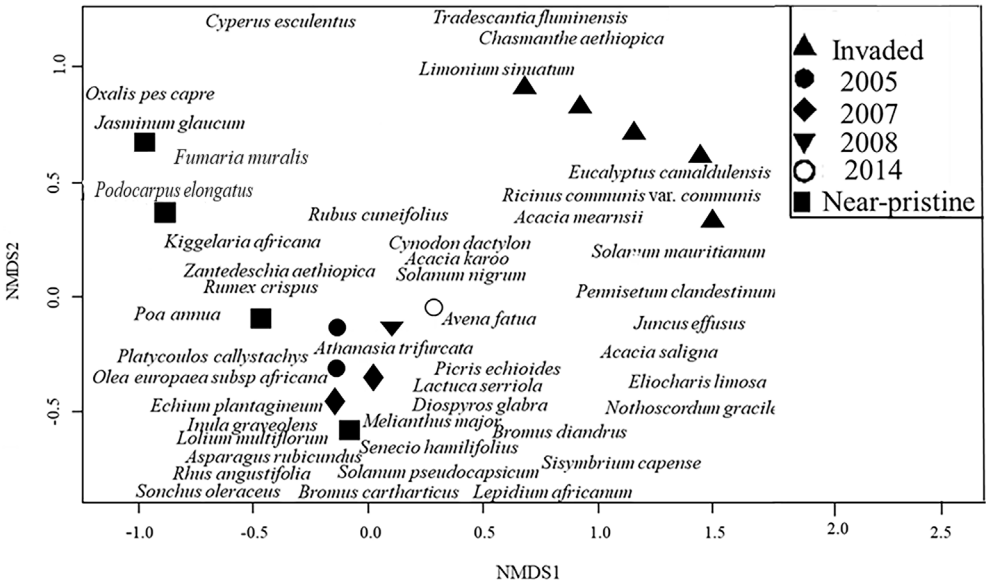

Fig. 4. Plant ordination (non-metric dimensional scaling (nMDS)) in invaded, cleared and near-pristine sites. Species abundances were used for similarity testing (Bray–Curtis diversity index) after square root transformation. Stress = 0.1.

collectively contribute 33% to the differences between the sites (Table S3).

3.3. Response of bird assemblages to Eucalyptus camaldulensis clearing

A total of 2049 birds from 52 species (26 species in invaded sites, 42 species in near-pristine sites and 41 species in cleared sites) were recorded (Table S4). Bird species richness was significantly lower in invaded sites compared to cleared and near-pristine sites ($F_{2,179} = 215.51$, $P < 0.001$; Fig. 5a). There are no clear patterns and no significant differences in bird species richness between time since clearing treatments ($F_{3,68} = 0.65$, $df = 3$, $P = 0.6$; Fig. 5b). Bird abundance was similar between cleared and near-pristine sites but significantly lower in invaded sites ($F_{2,179} = 474.63$, $P < 0.001$; Fig. 5c). There were no significant differences in bird abundance between time since clearing treatments ($F_{3,68} = 1.95$, $df = 3$, $P = 0.13$; Fig. 5d).

Eighteen bird species (mainly nectarivores, omnivores, granivores and frugivores) which occurred in near-pristine sites are absent from invaded sites. The nectarivores are entirely lacking from invaded sites. One year after clearing four feeding guilds are present – in large abundance – which increased to eight feeding guilds a decade after clearing (Fig. 6). Ten of the bird species missing from invaded sites returned after clearing but eight of them, including three raptors, were still missing a decade after clearing (Table S4). In addition, eight new species, four of them carnivores, were recorded at cleared sites but not in near-pristine sites.

3.4. Effect of habitat characteristics on bird assemblages

Site condition (invaded, cleared, near-pristine), canopy cover (%) and adjacent land use contributed significantly to bird species richness (Table 1). The interaction between site condition and canopy cover for bird richness was significant (Table S5), with invaded sites having a higher canopy cover and fewer birds (Table S6a).

Two interaction terms; season × plant species richness and adjacent land-use × plant species richness ($P < 0.05$, for all interactions, GLM; Table S5) were significant determinants of bird abundance, but due to absences of all site class combinations, no meaningful inferences on directions are possible (Table S6b).

