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# Invasive alien trees reduce bird species richness and abundance of mutualistic frugivores and nectarivores; a bird's eye view on a conflict of interest species in riparian habitats

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**Abstract** Invasive alien plants have major ecological effects, in particular in riparian habitats. While effects of alien tree invasions on riparian plants are well studied, effects on animals are less well understood. Invasive alien trees can have a positive effect by adding habitat and food sources, or have a negative effect, by replacing native food plants. Here we use birds as indicators to determine the impacts of an invasive *Eucalyptus* tree species in riparian areas of the Cape Floristic Region (CFR) of South Africa. Birds are an ideal study group because they are mobile, respond quickly to habitat changes and feed at different trophic levels. Fixed-point bird counts were done during winter and spring at near-pristine and *Eucalyptus camaldulensis* invaded riparian habitats. A total of 1142 birds from 44 species were recorded. Bird assemblages in invaded sites are almost a complete subset (24 species) of those in near-pristine areas (42 species). Invaded areas were missing 18 species and contained a total of 128 fewer individuals. This is due to declines in insectivores, frugivores, granivores, raptors and omnivores and the absence of nectarivores in invaded sites. From a bird's perspective, the prioritisation of *E. camaldulensis* removal from the CFR's river systems is justified, but whether bird species will return to cleared areas needs to be determined.

**Keywords** Bird feeding guilds · Cape Floristic Region · *Eucalyptus camaldulensis* · Nectar feeding birds · Plant invasions · Raptor

## Introduction

Riparian systems comprise only a small fraction of the landscape, but support a rich and distinct plant and animal community (Naiman and Decamps 1997; Robinson et al. 2002; Jacquemyn et al. 2010). Regular flooding in riparian areas results in high levels of moisture and nutrients, which at the same time facilitate propagule transportation (Planty-Tabacchi et al. 1996; Naiman and Decamps 1997). As a consequence, riparian areas are disproportionately rich in plant life and act as important habitats and movement corridors for fauna in highly transformed landscapes (Robinson et al. 2002). However, riparian zones are also more susceptible to invasion by alien plants due to the same factors that support this high species diversity (Planty-Tabacchi et al. 1996). Consequently riparian areas are some of the most invaded systems globally (Richardson et al. 2007).

Alien plant invasions in riparian areas displace native vegetation, changing the vegetation structure and floristic composition (Hejda and Pyšek 2006; Schwartz et al. 2006; Hejda et al. 2009; Terera et al. 2013). Although impacts on plant communities are relatively well studied, this is not the case for animals (Samways et al. 1996). The few studies available show that impacts on flora do translate into impacts on animals. For example, invasive alien plant species can lead to a reduction in riparian herbivorous insect populations (Greenwood et al. 2004; Gerber et al. 2008). Decline in insect populations may directly affect higher-trophic feeders such as birds through a decrease of primary food resources (Procheš et al. 2008). Furthermore, the displacement of native riparian vegetation by invasive woody plants simplifies habitat structure which results in a reduction

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of breeding and nesting sites and may indirectly affect riparian bird assemblages (Simberloff et al. 2010; Holland-Clift et al. 2011).

Birds are an ideal taxon to study the impacts of invasive alien vegetation. Firstly, they are mobile and easy to identify; secondly, they feed at higher trophic levels and thirdly, they respond quickly to changes in vegetation structure and plant composition (Dobson et al. 1997; Burnett et al. 2005). The response of bird assemblages to invasion by alien plants depends on the bird species in question, invading alien plant species and the affected ecosystem (Fraser and Crowe 1990; Sogge et al. 2008). Most studies that have explored the effects of invasive alien plants on bird assemblages report negative impacts (e.g. Dean et al. 2002; Greve et al. 2011; Holland-Clift et al. 2011). Usually these responses are linked to specialisation on certain food resources (Grass et al. 2013). For instance, thicket-forming invasive alien plants may become barriers to insectivores hunting for aerial insects (Avarind et al. 2010) whilst changes in plant species composition may render a habitat unsuitable for nectar feeding birds (Grass et al. 2013). In contrast, a few studies have found positive effects (Le Roux et al. 2010; Geerts et al. 2013; Rogers and Chown 2013). Insectivores and mixed feeders increased in abundance in sites dominated by invasive alien *Acacias* (Rogers and Chown 2013). Similarly, granivores and insectivores increased in response to *Acacia*, *Eucalyptus* and *Pinus* invasions (Fraser and Crowe 1990). The presence of fleshy-fruit bearing invasive plants such as *Lantana camara*, *Solanum mauritanium* and *Cinnamomum camphora* has been shown to lead to an increase in the abundance of obligate fruit-eating birds (Grass et al. 2013). Impacts can go beyond the immediate food source, for example large eucalypt trees have been found to offer perching and nesting sites for raptor species, increasing their numbers (Ewbank 2000). However, invasive alien plants can also have a neutral effect on bird assemblages (see for example Shanahan et al. 2011).

