

# Novel ecosystems support substantial avian assemblages: the case of invasive alien *Acacia* thickets

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## ABSTRACT

**Aim** Altered habitats may form entirely novel ecosystems that support new combinations of species. How indigenous species use invaded areas is, however, not well understood. Here, we investigate the value of Australian *Acacia* thickets as novel ecosystems in the Western Cape of South Africa by surveying bird assemblages within them.

**Location** Western Cape Province of South Africa.

**Methods** Birds were surveyed quantitatively in a variety of *Acacia* thickets in the south-western Western Cape in three seasons to examine species richness, abundance and functional diversity. We also examined the extent to which avian diversity was related to differences in patch-level vegetation structure.

**Results** Significant variation was observed in assemblage richness, density and biomass across sites. Diversity increased with productivity, but declined with stem density and canopy cover. On average, *Acacia* thicket patches were used by *c.* 20 species (with a regional richness of 76 species), had a mean density of 7.78 birds ha<sup>-1</sup> and a mean biomass of 0.224 kg ha<sup>-1</sup>. The most abundant feeding guilds were the mixed feeders and insectivores.

**Main conclusion** *Acacia* thickets in the Western Cape support a large subset of the region's birds with the most abundant species being small mixed feeders. Compared with other habitat types, *Acacia* thickets support avian assemblages with species richness and density similar to some natural sites in the region, but lacking typical nectarivores. Extrapolation to the area transformed by invasive acacias in the Cape Floristic Region suggests that these novel ecosystems support *c.* 22 million individual birds or 621 tonnes of avian biomass.

## Keywords

Biological invasions, body size, conservation value, local–regional assemblages, novel ecosystems.

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## INTRODUCTION

Landscape transformation by humans is one of the primary impacts on biodiversity (Pimm *et al.*, 1995; Sala *et al.*, 2000; Chown, 2010). The persistence of populations within and across modified landscapes depends in part on their ability to utilize resources in transformed habitats (Lindenmayer *et al.*, 2008; Markovchick-Nicholls *et al.*, 2008; Hodgson *et al.*, 2011). Indeed, as habitat transformation has reduced, fragmented and isolated native habitats, the relative value of altered habitats for conserving popula-

tions of indigenous species has increased (Edwards *et al.*, 2011).

Invasive alien species are important drivers of landscape transformation and contribute to local biodiversity loss and the homogenization of plant and animal communities (Richardson & van Wilgen, 2004; Olden, 2006; Simberloff *et al.*, 2012). However, invasive plants, in particular, may support indigenous species by providing habitat space or refugia in otherwise transformed landscapes, and/or replacement or novel food sources (Hobbs *et al.*, 2006; Foster & Robinson, 2007). Although controversial in part because of concerns

about the full extent of cost–benefit analyses (Simberloff *et al.*, 2012), several recent studies have highlighted the breadth of work demonstrating that indigenous species use and can benefit from landscapes that have been partially or substantially transformed by non-indigenous plants (Rodríguez, 2006; Quine & Humphrey, 2010; Schlaepfer *et al.*, 2011). Indeed, a recent meta-analysis has shown that the suitability of invaded habitats for indigenous populations depends on species- and context-specific responses to invasion (Pyšek *et al.*, 2012).

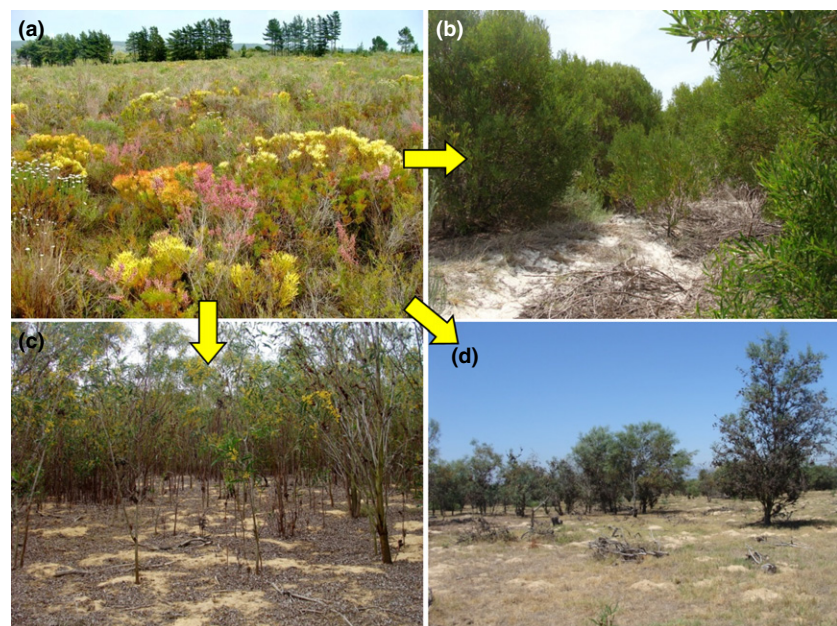
However, as a consequence both of the context-dependent nature of the impacts of invasion and of the absence of studies from many areas (in keeping with the situation for invasion biology generally, Pyšek *et al.*, 2008), the study concluded that investigations of species-specific impacts are necessary further to develop understanding in this area (see also Hulme, 2012). In other words, although novel ecosystems are becoming an increasingly important component of modern landscapes (Hobbs *et al.*, 2006, 2009), just how significant their contributions are to biodiversity maintenance remains unclear (Lindenmayer *et al.*, 2008; Chown & McGeoch, 2011).