3.5. Differences in bird community compositions between sites

Two near-pristine sites grouped with invaded sites whilst the other two near-pristine sites grouped with the cleared sites (Fig. 7; stress = 0.09). There was a significant difference in bird composition between invaded, cleared and near-pristine sites (PERMANOVA; $P < 0.05$). Pairwise tests showed that bird compositions were similar in cleared and near-pristine sites ($P = 0.32$) with invaded sites having different compositions than cleared ($P < 0.05$) and near-pristine sites ($P < 0.05$). Plant variables (plant species richness, total plants with seeds, maximum plant height, total plants with flowers, total plants with fleshy fruits and percentage canopy cover) together with environmental variables (adjacent land-use such as wheat farming, paddocks and/or fallow land, vineyards and/or pomegranate orchards) strongly influenced site groupings (Fig. 7). SIMPER shows that the Cape white-eye, Cape Robin-Chat, Brown-throated Martin, Yellow Canary, Cape Weaver and the Southern masked-weaver contributed up to 50% of the observed differences (Table S7).

4. Discussion

Clearing of *Eucalyptus camaldulensis* from riparian habitats coupled with a passive restoration approach result in a partial recovery of native plant and bird communities, a decade after clearing. A dearth of knowledge exists regarding the historical communities of the Berg River system and here we use the near-pristine sites as an alternative and pragmatic target community for restoration. The partial restoration of native plant assemblages several years after clearing is similar to Ruwanza et al. (2018) who also reported an incomplete recovery in native plant diversity after seven years following clearing of *E. camaldulensis*. Although plant and bird assemblages recover to levels comparable to those of near-pristine sites, ten native plant species (37%) and eight bird species (19%) were absent in cleared sites. The absence of a full complement of bird and plant assemblages in cleared sites suggests a need for a longer recovery time or that historically these sites were different. In particular, since the vegetation dynamics keep changing – with periodic fires historically, and more recently, flooding events – maintaining a herbaceous-shrubby vegetation interspersed by scrub forest. In patches with more herbaceous-shrubby vegetation, the shade from the invasive *Eucalyptus* would have excluded the more light-demanding herbaceous and shrubby species and facilitated the