*Eucalyptus camaldulensis* was initially introduced into South Africa from Australia for forestry (Forsyth et al. 2004) but has also become an important source of pollen and nectar for the apiculture industry during the dry summer months (Johannsmeier and Mostert 2001; Richardson et al. 2003). Concerns have been raised regarding the benefits and economic value of eucalypts in relation to the costs associated with invasion (Allsopp and Cherry 2004; van Wilgen 2012; Melin et al. 2014). Although species in the genera *Acacia*, *Hakea* and *Pinus* make up the bulk of invasive plant species in the Cape Floristic Region (Richardson and van Wilgen 2004), *Eucalyptus camaldulensis* is the most abundant invasive tree in many riparian areas (van Wilgen 2009; Dzikiti et al. 2016). In a rapid assessment, Forsyth et al. (2004), notes that 46% of rivers in the Cape Floristic Region, are invaded by *E. camaldulensis*. Very little is known about the impacts of invasive alien trees, and *Eucalyptus* trees' in particular, on bird assemblages in riparian areas.

Therefore, we assess how *E. camaldulensis*' invasion affects riparian bird assemblages. Specifically we compare (1) bird species richness (2) bird abundance and (3) bird feeding guilds between near-pristine (with few individuals of *E. camaldulensis* and *Acacia mearnsii*) and invaded sites. Subsequently, we compare our results with studies from non-riparian tree invaded habitat.

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## Methods

### Study area

The study was conducted along the upper catchment of the Berg River, near the town of Hermon, in the Cape Floristic Region of South Africa (33° 26'38.05''S; 18° 58'24.70''E) (Fig. 1). The Berg River is a perennial 300 km long river with a catchment area of approximately 9000 km<sup>2</sup> (de Villiers 2007; Dzikiti et al. 2016). The study area is located in the west coast renosterveld vegetation type of the fynbos biome (Mucina and Rutherford 2006). Climate is Mediterranean with a mean annual precipitation of 453 mm, with most rain received in June and the least in February (Mucina and Rutherford 2006). Mean daily temperatures range between 8 and 30 °C (Mucina and Rutherford 2006).

*Eucalyptus camaldulensis* is the most abundant and prominent invasive alien tree species in the riparian area of the Berg River with other invasive alien tree species, mainly *Acacia mearnsii* and *Populus* species, being less abundant (also see Geldenhuys 2008). *E. camaldulensis* invasion in the Berg River probably started about 100 years ago; however, knowledge of how or why eucalypts were introduced is scarce (Geldenhuys 2008). The remaining native vegetation occurs as small isolated remnants, dominated by *Kiggelaria africana*, *Olea europaea* subsp. *africana*, *Podocarpus elongatus*, *Diospyros glabra* and *Searsia angustifolia* (Tererai et al. 2013).

### Site selection

Two treatments were used for this study: near-pristine sites (Fig. 2a) with few individuals of *E. camaldulensis* and *Acacia mearnsii* and *E. camaldulensis* invaded riparian areas (Fig. 2b) (Table S1). The only four remaining near-pristine areas were used in this study with a minimum distance of 0.99 km between study sites (Tererai et al. 2013). Near-pristine sites are dominated by native vegetation with only a few individuals of *E. camaldulensis* occurring (less than 5% canopy cover; pers. obs.). Due to the presence of other invasive tree species, invaded sites are those in which *E. camaldulensis* cover exceeds 55% (mostly more than 85%) with the remainder consisting mainly of *A. mearnsii*.

## Bird surveys

A total of 108 fixed-point bird counts (six per season for the nine sites) were done (Bibby et al. 2000). Half of these were done between 9 May and 5 September 2014 to represent autumn/winter and the other half between 15 September and 13 November to represent spring/summer. Due to the small size of some near-pristine sites (Table S1) and to ensure independent samples, only one census point was sampled repeatedly for each site with a minimum of three days between sampling visits (Bibby et al. 2000). Vegetation in invaded sites could be dense; therefore a fixed maximum radius of 30 m was used. All birds within the 30 m fixed radius were identified audio-visually. Only birds that perched in the plot were recorded, except for the Brown-throated Martin and Yellow-billed Kite that rarely perch, and were therefore included when actively hunting for prey inside the plot.

Peak activity for most bird species occur between dawn and midday, and sampling was therefore done from 30 min after dawn until 11h00 (Bibby et al. 2000). Sampling was conducted on days without mist, strong wind, high temperature or rain as these conditions affect bird activity and detection (Bibby et al. 2000). Counts were preceded by a 2-min resting phase to allow birds to settle and resume normal behaviour (Bibby et al. 2000). The total of 10 min allocated to bird counting was sufficient to observe all species, including cryptic and skulking species (pers. obs.). A voice recorder was used to record bird calls to confirm the visual field identification. Bird species were classified into eight feeding guilds according to their primary food sources (Table S2; Hockey et al. 2005). With no significant difference in bird species richness and abundance between seasons [generalised linear model (GLM):  $\chi^2 = 1.84$ ;  $df = 1$ ;  $P = 0.174$ ] data were pooled for all subsequent analyses.