In the Western Cape of South Africa, invasion by Australian *Acacia* species has led to widespread landscape transformation, with 11% of lowland areas covered by dense thickets and a further 33% with low invasion density (Rouget *et al.*, 2003). Previously, these areas supported several vegetation types of the species rich Cape Floristic Region (CFR; Mucina & Rutherford, 2006). The extent to which *Acacia* invasion alters indigenous communities in the CFR depends on the traits of the *Acacia* species and the biotic and abiotic traits of the community invaded (Yelenik *et al.*, 2004; Gaertner *et al.*, 2011; Le Maitre *et al.*, 2011). Nonetheless, in lowland areas, *Acacia* thickets typically modify the physical structure

of habitats by forming dense woody thickets, changing the abiotic environment (Musil & Midgley, 1990) and outcompeting indigenous plant species (Holmes & Cowling, 1997). Indeed, these thickets form habitats with no contemporary indigenous analogue (Fig. 1), thus meeting the requirements of a novel ecosystem (Milton, 2003; Hobbs *et al.*, 2006).

Given the considerable landscape coverage of these novel ecosystems, their significance to biodiversity should be assessed for three key reasons. First, in the light of the substantial national effort to rehabilitate invaded systems in South Africa, firm data for cost–benefit and prioritization analyses are essential (Marais *et al.*, 2004). Second, in the urban/peri-urban/agriculture/conservation patchwork that is the Western Cape (and indeed much of the world – see Ellis & Ramankutty, 2008; Chown & McGeoch, 2011), understanding the biodiversity value of land that has been transformed by invasives, but is not under agricultural or urban development, is important, especially given that even relatively modestly sized areas may contribute to networks in the landscape ensuring connectivity between otherwise unconnected natural areas (Pryke & Samways, 2012). Third, data from this region will improve general understanding of the influence of invasive trees on indigenous biota given that previous work has been focused in northern systems (Pyšek *et al.*, 2012).

Here, we therefore assess the role of *Acacia*-dominated patches in supporting avian diversity in the Western Cape. Bird habitat occupancy is influenced by local habitat structure and composition, food resource abundance and diversity, and landscape-level patterns in habitat fragmentation and cover (Willson, 1974; Wiens, 1989; Lindenmayer *et al.*, 2008; Sweeney *et al.*, 2010), making birds an excellent model group to investigate indigenous species use of a widespread, novel ecosystem. Our work builds on a set of previous stud-



**Figure 1** Indigenous lowland vegetation shown in the foreground of image (a) significantly changes with *Acacia* invasion. Habitats formed by invasive *Acacia* range from dense thickets of *A. cyclops* (b) and *A. saligna* (c), to more open savanna habitats formed by *A. saligna* (d).

ies in the region that were either more restricted or focused predominantly on richness rather than diversity estimates in transformed areas (Winterbottom, 1970; Fraser & Crowe, 1990; Dures & Cumming, 2010).

## METHODS

### Study area

This study was conducted in the south-western region of the Western Cape Province, South Africa (Fig. S1). The majority of the CFR is comprised of the Fynbos Biome, and the indigenous lowland fynbos is characterized by vegetation types such as Renosterveld, Cape Flats Sand Fynbos and Coastal Strandveld (Mucina & Rutherford, 2006). Birds were surveyed at eight sites (90–500 ha *Acacia* patches) across the region, which represented different landscape contexts (Table 1), and varying levels of *Acacia* dominance. Final site selection was based on total patch area (sites had to be >80 ha to allow space for at least 10 survey points per site), accessibility and site safety. Although we considered choosing remnant patches of lowland fynbos for baseline comparisons, previous work in the area has demonstrated that remnant patches are highly influenced by anthropogenic landscape transformation (Dures & Cumming, 2010). Thus, we elected rather to make comparisons with previous studies of less transformed sites, which have adopted similar methods (Greve *et al.*, 2011).

### Bird surveys

Bird surveys were conducted using the point-count method (Bibby *et al.*, 2000). For each site, points were located 100 m from the patch edge to minimize the influence of edge effects on bird activity and at least 200 m apart to ensure independent samples of bird density (Buckland *et al.*, 2001). Sites were mapped in ArcGIS version 10 (ESRI, 2011) and point-count locations were selected by overlaying maps of the site with randomly placed grids containing evenly spaced points. Of the points which fell within a site, ten were randomly selected to meet the above criteria. All sites had evidence of human disturbance, such as woodcutting, wildlife poaching and building of temporary human shelters. Point locations were changed if they fell within 200 m of human shelters, or if woodcutting was found within 100 m of a point. Sites were visited six times in a season. Seasonal surveys were conducted during February to March (summer), June to July (winter) and September to December (spring), of 2010, to capture variation in bird communities over the course of the year. Not all sites were surveyed in each season. Some sites were not surveyed after woodcutting or if fire reduced total patch area such that the 10 point counts could not be conducted. Additional sites were added in spring as this coincides with the peak breeding for many species (Hockey *et al.*, 2005). For the analysis, the term 'survey' refers to observations made at an individual site during a particular season.