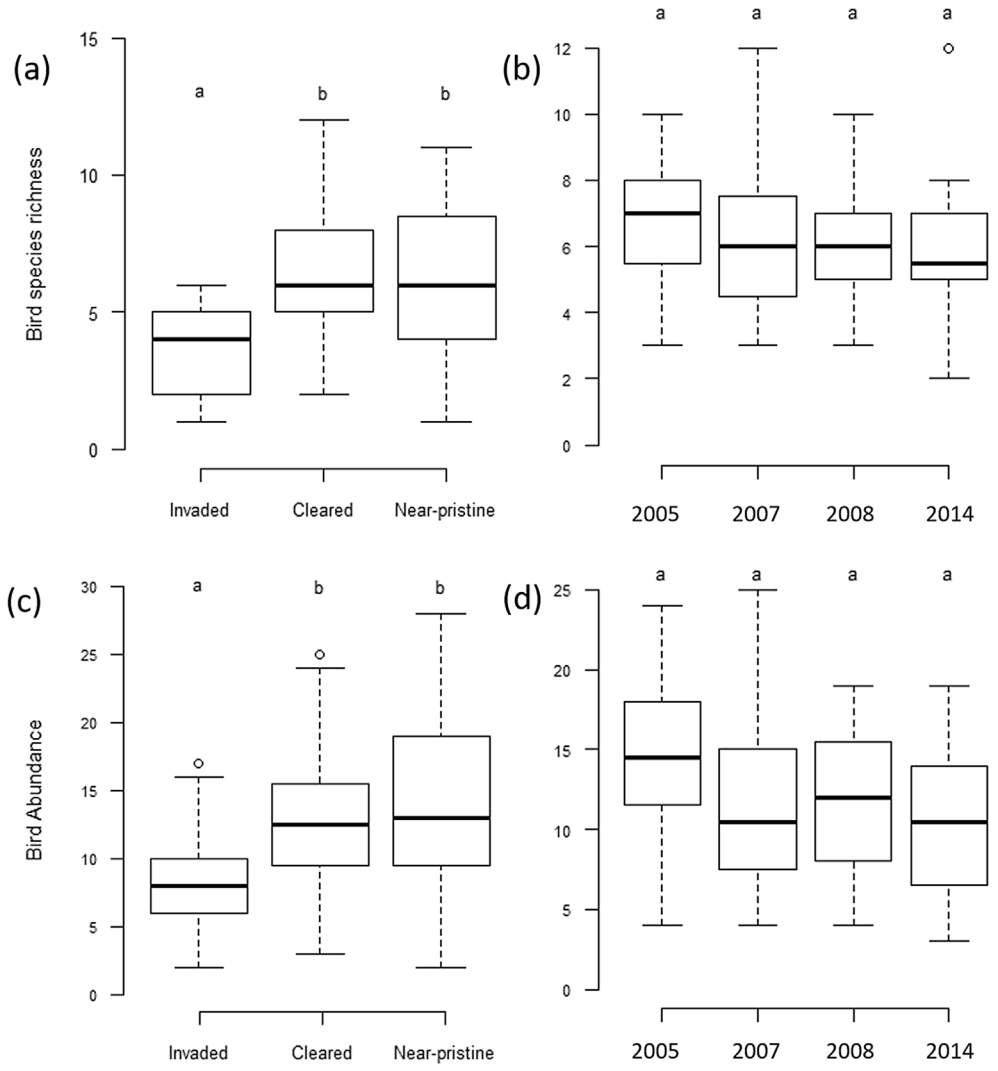

Fig. 5. Comparison of (a) bird species richness in invaded, cleared and near-pristine sites; (b) bird species richness with time since clearing; (c) bird abundance in invaded, cleared and near-pristine sites and (d) bird abundance in sites with different post clearing ages. Box plots display median, 25th and 75th percentiles, and data range. Open circles indicate outliers. Different letters indicate significant differences.

establishment of the relatively more shade-tolerant forest tree species.

Therefore, attempting to actively restore should be carefully considered, since other than being costly and often failing (Ruwanza et al., 2013b), active restoration might be impossible when biotic and abiotic thresholds have been surpassed (Gaertner et al., 2012). Natural recovery of native plant species, through native soil-stored seed banks and recruitment from remnant natural vegetation saves costs and is desirable for any restoration project (Blanchard and Holmes, 2008; Morris et al., 2008). However, if conditions for germination have become unsuitable for some species or no dispersal from nearby areas is possible (Galatowitsch and Richardson, 2005; Holmes et al., 2005; Ruwanza et al., 2013a), secondary invasions will make up a large component of the vegetation as those aliens are better suited to establish after the disturbance on cleared sites (Ruwanza et al., 2018).

In fact, cleared sites had the highest plant species richness, which can be largely attributed to alien grasses, shrubs and forbs. Other studies have shown that invasive alien plant clearing triggers the natural phenomenon where pioneer plants, mostly alien, move in and dominate cleared areas (Morris et al., 2008; Reinecke et al., 2008; Ruwanza et al., 2013a, b). The increase in availability of water, nutrients, space and sunlight also facilitates revegetation from soil-stored seed banks and from propagules dispersed from plants in nearby areas (Galatowitsch and Richardson, 2005; Morris et al., 2008; Reinecke et al., 2008; Ruwanza et al., 2013a, b, González et al., 2017a). Native tree recovery could be assisted by thinning *E. camaldulensis* trees over a number of years or alternatively kill trees and leave them standing. This aids shade-intolerant native species to establish while supressing light-demanding alien plant species (Geldenhuys and Bezuidenhout, 2008). The fast-growing and light-demanding pioneer species are unlikely to outcompete native plants over the long run, and are usually replaced by the slow-growing and shade-tolerant woody plant species (Geldenhuys et al., 2017). However, under regular disturbances and nutrient enrichment, alien invasive grasses are able to replace indigenous plant species (Milton, 2004). The Berg River system is prone to disturbance events through flooding, and several more years may be required for alien plant species richness in cleared sites to diminish. Encouraging though is that the abundance of plant species that provide food for birds increased in cleared sites. This is a long-term process however, since although many plant species reproduce within a few years, tree species may take a decade or more.

Only two native tree species (*Olea europaea* subsp. *africana* and *Kiggelaria africana*) were recorded in cleared sites. Nevertheless, eleven new species, six of them native forbs – and not recorded in invaded or near-pristine sites – came up after clearing, indicating early stages of recovery (Geldenhuys and Bezuidenhout, 2008; Geldenhuys et al., 2017). Due to the absence of a reference condition, and the long time to