## Vegetation surveys

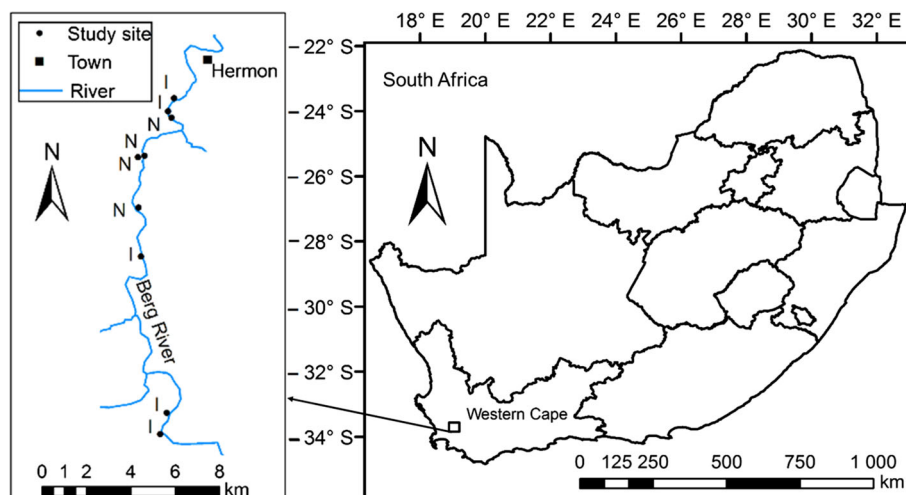
Vegetation parameters included in this study are maximum plant height and percentage canopy cover. Two plant surveys were conducted per site ( $n = 9$ ) in winter and spring for a total of 18 surveys. Surveys were done using line transects extending 30 m from the centre of each bird counting point (James and Shugart 1970). Vegetation on the river bank and adjoining floodplains were included but we excluded aquatic submerged and emergent species. The point intercept method was used; dropping a vegetation height pole every 2 m along transects. The height of all plants that came into contact with the vegetation pole was determined and the species identified. Canopy cover was scored as present or absent at the same 2 m intervals and used to calculate total percentage canopy cover.

## Comparison of bird communities between riparian and non-riparian habitats

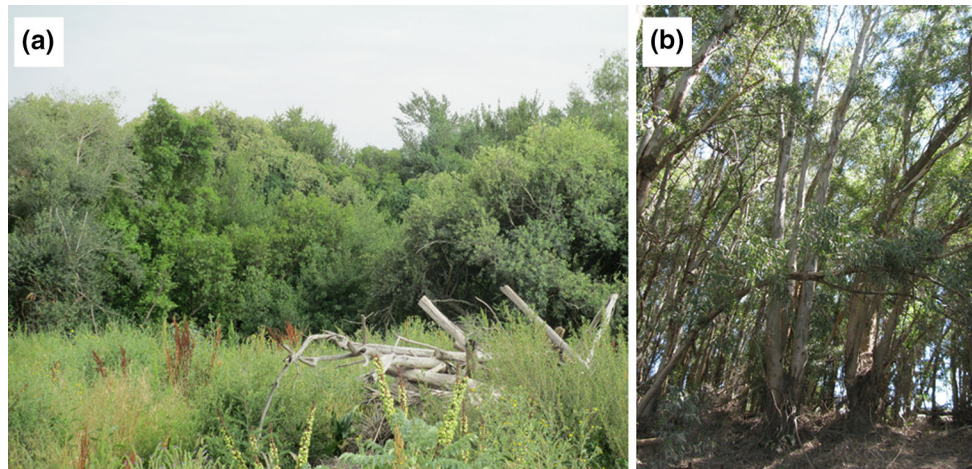
We compare the effect of alien tree invasion on bird assemblages in this study with that of non-riparian habitats (Greve et al. 2011; Rogers and Chown 2013; Thorpe 2013). These three studies were selected since they (1) are recent (2) used comparable methods and (3) were done in the same biome. To control for differences in time and area sampled, bird species richness and abundance data was divided by the sampling effort (time and area).