**Table 1** Site characteristics. The list of woody invasive species includes all invasives recorded on site, but in all sites, *Acacia* species were the dominant invaders. The *Acacia* stand at site 4 was cut down before vegetation surveys could be conducted

Site	Name	Manager	Area (ha <sup>2</sup> )	Woody invasive species	Native vegetation	GPS location (Decimal degrees)	Mean vegetation height (cm) ± SE	Mean stem density (m <sup>2</sup> ) ± SE	Mean canopy cover (%) ± SE
1	Koeberg NR*	Eskom	306.82	<i>Acacia cyclops</i> , <i>A. saligna</i>	Coastal Strandveld	-33.6431 18.4263	110 ± 1.85	1.23 ± 0.295	13.1 ± 3.43
2	Rooisands NR*	Cape Nature	302.88	<i>Acacia cyclops</i> , <i>A. saligna</i> , <i>Pinus</i> spp., <i>Leptospermum laevigatum</i>	Coastal Strandveld, Renosterveld	-34.3468 19.0872	200 ± 2.42	2.32 ± 0.488	32.6 ± 4.34
3	Penhill Estates	Private	160.55	<i>Acacia saligna</i> , <i>Eucalyptus</i> spp.	Cape Flats Sand Fynbos	-33.9904 18.7431	308 ± 4.73	0.869 ± 0.145	32.7 ± 3.74
4	Zevenwacht Estates	Private	136.00	<i>Acacia saligna</i> , <i>Eucalyptus</i> spp., <i>Pinus</i> spp.	Cape Flats Sand Fynbos	-33.9187 18.7071	NA	NA	NA
5	Kerk te Koe Farm	Private	122.54	<i>Acacia cyclops</i> , <i>A. saligna</i> , <i>Leptospermum laevigatum</i>	Cape Flats Sand Fynbos	-33.7133 18.5333	319 ± 3.07	1.65 ± 0.317	40.0 ± 3.12
6	DeGrendel Estates	Private	90.04	<i>Acacia saligna</i> , <i>Eucalyptus</i> spp.	Cape Flats Sand Fynbos	-33.8576 18.5671	391 ± 3.85	2.00 ± 0.336	34.4 ± 3.53
7	Riverlands NR*	Cape Nature	499.52	<i>Acacia saligna</i>	Cape Flats Sand Fynbos	-33.4888 18.5837	70 ± 1.1	0.0179 ± 0.00751	0
8	Bottelary Conservancy	Private	119.35	<i>Acacia saligna</i> , <i>Pinus</i> spp.	Renosterveld	-33.9208 18.7299	153 ± 1.96	0.555 ± 0.129	5.36 ± 2.67

NR\*, nature reserve.

To provide estimates of density, birds seen or heard within 65 m of point-count locations were identified to species and the distance to the birds was recorded. Distances from the point to visually sighted birds were measured with a Bushnell Sport laser range finder. Birds that were heard, but not seen, were judged to be within one of seven distance intervals, 0–7, 8–15, 16–25, 26–35, 36–45, 46–55 and 55–65 m, from the point. Surveys were conducted by one observer to minimize observer bias. Each point count lasted nine minutes, and a three-minute quiet phase allowed birds to resume normal behaviour before the six-minute survey during which birds were recorded (Bibby *et al.*, 2000). Surveys were conducted over three-and-half hours starting at sunrise. Surveys were not conducted on windy, misty or rainy days. All birds seen or heard during each count session were recorded for estimates of species richness. Birds flying over the study site were not recorded. Raptors observed circling over the point count, during the count session, were recorded as it is possible they were hunting at the site (Bibby *et al.*, 2000).

### Habitat characteristics

A modified version of James & Shugart (1970) plots was used to capture variation in habitat structure in three 30-m transects radiating out from each point used for the avian density estimates. Tree stem density was measured by counting all stems 1.5 m, or taller, that fell within 1 m, on either side of the transect line. Vegetation height profiles were recorded every 2 m along the transect by placing a pole with 10 cm demarcations vertically and recording the height at which the vegetation touched the pole. Canopy cover was recorded by counting the presence or absence of canopy every 2 m along the transect using a canopy spotting scope (James & Shugart, 1970). Vegetation surveys were conducted once at each point, from November 2009 to February 2010.

Vegetation productivity for each surveyed area was measured using images of enhanced vegetation index (EVI) from the Moderate Resolution Imaging Spectroradiometer on NASA's Earth Observing System-Terra platform. EVI measures reflectance from near infrared, red and blue light sources allowing for an evaluation of vegetative growth, which is sensitive to seasonal differences in total leaf area, canopy density and structural variation in vegetation (Huete *et al.*, 2002). EVI data were obtained as raster images with 250 m by 250 m pixel resolution, compiled over 16 days intervals, for the months January through December in 2009 (NASA Land Processes Distributed Active Archive Center, 2011). EVI measurement scores were extracted for each pixel which overlapped with projected field sites in ArcGIS. Mean EVI for each site was calculated using pooled data for each month and season.

To quantify differences in landscape context between sites, surveyed *Acacia* thickets were mapped using the 2009 aerial photos in Google Earth (Google Inc., 2009) and projected in ArcGIS version 10 (ESRI, 2011). Site characteristics measured included distance to nearest urban area, distance to nearest natural area as well as total site area.

### Analysis

Species richness and its variance were computed by bootstrap, sampling with replacement using 500 randomizations and the Jackknife 2 (SJack2) estimator in EstimateS (Colwell, 2009). Total richness was calculated using data pooled from all sites, and survey richness was calculated using data from the six visits made to a site in a particular season. Differences in survey richness were assessed using Kruskal–Wallis rank sum tests in R (R Development Core Team, 2011).

Distance observations for all birds were pooled over the six visits for each survey. Bird density was calculated using Distance (Thomas *et al.*, 2010). Analyses used the Covariate Distance Sampling engine and detection functions were fitted to the data with final model selection determined using Akaike's information criterion (Buckland *et al.*, 2001). Final density estimates and their variance were generated using a uniform model with a simple polynomial adjustment term in which the samples were bootstrapped 999 times (Buckland *et al.*, 2001). The fit of the models indicated that detection of birds was low beyond 45 m; therefore, density data were truncated at 45 m for all subsequent analyses. Survey density was calculated using data pooled from the six visits. Mean bird density for the entire study was calculated using data pooled from all surveys. Differences in bird density between surveys were assessed using Kruskal–Wallis rank sum test in R (R Development Core Team, 2011). Assemblage evenness across sites was evaluated using rank abundance curves.