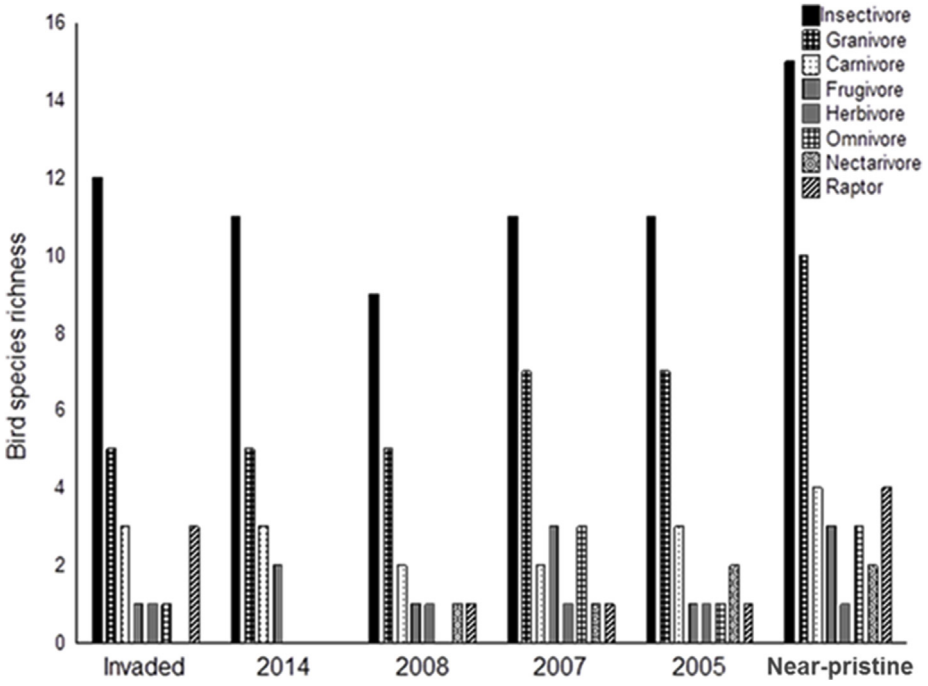

Fig. 6. The number of bird species per feeding guild in cleared sites compared to invaded and near-pristine sites.

recovery, whether these plant communities will become herbaceous or scrub forest communities, remains unknown. If scrub forest, Ruwanza et al. (2018) showed that several years after clearing the presence of alien shrubs and trees remains high and slows down the recovery of native trees. It is well known that the recovery process of native tree species take decades, even if adjacent to mature forests (Lubbe and Geldenhuys, 1991; Geldenhuys, 1994). Here this might be exacerbated by the limited number of natural remnants that can act as seed sources. Added to this is the potential disturbance by periodic flooding events – all of which will in turn influence bird assemblages.

In other studies from Mediterranean regions, the recovery of bird assemblages after a disturbance relied largely on vegetation succession (Herrando and Brotons, 2002; Chalmandrier et al., 2013). Species composition tend to shift from tree-dwelling species to ground-dwelling species in cleared areas (Domer et al., 2019). We found that some generalist bird species such as the insectivores (Cape Wagtail, African Reed-warbler and Levaillant's Cisticolla) granivores (Yellow Canary, Cape Sparrow, Streaky-headed Seedeater, the pin-tailed Whydah, Common Quail and Yellow bishop) and the carnivore (Maccoa duck), which are absent in invaded sites, were present even in recently cleared sites. The granivores in particular can be linked to the many weedy (both native and alien) species colonising cleared sites and producing abundant seeds (Table S2). Specialist nectar feeders such as the Malachite Sunbird and the Southern Double-collared Sunbird, which were completely absent from invaded sites (Mangachena and Geerts, 2017; Mangachena, 2017), only returned to cleared areas once nectar rich bird pollinated plants such as *Melianthus major* and *Halleria elliptica* started to flower. Similarly, Chalmandrier et al. (2013) found that post fire changes in vegetation structure and plant functional composition over time lead to a shift from generalist and granivorous bird species to specialists and nectarivorous species. However, in this study due to the low number of plants flowering, the patchy nature of these resources and the many years before some species start flowering, we did not find a strong link between food sources and bird assemblages.

More importantly, plants with flowers only influence certain guilds, such as nectar feeders, which are important in pollination but consist of very few species and therefore might have contributed little to overall diversity and abundance patterns (Geerts and Pauw, 2012; Geerts, 2011, 2016). Despite this, the restoration of this ecosystem function (bird pollination) is important for many plant species and ecosystem resilience in general (Handel, 1997; Geerts and Pauw, 2009; Geerts et al., 2012).

Table 1
Results from main effects analysis from a generalised linear model showing variables potentially predicting bird species richness and bird abundance. α level of significance = 0.05.