## Data analyses

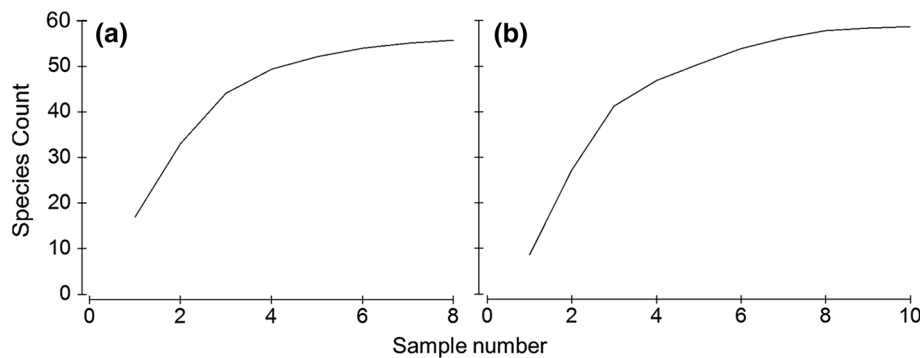
To assess if sampling had been adequate, sample-based rarefaction curves were calculated using Jackknife 2 in Primer version 6 (Clarke and Gorley 2006). This method



**Fig. 1** Locations of near-pristine (N) and *Eucalyptus camaldulensis* invaded (I) study sites along the Berg River in the Western Cape of South Africa



**Fig. 2** Near-pristine riparian vegetation (a) and *Eucalyptus camaldulensis* invaded (b) riparian area



**Fig. 3** Species accumulation curves for near-pristine (a) and invaded (b) sites. Species estimates are based on Jackknife 2

calculates the expected number of species when a given number of samples are drawn randomly, without replacement from a set of samples collectively representing an assemblage (Gotelli and Colwell 2001).

Species richness ( $S$ ), the Simpson diversity index ( $1-D$ ) and the Simpson's evenness index ( $E_{1/D}$ ) were used to compare bird assemblages between near-pristine ( $n = 4$  sites) and invaded ( $n = 5$  sites) areas. Diversity indices were calculated in PAST version 3 (Hammer et al. 2001). A Mann–Whitney U test (Statistica version 12; StatSoft Inc. 2015, Tulsa, USA) was used to compare Simpson's diversity and Simpson's evenness between near-pristine and invaded sites. The Simpson diversity index ( $1-D$ ) increases with an increase in bird diversity (Magurran 2004). Simpson's evenness index ( $E_{1/D}$ ) increases when bird abundance is equally distributed

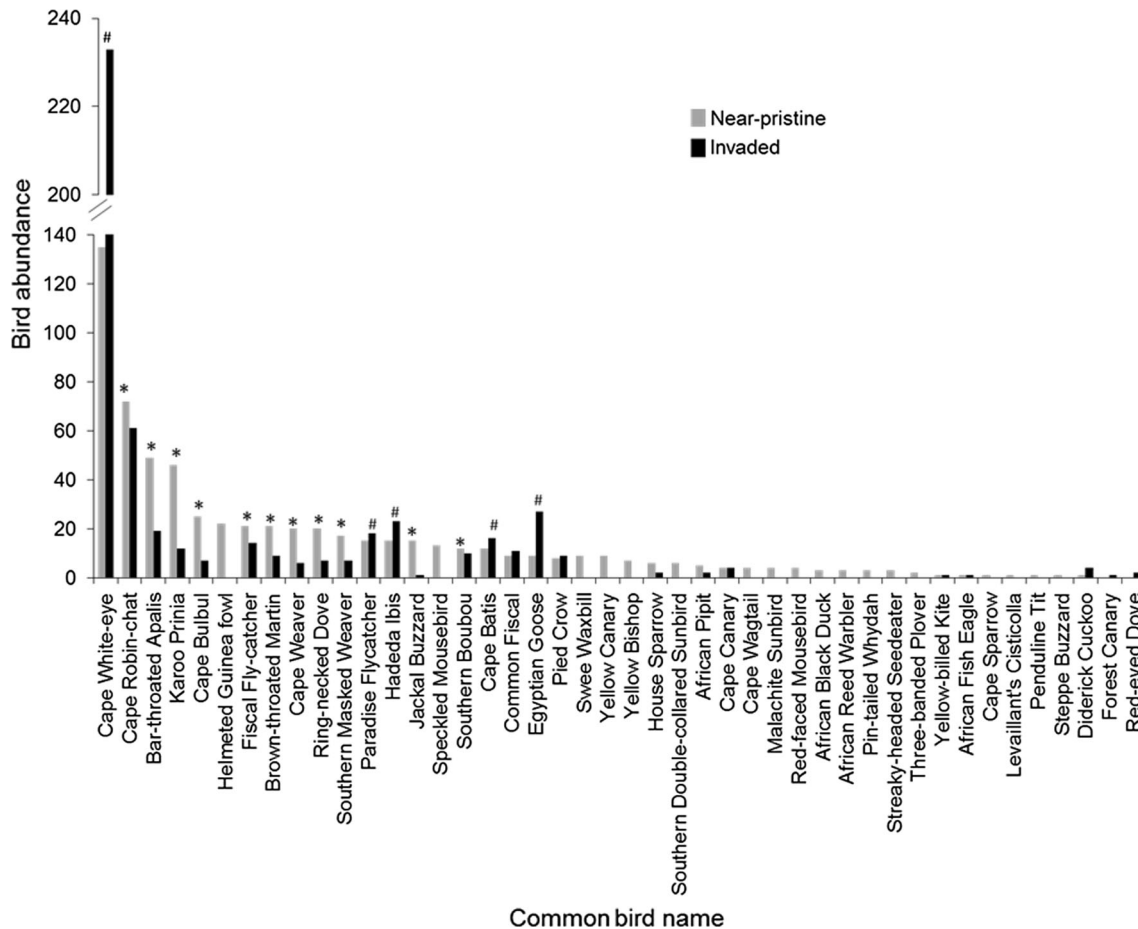
among species in the area and there are no few dominant bird species (Magurran 2004).