The avian biomass for each survey was estimated as the biomass observed within 45 m around each point count, using each visit to a point as an independent sample of biomass. Biomass around each point was calculated as the abundance of each species multiplied by the mean mass of each species summed for the assemblage at each point. The mean biomass observed across all points, per survey, was then used to estimate mean biomass per survey. Species-appropriate mass (Table S1) was calculated following Greve *et al.* (2008). The biomass from each survey was compared using a Kruskal–Wallis rank sum test.

Feeding guild density was estimated in the programme Distance by post-stratification of the pooled data from all surveys using the same model selection procedures as described for total bird density. Species were grouped into six feeding guilds (Table S1) – frugivore, granivore, insectivore, mixed, nectarivore and predator – using diet descriptions in Hockey *et al.* (2005). Differences in feeding guild abundances were assessed using Kruskal–Wallis rank sum tests in R (R Development Core Team, 2011).

Body size can influence how birds utilize different habitats (Polo & Carrascal, 1999). Therefore, the body size frequency distribution (BSFD) for birds observed in this study was compared with the Western Cape BSFD for terrestrial species. The species list for the Western Cape came from the South African Bird Atlas Project (Harrison *et al.*, 1997), and seabirds and aquatic birds were removed. The BSFD for *Aca-*



*cia* was generated using the cumulative species list for the entire study. Body mass was used as a surrogate for body size, and mass measurements were obtained from Hockey *et al.* (2005), and species-appropriate body mass was calculated using the methods described above. Body mass was  $\log_{10}$ -transformed, and frequency distributions were generated by plotting the number of species occurring in equal-sized body classes (Greve *et al.*, 2008; Coetzee *et al.*, 2013). The *Acacia* BSFD included 72 species compared with 292 for the Western Cape. BSFDs were compared by analysis of variance and Welch's two sample *t*-tests implemented in R.

### Avian diversity correlates

Vegetation characteristics from the vegetation survey included mean vegetation height, canopy cover and stem density. For each site, structural traits were calculated as the mean value from all vegetation transects conducted at a site. Differences between vegetation characteristics were compared among sites using a one-way analysis of variance implemented in R. To assess vegetation productivity, EVI was compared across months and across surveys using Kruskal–Wallis rank sum tests.

The influence of site characteristics on bird assemblage measures was examined using generalized linear models (GLM) implemented in R (R Development Core Team, 2011). Explanatory variables included site (to account for spatial position), stem density, canopy cover, mean vegetation height, mean EVI value, distance to urban areas, distance to indigenous vegetation and total habitat area. Response variables tested were species richness, density and biomass. Explanatory variables were included in final models if they had a variance inflation factor of less than four to

account for collinearity. Following recommendations from Zuur *et al.* (2009), both Poisson (scaled to compensate for overdispersion) and negative binomial error distributions were used, and model simplification was performed using the 'drop1' function (for Poisson errors) or 'step' function (for Negative Binomial errors) in the MASS package (Venables & Ripley, 2002).

## RESULTS

### Avian diversity

In total, 76 species from 5 954 individual bird records were observed in the *Acacia* patches. Species richness estimates for the study spanned a difference of 12 species (Mao Tau = 68 species, SJack2 = 80 species). Sample-based rarefaction curves for the entire study reached asymptotes, suggesting that the survey captured most species utilizing *Acacia* thickets (Fig. S2). Species richness estimates calculated for each survey independently, using the second-order Jackknife, ranged from 23 to 40 species, and significant differences were found among surveys (Kruskal–Wallis  $\chi^2 = 1830$ , d.f. = 15,  $P < 0.0001$ , Table 2). Species accumulation curves for individual surveys began to level off but did not reach a complete asymptote suggesting that patches may include more of the regional richness for such habitats, as was clearly reflected by the differences in richness among seasons. Nonetheless, overall, richness was adequately captured by the survey.

Mean ( $\pm$ SE) density of the avian assemblages was  $7.87 \pm 1.11$  birds  $\text{ha}^{-1}$ , with substantial and significant variation among surveys ( $3.12 \pm 0.134$  to  $21.1 \pm 0.0718$  birds  $\text{ha}^{-1}$ , Kruskal–Wallis  $\chi^2 = 7170$ , d.f. = 15,  $P < 0.0001$ , Table 2). Rank abundance curves for seasonal surveys (Fig. S3)

**Table 2** Assemblage characteristics for each survey and all sites pooled. Estimates of density and number of individuals represent the mean bootstrapped values from the programme Distance (Thomas *et al.*, 2010). Species richness estimates are the mean bootstrapped SJack2 values from EstimateS (Colwell, 2009). Biomass for each assemblage calculated by assigning species-appropriate mean body masses, from Hockey *et al.* (2005), to individuals observed within 45 m of point counts