Independent variable	Bird species richness				Bird abundance			
	Est.	S.E	z-value	*P*	Est.	S.E	z-value	*P*
Site condition: Near-pristine	0.754	0.241	3.119	**0.001**	0.823	0.165	5.000	< **0.001**
Site condition: Invaded	0.455	0.367	1.237	0.216	0.500	0.256	1.959	**0.050**
Adjacent land-use: vineyards/pomegranate,	0.393	0.122	3.198	**0.001**	0.325	0.081	4.609	**0.001**
Adjacent land-use: Wheat	0.447	0.141	3.181	**0.002**	0.433	0.094	4.609	**0.001**
Canopy cover (%)	−0.008	0.003	−2.654	**0.008**	−0.010	0.002	−4.449	0.001
Season	−0.275	0.151	−1.821	0.069	0.182	0.102	−1.781	0.075
Plant species richness	0.009	0.016	0.551	0.581	0.002	0.010	0.181	0.856
Plants with fruits	0.009	0.018	0.470	0.639	0.021	0.013	1.718	0.086
Plants with flowers	0.014	0.014	1.032	0.302	0.002	0.009	−0.164	0.870
Plants with seeds	−0.039	0.024	−1.619	0.105	−0.006	0.016	−0.390	0.696
Maximum plant height (m)	−0.033	0.037	−0.912	0.361	−0.008	0.026	−0.320	0.749

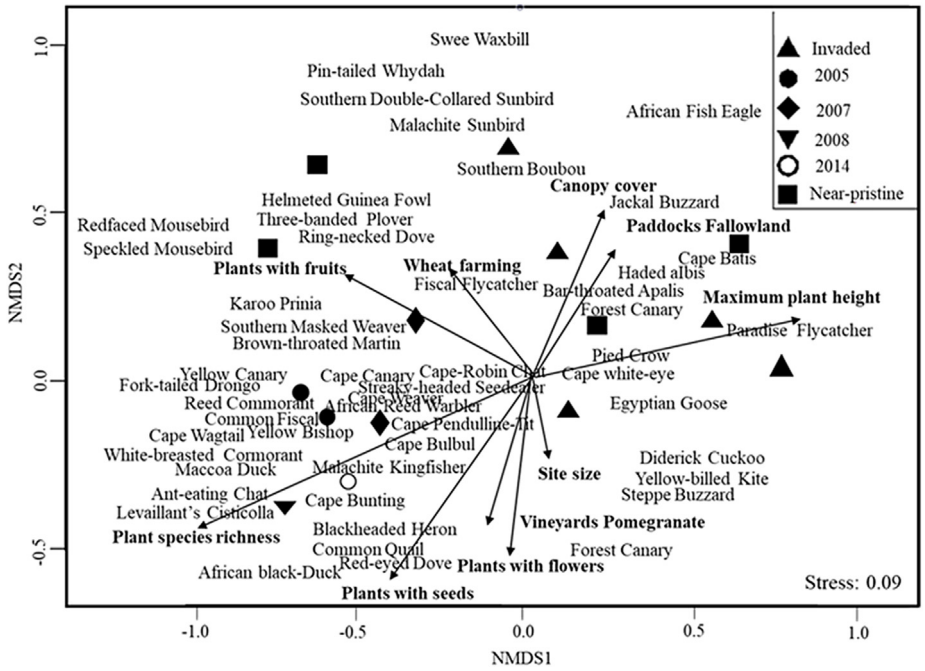

Fig. 7. Bird ordination (non-metric dimensional scaling (nMDS)) in invaded, cleared and near-pristine sites. Species abundances were used for similarity testing (Bray–Curtis diversity index) after square root transformation. Stress = 0.09.