Differences in bird abundance per feeding guild, between near-pristine and invaded sites, was assessed with a generalised linear model (GLM) with Poisson distribution and a log-linked function in R (R Core Team 2012). We assessed whether birds' body size is an important predictor of bird response to *E. camaldulensis* invasion (Polo and Carrascal 1999; Coetzee et al. 2013; Rogers and Chown 2013). Bird weight as a proxy for body size was compared between near-pristine and invaded areas with a Mann–Whitney U test (Statistica version 12; StatSoft Inc. 2015, Tulsa, USA).

Differences in bird composition between near-pristine and invaded sites were explored using non-metric multidimensional scaling (nMDS) in Primer version 6

**Table 1** Simpson's diversity index ( $1-D$ ) and Simpson's evenness ( $E_{1/D}$ ) for near-pristine and *Eucalyptus camaldulensis* invaded sites along the Berg River, South Africa

	Near-pristine	Invaded	Mann–Whitney U test
Simpson's diversity $\pm$ SD	0.92 $\pm$ 0.03	0.76 $\pm$ 0.02	$P = 0.04$
Simpson's evenness $\pm$ SD	0.51 $\pm$ 0.03	0.34 $\pm$ 0.03	$P = 0.02$



**Fig. 4** Bird abundance for species observed in near-pristine and invaded sites. Bird abundance is the total number of individual birds recorded in near-pristine and invaded sites. The *asterisk* indicates species with significantly higher abundances in near-

pristine sites, while the *hash* indicates species with significantly higher abundances in invaded sites. Only bird species with more than ten sightings were included in the analyses

(Clarke and Gorley 2006). Before nMDS analysis, similarities between sites were calculated using the Bray–Curtis index and bird species abundances for each site were subsequently square root transformed. On two dimensions, nMDS was performed running 50 restarts with a minimum stress of 0.01. The difference in bird composition between near-pristine and invaded sites was analysed with a one-way multivariate permutational analysis of variance (PERMANOVA). Maximum plant height and percentage canopy cover were included in the analysis as covariates. Similarity percentage analysis (SIMPER) was used to identify the bird species contributing strongly to similarities and differences between near-pristine and invaded sites.

## Results

### Bird species richness and abundance

Sampling was adequate; since the species accumulation curves flattened off for both near-pristine (Fig. 3a) and

invaded sites (Fig. 3b). In the near-pristine sites, a total of 635 individual birds from 42 different species were observed versus 507 birds from 26 species in invaded sites. The Simpson's diversity index and Simpson's evenness were higher in near-pristine sites when compared to invaded sites (Table 1).

Eighteen species occurred in near-pristine sites only, whilst 24 species were shared between near-pristine and invaded sites (Fig. 4). Two species, the Red-eyed Dove and Forest Canary, occurred only in invaded sites. Carnivorous and herbivore bird species occurred in equal numbers in invaded and near-pristine sites (Fig. 5). The total number of species for the remainder of the feeding guilds was lower for the invaded sites, with the nectar feeding guild absent from invaded sites (Fig. 5). Nectar feeding bird abundance differed significantly between near-pristine and invaded sites ( $P < 0.01$  from a Chi squared test comparing generalised linear models with and without treatment as a factor; Fig. 6; Table S3). Invaded sites had significantly lower bird abundance for insectivores, omnivores, granivores, frugivores and raptors but with a significantly higher abundance of carnivores and herbivores