Site	Season	Density (ha) $\pm$ SE	Total individuals $\pm$ SE	SJack2 $\pm$ SE	Biomass (g $\text{ha}^{-1}$ ) $\pm$ SE
1	Summer	9.8 $\pm$ 0.0873	3008 $\pm$ 21.9	26.4 $\pm$ 0.178	396 $\pm$ 100
2	Summer	5.98 $\pm$ 0.0643	1812 $\pm$ 5.58	25.4 $\pm$ 0.227	239 $\pm$ 60.1
3	Summer	9.35 $\pm$ 0.0843	1501 $\pm$ 13.5	29.1 $\pm$ 0.258	166 $\pm$ 23.5
4	Summer	11.3 $\pm$ 0.0693	1544 $\pm$ 9.41	26.8 $\pm$ 0.204	193 $\pm$ 38.6
1	Winter	7.27 $\pm$ 0.0423	2232 $\pm$ 12	27.9 $\pm$ 0.264	147 $\pm$ 17.7
2	Winter	4.81 $\pm$ 0.0582	1456 $\pm$ 2.24	27.9 $\pm$ 0.268	94 $\pm$ 11.6
3	Winter	6.24 $\pm$ 0.1115	444 $\pm$ 1.1	25.7 $\pm$ 0.226	321 $\pm$ 140
4	Winter	5.82 $\pm$ 0.0826	791 $\pm$ 7	24.9 $\pm$ 0.261	207 $\pm$ 57.9
5	Winter	4.77 $\pm$ 0.0619	584 $\pm$ 0.898	27.5 $\pm$ 0.368	135 $\pm$ 26.7
1	Spring	11.31 $\pm$ 0.0409	3471 $\pm$ 12.7	24.2 $\pm$ 0.221	388 $\pm$ 90.3
2	Spring	6.71 $\pm$ 0.0390	2033 $\pm$ 9.83	23.9 $\pm$ 0.144	147 $\pm$ 31.7
3	Spring	8.47 $\pm$ 0.0560	603 $\pm$ 2.24	23.5 $\pm$ 0.217	330 $\pm$ 79.3
5	Spring	13.8 $\pm$ 0.0460	1691 $\pm$ 5.61	26.2 $\pm$ 0.245	227 $\pm$ 23.8
6	Spring	12.3 $\pm$ 0.0725	1107 $\pm$ 6.52	22.3 $\pm$ 0.163	138 $\pm$ 19.3
7	Spring	3.12 $\pm$ 0.134	1559 $\pm$ 11.6	23.4 $\pm$ 0.307	102 $\pm$ 48.9
8	Spring	21.1 $\pm$ 0.0718	2518 $\pm$ 8.55	40.8 $\pm$ 0.341	303 $\pm$ 39.1
Entire study		7.87 $\pm$ 1.11	3100 $\pm$ 45.2	80.1 $\pm$ 0.381	224 $\pm$ 15.4

revealed that assemblages were dominated by five species – Karoo Prinia, Cape Robin Chat, Cape White-eye, Cape Canary and Cape Bulbul. Together these five species constituted 63.5% of all observations. Mean biomass also differed significantly among surveys ( $94 \pm 11.6 \text{ g ha}^{-1}$  to  $396 \pm 100 \text{ g ha}^{-1}$ , Kruskal–Wallis  $\chi^2 = 150.3$ , d.f. = 15,  $P < 0.0001$ , Table 2), with a grand mean across surveys of  $224 \pm 15.4 \text{ g ha}^{-1}$ .

Significant differences in density were found among feeding guilds (Kruskal–Wallis  $\chi^2 = 6800$  d.f. = 6,  $P < 0.0001$ , Fig. 2). Mixed feeders ( $3.98 \pm 0.009 \text{ birds ha}^{-1}$ ) were the most abundant feeding guild, followed by insectivores ( $3.01 \pm 0.01 \text{ birds ha}^{-1}$ ) and granivores ( $1.03 \pm 0.004 \text{ birds ha}^{-1}$ ). The low numbers of frugivores, nectarivores and predators made the fitting of density detection functions more difficult, and estimates of density for these guilds should be treated with caution.

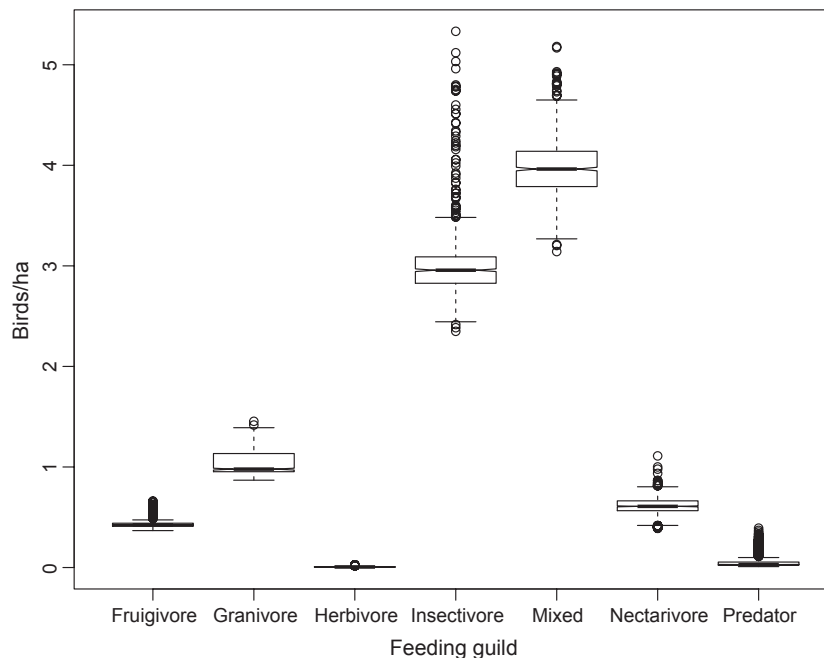
The BSFD for the assemblage of species found in the *Acacia* patches differed from that of the Western Cape terrestrial species in variance ( $F = 6.072$ , d.f. = 2886,  $P < 0.0001$ ), but not in range and mean (Welch's two sample  $t$ -test:  $t = 1.82$ , d.f. = 2550,  $P = 0.0684$ ; Fig. 3).