The species richness of fruit feeding birds such as the Cape Bulbul, Red-faced Mousebird and the Speckled Mousebird also recovers over time although the abundance remains low. This lack of a significant increase in overall bird abundance with time since clearing can be attributed to the low occurrence and immature state of fleshy fruit-bearing plants such as *Kiggelaria africana*, *Searsia angustifolia* and *Olea europaea* subsp. *africana*. This, despite *K. africana* trees being present in small clumps of mature trees which developed under the *E. camaldulensis* canopy. *Searsia angustifolia* and *O. europaea* subsp. *africana* could have been dispersed by birds from near-pristine sites. In their study, Galatowitsch and Richardson (2005) reported the importance of remnant vegetation as an important source of seeds for re-vegetation. *Searsia angustifolia* and *O. europaea* subsp. *africana* are also colonising species which establish well in a variety of habitats including exposed environments (Manders and Richardson, 1992). *Podocarpus elongatus* – which is also a fleshy-fruit bearing species – produces more fruit when growing in the open, but is absent in cleared sites. *Podocarpus elongatus* is a shade-tolerant forest species which requires the shade of other plants for it to establish (Geldenhuys et al., 2017), but even once established, it takes many years to become reproductively mature, and even then, fruits are not produced every year. Despite this, the occurrence of non-fruit bearing trees in restored sites are also important as these could act as perches for seed dispersing birds (Galatowitsch and Richardson, 2005).

Forest granivore species – such as the Ring-necked Dove and the Swee Waxbill – that occurred in invaded and near-pristine sites, were not recorded in cleared sites. The occurrence of these species in nearby invaded habitat highlights the importance of vegetation structure. The high numbers of granivores we found in cleared sites could accelerate restoration because these species act as valuable seed dispersers, but their occurrence can also facilitate invasion by alien plants (Heleno et al., 2010).

Similar to granivores, insectivorous bird assemblages still differ from near-pristine areas a decade after clearing. On the one hand, invasive alien plants can have a negative effect on insectivores through the depletion of invertebrate communities (Samways and Taylor, 2004), whilst clearing of alien trees can have a positive effect via the removal of obstacles for birds actively hunting insects (Avarind et al., 2010). For forest species gleaning insects off leaves, such as the Paradise Flycatcher, the absence of large trees in cleared sites could explain the absence of this species. In contrast, four new carnivores namely; the Reed Cormorant, White-breasted Cormorant, Common Fiscal and the Black-headed Heron make use of cleared sites. This might be linked to the improvement of river water quality which in turn increase fish and aquatic invertebrate diversity with increase in time since clearing (Magoba and Samways, 2010).

Only one raptor species, the Yellow-billed Kite, occurred in cleared sites. The absence of other raptors such as the African Fish Eagle, the Jackal Buzzard and the Steppe Buzzard could be due to absence of large trees (native or alien) used by these species for nesting, roosting and as a vantage point for hunting (Ewbank, 2000; Suddjian, 2004; Cilliers and Siebert, 2012). In contrast, the removal of alien invasive trees simulates the natural open areas with scattered scrub forest clusters of trees which creates an ideal open hunting ground for the Yellow-billed Kite whose prey consists mainly of seed eating rodents and birds, which are attracted by the abundance of seed produced by grasses in cleared sites (Hockey et al., 2005).

Sites grouped together based on bird communities, but also based on environmental variables. Similarly, other studies have shown that there is a close relationship between bird communities and environmental factors as well as plant assemblages (Herrando and Brotons, 2002; Chalmandrier et al., 2013). We conclude that plant composition and canopy cover influence bird assemblages. Surrounding vegetation – included here as adjacent land-use type –also has an influence on bird assemblages. This is largely because of the small size of these riparian areas (whether near-pristine, invaded or cleared), within an agricultural landscape. Although invasion status does influence bird assemblages, surrounding land use could be important in post clearing bird community recovery – through a spill-over effect – and warrants attention in future studies. Lastly, from a bird perspective, we support the approach of selectively clearing invasive trees – rather than active re-introduction of trees – to allow for a natural succession process. This requires further study, in particular since in riparian areas this is complicated by regular flooding.

In conclusion, in this study we considered the potential impacts of clearing alien invasive *Eucalyptus* trees from a riparian mosaic of

herbaceous-shrubby vegetation interspaced by scrub forest patches influenced by regular flooding on plant and bird communities. Cleared areas had higher bird species richness than invaded sites, but were similar to near-pristine sites. For plants, cleared areas had similar native species richness to near-pristine areas but higher than that of invaded areas. Cleared sites had more plant species than near-pristine sites due the secondary invasions by weedy species. The complete absence of large trees and surrounding land use are important in shaping bird communities, but less so than the time since clearing. However, due to a lack of a reference condition and considering the flood dynamics of the area, we expect that vegetation recovery in the riparian zone is likely going to become scrub forest in more protected areas and herbaceous-shrubby in the more exposed areas. In turn, this will influence ecosystem function. Therefore the monitoring of not only the floral component but also of the fauna in cleared sites, is vital to evaluate recovery success and to guide further management interventions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2019.103483.

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