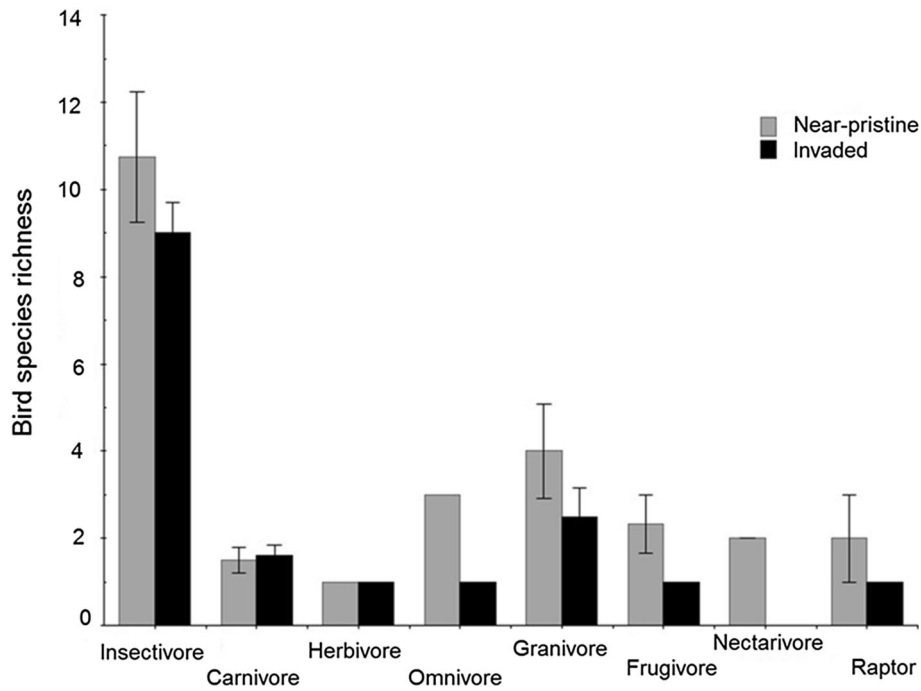


Fig. 5 Bird species richness per feeding guild (total per site) for near-pristine and invaded conditions. Bars show totals  $\pm$ SD

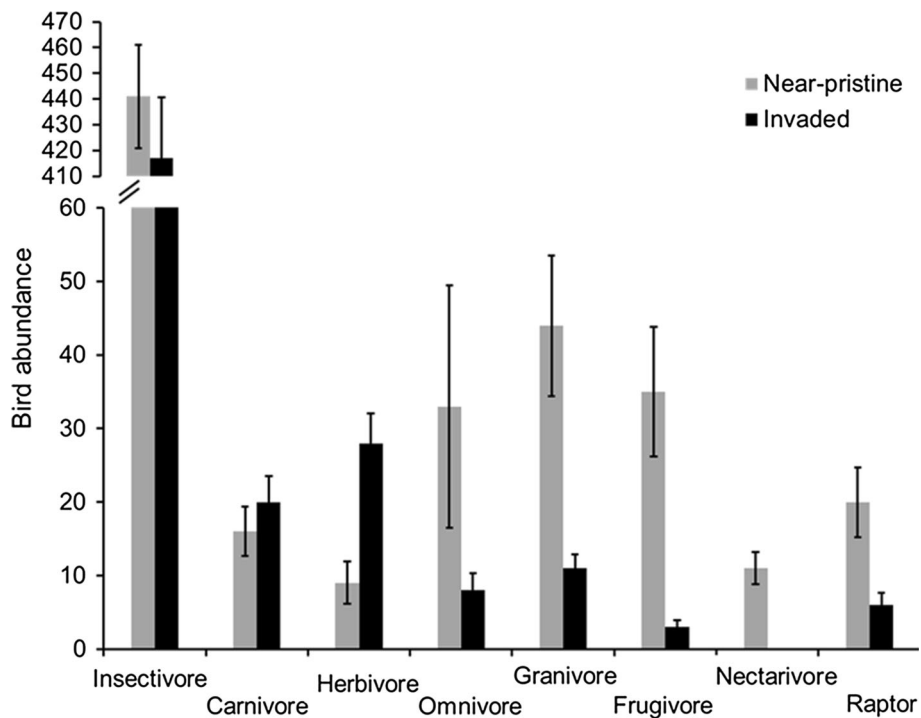
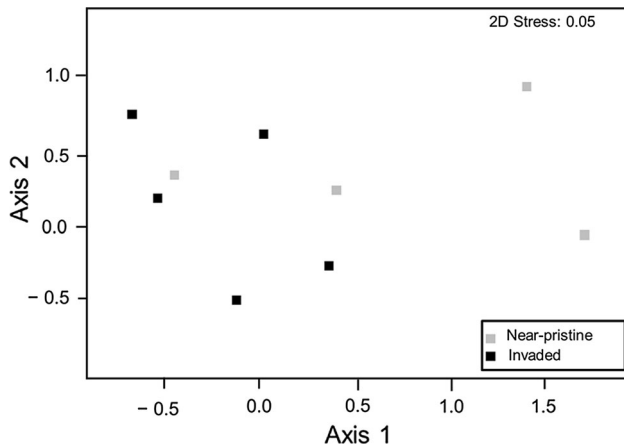


Fig. 6 Number of individual birds recorded per feeding guild for near-pristine and invaded sites. Bars show totals  $\pm$ SD

(Fig. 6;  $P < 0.05$ ). Bird body weight did not differ between near-pristine and invaded sites ( $Z = 0.53$ ;  $df = 1$ ;  $P = 0.6$ ).

Invaded sites grouped together, with two of the near-pristine sites grouping closely to invaded sites (Fig. 7).