### Habitat correlates of avian diversity

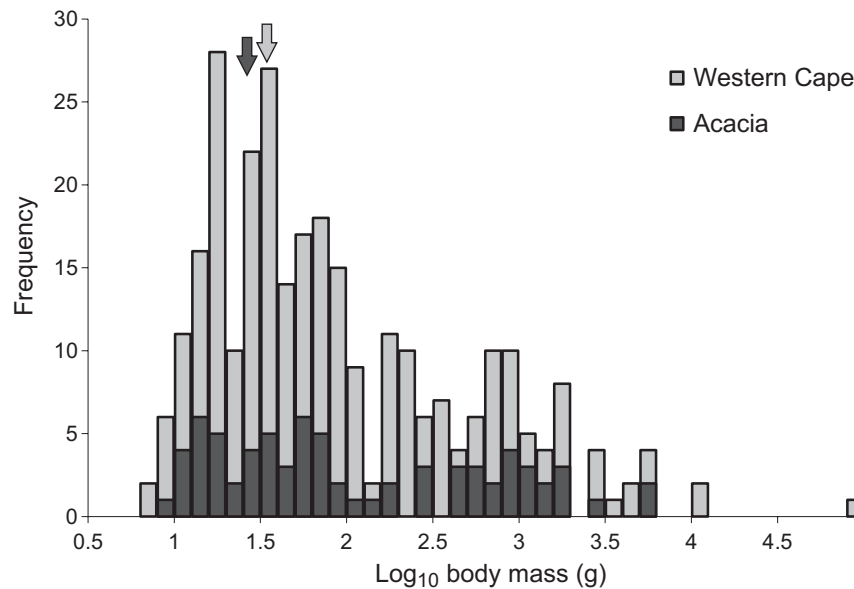
Across sites, mean vegetation height ranged from 0.7 to 3.91 m, mean stem density ranged from 0.0179 to 2.32 stems  $\text{m}^{-2}$ , and mean canopy cover ranged from 0 to 40% (Table 1). Sites differed in mean vegetation height ( $F_{(6, 57)} = 21.1$ ,  $P < 0.0001$ ), stem density ( $F_{(6, 57)} = 4.37$ ,

$P = 0.00107$ ) and percentage canopy cover ( $F_{(6, 57)} = 17.1$ ,  $P < 0.0001$ ). Mean vegetation productivity across all sites varied over the 10 months of the study from 2349 to 2879 (EVI) and showed significant differences (Kruskal–Wallis  $\chi^2 = 369.6$ , d.f. = 10,  $P < 0.0001$ ). Across surveys, mean vegetation productivity ranged from 1762 to 3364 (EVI) and showed significant differences (Kruskal–Wallis  $\chi^2 = 1271.364$ , d.f. = 15,  $P < 0.0001$ ; Fig. S4). Productivity was highest from June through October corresponding to the winter and spring seasons.

Generalized linear models with Poisson errors corrected for overdispersion provided the best fit minimal adequate models (Table 3). Species richness showed a significant positive relationship with EVI (coefficient = 0.000375,  $t$ -value = 3.53,  $P = 0.00778$ ) and site (coefficient = 0.0344,  $t$ -value = 2.55,  $P = 0.0341$ ), while a significant negative relationship was observed with mean vegetation height (coefficient =  $-0.00136$ ,  $t$ -value =  $-34.15$ ,  $P = 0.00321$ ) and spring (coefficient =  $-0.191$ ,  $t$ -value =  $-2.44$ ,  $P = 0.0403$ ). Avian density showed a significant positive relationship with EVI (coefficient = 0.00132,  $t$ -value = 4.48,  $P = 0.00153$ ), a negative relationship with canopy cover (coefficient =  $-1.85$ ,  $t$ -value =  $-3.05$ ,  $P = 0.0138$ ) and a negative relationship with the winter season (coefficient =  $-0.616$ ,  $t$ -value =  $-2.52$ ,  $P = 0.033$ ). Biomass across surveys showed a positive relationship with EVI (coefficient = 0.00154,  $t$ -value = 4.16,  $P = 0.00424$ ) and site (coefficient =  $-0.153$ ,  $t$ -value =  $-3.64$ ,  $P = 0.00831$ ), while showing a negative relationship with stem density (coefficient =  $-0.608$ ,  $t$ -value =  $-4.39$ ,  $P = 0.00321$ ).



**Figure 2** Significant differences were found between the densities of each feeding guild (Kruskal–Wallis  $\chi^2 = 6800$ , d.f. = 6,  $P < 0.0001$ ). Densities were calculated based on guild abundance across all sites. Horizontal lines in the boxes represent median values, and lower and upper box boundaries indicate 25th and 75th percentiles. Whiskers span two standard deviations of the mean, and points beyond the whiskers are outliers. Non-overlapping notches indicate significant differences between medians.



**Figure 3** Species body size frequency distribution for log-transformed body mass for the Western Cape (292 species, in grey) and for the species found in *Acacia* from this study (76 species, in black). Arrows mark mean log body size for the Western Cape (1.56) and for *Acacia* (1.47) and are not significantly different between the distributions (Welch’s two sample *t*-test:  $t = 1.82$ , d.f. = 2550,  $P = 0.0684$ ).