The other two near-pristine sites are distinctively separate from the invaded sites (stress = 0.05). There was a significant difference in bird composition (PERMANOVA,  $F = 3.619$ ,  $df = 1$ ,  $P = 0.001$ ), maximum plant height (PERMANOVA,  $F = 2.063$ ,  $df = 8$ ,



**Fig. 7** Ordination analyses (non-metric dimensional scaling (nMDS)) of near-pristine and invaded sites. Species abundances were used for similarity testing (Bray–Curtis diversity index) after square root transformation. Stress = 0.05

$P = 0.004$ ) and percentage canopy cover (PERMANOVA,  $F = 1.791$ ,  $df = 8$ ,  $P = 0.017$ ) between near-pristine and invaded sites. There was an overall dissimilarity of 58.5% between invaded and near-pristine sites with the Cape White-eye, Cape Robin-Chat, Bar-throated Apalis, Karoo Prinia and Cape Bulbul contributing 40% of the observed differences (Table S4).

#### Comparison of bird communities between riparian and non-riparian habitats

Comparatively, riparian areas (whether near-pristine or invaded) have higher bird species richness and abundance than non-riparian habitats (Table 2). For both riparian and non-riparian habitats, bird species richness and abundance is highly variable but is lower in alien tree invaded habitats. *Acacia* invasions had the highest negative impact on bird communities, followed by *E. camaldulensis* invaded riparian areas (Table 2).

## Discussion

Bird assemblages in *Eucalyptus camaldulensis* invaded riparian habitats are largely a subset of those in near-pristine habitats. While invaded sites gained only two bird species (Red-eyed Dove and the Forest Canary), almost half of the 42 bird species present in near-pristine sites are lost in *Eucalyptus* invaded areas. But with only one Forest Canary and two Red-eyed Doves sighted, no inference can be made for the existence of the two species in invaded sites.

Five species, namely: Cape White-eye, Paradise Flycatcher, Hadedda Ibis, Cape Batis and the Egyptian Goose had a significantly higher abundance in invaded sites. Whilst the Cape Batis and Paradise Flycatcher are forest dwellers, the Cape White-eye, Hadedda Ibis and the Egyptian Goose are opportunistic and are known to move into transformed habitats (Macdonald et al. 1986; Schwarzenberger and Dean 2003; van Rensburg et al. 2009; Dures and Cumming 2010). Invasive alien plants change the availability of resources, in particular food and nesting sites, which to a large extent determine the occurrence of birds (Holland-Clift et al. 2011). The Cape White-eye, Cape Batis and Paradise Flycatcher are foliage gleaners and their high abundance in invaded sites could indicate an increase in insect abundance (Fraser and Crowe, 1990) whilst the availability of nesting sites in the tall eucalypt trees could explain the higher abundance of the Hadedda Ibis and the Egyptian Goose (Fraser and Crowe 1990; pers. obs.).

Of the bird species occurring in both near-pristine and invaded sites, eleven species occur at significantly higher abundance in near-pristine sites (Fig. 4). Lower bird abundance in invaded sites might be attributed to low native plant diversity in invaded sites (Tererai et al. 2013). Other than outcompeting native trees, the dense *E. camaldulensis* canopy cover reduces sunlight for understory plants, resulting in lower plant diversity (Tererai et al. 2013). This will reduce food resources diversity, which largely determines the feeding guilds present in a bird community (Symes et al. 2002).

**Table 2** Comparison of invasive tree impact on bird species richness and abundance in riparian and non-riparian areas of the Cape Floristic Region

Habitat type	Species richness (total)	Species richness $h^{-1} ha^{-1}$	Bird abundance (total)	Bird abundance $h^{-1} ha^{-1}$	References
<i>Pinus radiata</i> forests	26	1.1	819	34.9	Greve et al. (2011)
Mountain fynbos	33	1.4	1199	51.02	Greve et al. (2011)
<i>Acacia</i> : high density	33	0.09	2122	5.8	Rogers and Chown (2013)
Medium density	36	0.29	2154	17.6	Rogers and Chown (2013)
Low density	32	0.96	625	18.7	Rogers and Chown (2013)
<i>Acacia</i>	8	0.85	21	2.2	Thorpe (2013)
Strandveld	11	1.16	84	8.9	Thorpe (2013)
<i>Eucalyptus camaldulensis</i>	26	1.84	507	35.8	Current study
Riparian	44	4.86	635	70.2	Current study

Bird species richness and abundance is presented as birds per hour per hectare ( $h^{-1} ha^{-1}$ ). Values were calculated from paper appendices or from data provided by the authors

Seven of the eight bird feeding guilds still occur in the invaded sites but frugivores, granivores and omnivores have fewer species when compared to near-pristine sites. The low species richness of frugivores, granivores and omnivores could be due to a decrease in the guilds' food resources in invaded sites (Hajzlerova and Reif 2014). In their study, Tererai et al. (2013) note that invasion by *Eucalyptus camaldulensis* results in the replacement of a forest habitat by woodland with changes in understorey plant species composition. The decrease in the species richness of frugivores in *E. camaldulensis* invaded sites is in consistence with other studies where frugivores were also negatively affected by invasive alien plants (Fraser and Crowe 1990; Holland-Clift et al. 2011; Rogers and Chown 2013). As with other invasive alien woody plant species, *E. camaldulensis* invasion negatively impacts understorey plants, affecting germination, growth and establishment of native plant species (Le Maitre et al. 2011; Tererai et al. 2013). For example, *Eucalyptus* trees affect soil physico-chemical properties through a decrease in soil pH, nitrogen and total carbon and an increase in soil water repellency which all negatively affect native plant growth (Kerr and Ruwanza 2016). This effect on native plant species also indirectly affects bird assemblages, in particular the specialist bird species.

The nectar feeding bird guild in the CFR is highly specialised and usually consists of only two or three species in a community (Geerts and Pauw 2009b). In this study, the two species found in near-pristine sites is thus not unusually low. However, no specialist nectar feeding bird species occur in invaded sites (Fig. 5). Consequently nectar feeding bird abundance also changes from eleven birds in near-pristine to no birds in invaded areas (Fig. 6). Specialist nectar feeding birds are strongly linked to their specialised food resources and the absence of bird pollinated plants such as *Chasmanthe aethiopica* and *Halleria elliptica* in *Eucalyptus* invaded sites can explain the absence of this guild (Grey et al. 2007; Geerts and Pauw 2009a; Geerts et al. 2011). Similarly, other studies have found invasive alien plants to displace specialist nectar feeding birds (Fraser and Crowe 1990; Greve et al. 2011; Rogers and Chown 2013; Thorpe 2013). However, the opposite is true when the invasive alien plant species provides an abundant nectar source (Le Roux et al. 2010; Geerts et al. 2013).

The importance of eucalypts to raptor species is not apparent from this study as the richness and abundance of raptors is slightly lower in invaded sites. This dilutes the argument that eucalypts are important for raptor species for roosting, nesting and to serve as hunting platforms (Ewbank 2000; Suddjian 2004, unpublished conference notes; Cilliers and Siebert 2012; Carnie 2015). The importance of *Eucalyptus* trees as a hunting platform might be explained when an occasional tall *Eucalyptus* tree occurs within indigenous vegetation or in an urban environment where large trees are absent (Cilliers and Siebert 2012), but here we show that this effect disappears in a *Eucalyptus* dominated landscape.

Alternatively, low raptor species richness and abundance may be attributed to a decrease in prey species in monospecific *Eucalyptus* stands (Dean et al. 2002). However, with only 14 sightings of four raptor species, this requires more study.

Two near-pristine sites group together with invaded sites suggesting a similarity of the site characteristics and bird assemblages. A potential reason for the close grouping of these sites with invaded sites, and strangely so, is the high percentage canopy cover, resulting in the lack of understorey in near-pristine sites, which is also typical of *E. camaldulensis* invaded areas. Another reason could be that the bird species contributing the most towards site similarity (which includes the Cape White-eye, Cape Robin-Chat, Bar-throated Apalis and Karoo Prinia) are all insectivores pointing to a high similarity in food resources between these sites (Fraser and Crowe 1990).

Bird species richness in invaded vegetation from all four studies (Table 2); that is in *E. camaldulensis* woodlands, *P. radiata* forest or *Acacia* stands is lower when compared to near-pristine sites. We acknowledge that even though we corrected for sampling intensity (time and space), longer observation periods will always result in fewer species per time unit. Despite this, a strong pattern provides confidence in the riparian versus non-riparian comparison with impacts on bird assemblages being higher in riparian invaded areas, than in non-riparian invaded areas. Lower effects from invasion by *Acacia* and *P. radiata* might be attributed to the type of ecosystem affected (Sogge et al. 2008). It is also possible that the lesser effect in non-riparian invaded habitat is due to a larger regional pool of bird species that can adapt and tolerate habitat change through invasion (Brown et al. 2001). Thus, bird species from surrounding areas migrate into the invaded non-riparian habitat, compensating for losses from invasion (Brown et al. 2001; Rogers and Chown 2013).

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## Conclusion

Riparian habitats act as important refugia for wildlife in highly transformed landscapes, but here we support the hypothesis that the invasion by alien trees has negative impacts on bird assemblages. Significantly though is that we show that some of the most critical avi-faunal ecosystem services are impacted the most, namely seed dispersal and pollination. Consequently, and as a first step to restore these ecosystem processes, this study supports *Eucalyptus camaldulensis* removal from riparian areas. Furthermore, the high reduction in bird richness and abundance in *Eucalyptus* invaded riparian habitat, relative to other invaded habitats, lends support to the prioritisation of riparian areas for restoration activities. However, whether the current practice of passive restoration can restore riparian bird assemblages to pre-infestation levels needs to be determined.



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