**Table 3** Results from models of the relationship between site-level characteristics and species richness, density and biomass. Non-significant explanatory variables included in the final models were retained if they decreased model variance

Response variable	Error distribution	Deviance explained	Explanatory variables	Coefficient	Standard error	<i>t</i> -value	<i>P</i>
Species richness	Poisson*	7.02/8.98 (78.11%)	(Intercept)	2.43	0.270	9	1.85E-05
			Site	0.0344	0.0135	2.55	0.0341
			EVI	0.000375	0.000106	3.53	0.00778
			Mean vegetation height	-0.00136	0.000327	-4.15	0.00321
			Season (spring)	-0.191	0.0783	-2.44	0.0403
			Season (winter)	-0.0676	0.0767	-0.883	0.403
Density	Poisson*	23/28.69 (80.16%)	(Intercept)	-1.09	0.796	-1.37	0.203
			EVI	0.00132	0.000294	4.48	0.00153
			Canopy cover	-1.85	0.608	-3.05	0.0138
			Season (spring)	-0.103	0.209	-0.494	0.633
			Season (winter)	-0.616	0.245	-2.52	0.033
			Biomass	Poisson*	553.39/652.75 (84.78%)	(Intercept)	2.145
Site	-0.153	0.042				-3.64	0.00831
EVI	0.00154	0.000369				4.16	0.00424
Stem density	-0.608	0.139				-4.39	0.00321
Season (spring)	-0.156	0.193				-0.812	0.444

\*Scaled to compensate for overdispersion.

**DISCUSSION**

In keeping with the strong influence of habitat structure and productivity on avian assemblages generally (Wiens, 1989; Polo & Carrascal, 1999; van Rensburg *et al.*, 2000; Hurlbert & Haskell, 2003; Pautasso *et al.*, 2011), the current study revealed positive relationships between richness, bird density, and biomass and productivity, and negative relationships between diversity and measures of increasing *Acacia* dominance (canopy cover, stem density and vegetation height). Seasonality also had a significant effect on diversity. Further

survey and experimental work would be required to determine the cause of these relationships. Nonetheless, the positive relationship with productivity and with the productive late winter to spring season is in keeping with the growing and flowering season for Australian *Acacias* in the region (Milton & Moll, 1982) and corresponds with changing insect abundance, which rises from early winter to mid-summer in the region (Procheş *et al.*, 2008). This outcome is also in keeping with the high densities of mixed feeders and insectivores in the *Acacia* sites, with three of the dominant species belonging to these groups (Insectivore: Karoo Prinia; Mixed

feeders: Cape Robin Chat, Cape White-eye). Nonetheless, changing detectability (Bibby *et al.*, 2000) cannot be ruled out as a partial contributor to these seasonal differences.

By contrast, the declining suitability of sites (measured as declining richness, density or biomass) with increasing canopy cover, vegetation height and stem density reflects the decrease in habitat quality as *Acacia* comes to dominate the sites (Le Maitre *et al.*, 2011). This may be a consequence of a decline in suitable food resources in thick *Acacia* stands, given that indigenous plant species are less abundant in such stands (Holmes & Cowling, 1997), and insect abundance (especially herbivores) tends to be lower on Australian *Acacias* than on related indigenous species (Procheş *et al.*, 2008). Changing nest site availability may also play a role (Fraser & Crowe, 1990). In consequence, some level of disturbance of sites, either as a consequence of informal use for woodcutting or through a managed thinning programme, is likely to benefit avian diversity in such sites by reducing *Acacia* density and presumably maintaining structural diversity. The significance of the latter for avian diversity has been demonstrated in other areas dominated by invasive woody plants (Fleishman *et al.*, 2003). For many *Acacia*-dominated sites in the general region, proximity to urban or peri-urban areas is likely to mean ongoing use for various purposes (Kull *et al.*, 2011). However, in protected areas where eradication is not underway or planned, it should be kept in mind that stand thickening is likely to reduce the value of the area not only for indigenous plants (Holmes & Cowling, 1997), but also for birds.

Accepting variation in diversity with changing *Acacia* dominance, our data nonetheless indicate that *Acacia* patches in the size range we examined support on average eight birds per ha, 224 g ha<sup>-1</sup> of bird biomass and 27 species. Such diversity is within the range of local scale species diversity

determined previously for the region (Table 4), although density was much lower (by an order of magnitude) than two coastal sites north of Cape Town (Fox & Hockey, 2007). Avian density at these latter sites is, however, similar to that found elsewhere (Pautasso & Gaston, 2005; Fuller *et al.*, 2009), suggesting that both Fynbos (Fraser & Crowe, 1990) and *Acacia*-dominated areas support relatively low avian densities. Nonetheless, overall, the *Acacia*-dominated sites housed 76 species, similar to values typically found for the region (Table 4). All species observed were native to Southern Africa, although several species, such as the African Goshawk, Hadeda Ibis, Fork-Tailed Drongo, Sweet Waxbill and Blacksmith Lapwing, have experienced recent range expansions into the Western Cape (Hockey & Midgley, 2009; Hockey *et al.*, 2011). Additionally, species that might typically be expected for lowland areas dominated by Fynbos or Renosterveld were nonetheless conspicuously absent, and particularly nectarivores (for a comparison, see e.g. Dures & Cumming, 2010; Greve *et al.*, 2011), although the effect on the overall BSHD was not marked. Indeed, from this perspective, the *Acacia*-dominated sites resemble BSHDs that are typically found at local scales across the continent (Coetsee *et al.*, 2013). Nonetheless, these assemblages are in some ways very different to those found in undisturbed fynbos vegetation as a consequence of the virtual absence of the more typical nectarivores and other habitat specialists such as the Cape Sugarbird, Orange-Breasted Sunbird, Cape Grassbird and Grey-Backed Cisticola (Fox & Hockey, 2007; Greve *et al.*, 2011). Thus, the *Acacia*-dominated habitats are functioning as quite different systems, hosting lower plant diversity, fewer insect herbivores and altered avian assemblages (Fraser & Crowe, 1990; Holmes & Cowling, 1997; Procheş *et al.*, 2008). In this respect, they resemble both the extant novel ecosystems found on other continents

**Table 4** Bird density, biomass and species richness reported for available habitat types in the Western Cape. Values are those published in the original paper or calculated from data in the attached appendices. Species richness values are the total number of species observed, reported in the study for a single habitat type. Density is the average density for a habitat type or was calculated for papers which reported both bird abundance and survey area. Boldfaced values indicate estimates for an entire study. Values for individual patches are indicated in parentheses where available

Reference	Habitat	Species richness	Density (birds ha <sup>-1</sup> )	Biomass (g ha <sup>-1</sup> )
Fraser & Crowe (1990)	Mountain Fynbos	<b>9</b>	<b>3.3</b>	<b>64.9</b>
	Restionaceous tussock marsh	<b>9</b>	<b>2.2</b>	<b>37.6</b>
	<i>Acacia</i> thickets	<b>23</b> (13–19)	(3.4–5.0)	(101.6–161.1)
	Mixed alien trees	<b>22</b> (10–17)	(2.6–5.7)	(56.9–709.9)
Armstrong & Van Hensbergen (1994)	Pine forest	<b>32</b> (6–19)	NA	NA
	Riparian vegetation	<b>23</b> (15–23)	NA	NA
Mangnall & Crowe (2003)	Agricultural land	<b>83</b> (16–81)	NA	NA
	Fynbos	<b>49</b>	NA	NA
Fox & Hockey (2007)	Strandveld	<b>40</b> (8–16)	<b>95.9</b> (24.6–145.5)	NA
	Golf estate	<b>34</b> (5–16)	<b>80.2</b> (29–143)	NA
Dures & Cumming (2010)	Cape Flats Sand Fynbos fragments	<b>79</b>	NA	NA
Greve <i>et al.</i> (2011)	Mountain Fynbos	<b>33</b> (9)	<b>42</b>	NA
	Pine forest	<b>25</b> (8)	<b>28</b>	NA



(Lindenmayer *et al.*, 2008), and those forecast to develop as landscapes continue to be transformed in various ways (Stralberg *et al.*, 2009).

Recognizing that approximately 2,773,498 ha of the CFR are invaded by Australian *Acacia* species (Kotzé *et al.*, 2010) and that *Acacia*-dominated sites support on average  $7.87 \pm 1.11$  birds  $\text{ha}^{-1}$  or  $224 \text{ g ha}^{-1}$  suggests that these novel ecosystems support *c.* 22 million individual birds or 621 tonnes of avian biomass. For comparison, the estimated total number of individual birds of all species in South Africa lies between 1.9 and 2.35 billion (Hui *et al.*, 2009). Compared with a more temperate system, the number of individual birds supported by *Acacia*-transformed habitats is high, with the total number of wild birds estimated for the UK at 126.5 million (Gaston & Evans, 2004) and 602 995 in the city of Sheffield (Fuller *et al.*, 2009).

Having said this, the current study provides no information on the extent to which the local avifauna is supported by the *Acacia*-dominated sites. In other words, the study was based largely on point counts rather than on methods such as territory mapping and assessment of reproductive success that might enable estimates to be made of the extent to which habitats are positively contributing to population persistence. However, investigations of avian diversity and diversity of other groups, in other settings, such as among habitats in protected areas or among different landscape types (van Rensburg *et al.*, 1999; Waltert *et al.*, 2005; García *et al.*, 2008; Fuller *et al.*, 2009), similarly cannot provide such information directly. Rather, they provide an assessment of the assemblages likely to be supported by the areas investigated. In consequence, the same assumptions – that the habitats in fact support population persistence for many species – should be made with regard to the current sites, especially since during field observations, it appeared that species were more than simply transient visitors. However, only banding and population-level studies will enable the full extent of the significance of *Acacia*-dominated systems to be ascertained, both in terms of population persistence and as corridors through substantially modified habitats (see discussion in Rouget *et al.*, 2003; Rodewald, 2011; Pryke & Samways, 2012).

In conclusion, the novel ecosystems represented by *Acacia*-transformed sites in the Western Cape of South Africa support significant numbers and species of birds in the region. Mild disturbance to limit height and canopy cover, such as that associated with woodcutting, may contribute to diversity. Nonetheless, these novel ecosystems tend to have a suite of species different to those found in lowland Fynbos or Renosterveld habitats. Thus, they should not be seen as having no impact on avian diversity (see Discussion in Pyšek *et al.*, 2012). Rather, they have a biodiversity value that is different to other aspects of the landscape. In consequence, decisions about investment in various forms of landscape management across the region should take explicit cognizance of this value. Such evidence-based decision making lies at the heart of sound conservation practice (Sutherland *et al.*, 2004; Lindenmayer *et al.*, 2008).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Species list, species mass and feeding guild.

**Figure S1.** Map of study region.

**Figure S2.** Rarefaction curves for each survey grouped by season.

**Figure S3.** Rank abundance curves.

**Figure S4.** EVI values.

## BIOSKETCHES

**Andrew Rogers** is a Masters graduate of the Centre for Invasion Biology at Stellenbosch University whose research interests include invasion biology, novel ecosystem interactions, restoration and conservation management.

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Author contributions: A.M.R. and S.L.C. conceived the ideas; A.M.R. collected and analysed the data with support from S.L.C.; A.M.R. and S.L.C. led the writing.

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