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−1 and a mean biomass of 0.224 kg ha−1. 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.

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 populations 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 (Rodriguez, 2006; Quine & Humphrey, 2010; Schläepfer 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 (Pysek 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, Pysek 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 (Pysek 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](image.png) 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 invaders 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) | Woody invasive species | Native vegetation | Native stem density (m²) | Mean vegetation height (cm) | Mean canopy cover (%) | GPS location (Decimal degrees) | Erected | Mean vegetation height (cm) | Mean stem density (m²) | Mean canopy cover (%) |
|------|------|---------|-----------|-----------------------|------------------|-------------------------|----------------------------|------------------------|----------------------------|---------|-----------------------------|----------------------|-----------------------|
| 1    | Keerberg NR* | Escom | 306.82 | Acacia cyclops, A. saligna | Coastal Strandveld | -33.6431 | 100 ± 1.95 | 12.3 ± 0.295 | 38.0248, 18.6606 | 36 | 305 ± 1.95 | 12.4 ± 0.295 | 37.0248, 18.6606 |
| 2    | Rooielsand NR* | Cape Nature | 302.88 | Acacia cyclops, A. saligna, Pinus spp., Leptospermum laevigatum | Coastal Strandveld | -34.0872 | 200 ± 24.2 | 2.3 ± 0.488 | 38.0248, 18.6606 | 36 | 293 ± 24.2 | 2.3 ± 0.488 | 37.0248, 18.6606 |
| 3    | Penhill Estates | Private | 160.55 | Acacia saligna, Eucalyptus spp. | Leptospermum laevigatum | -33.9904 | 300 ± 4.73 | 2.4 ± 0.73 | 38.0248, 18.6606 | 36 | 293 ± 4.73 | 2.4 ± 0.73 | 37.0248, 18.6606 |
| 4    | Zevenwacht Estates | Private | 136.00 | Acacia saligna, Eucalyptus spp. | Leptospermum laevigatum | -33.9187 | 300 ± 3.07 | 3.0 ± 0.37 | 38.0248, 18.6606 | 36 | 293 ± 3.07 | 3.0 ± 0.37 | 37.0248, 18.6606 |
| 5    | Kerkke Keet Roe Farm | Private | 122.54 | Acacia saligna, Eucalyptus spp. | Leptospermum laevigatum | -33.7133 | 319 ± 3.07 | 3.0 ± 0.37 | 38.0248, 18.6606 | 36 | 293 ± 3.07 | 3.0 ± 0.37 | 37.0248, 18.6606 |
| 6    | DeGrendel Estates | Private | 90.04 | Acacia saligna, Eucalyptus spp. | Leptospermum laevigatum | -33.8576 | 319 ± 3.07 | 3.0 ± 0.37 | 38.0248, 18.6606 | 36 | 293 ± 3.07 | 3.0 ± 0.37 | 37.0248, 18.6606 |
| 7    | Riverlands NR* | Cape Nature | 493.52 | Acacia saligna, Pinus spp. | | -33.4887 | 290 ± 3.07 | 3.0 ± 0.37 | 38.0248, 18.6606 | 36 | 293 ± 3.07 | 3.0 ± 0.37 | 37.0248, 18.6606 |
| 8    | Bottelary Conservancy | Private | 119.35 | Acacia saligna, Pinus spp. | | -33.9208 | 70 ± 11 | 1.9 ± 0.55 | 38.0248, 18.6606 | 36 | 293 ± 11 | 1.9 ± 0.55 | 37.0248, 18.6606 |

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, complied 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 Acacia thicket
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 ranged from 12 species (Mao Tau = 68 species, SJack2 = 80 species). Sample-based rarefaction curves for the entire survey captured species utilizing Acacia thicket (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 (Mao Tau–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 ha$^{-1}$, with substantial and significant variation among surveys (1.12 $\pm$ 0.134 to 21.1 $\pm$ 0.0718 birds 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$^{-1}$) $\pm$ SE | Total individuals $\pm$ SE | SJack2 $\pm$ SE | Biomass (g 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 $\pm$ 6.32             | 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 ± 11.6 g ha⁻¹ to 396 ± 100 g ha⁻¹). Kruskal–Wallis χ² = 150.3, d.f. = 15, P < 0.0001, Table 2), with a grand mean across surveys of 224 ± 15.4 g ha⁻¹.

Significant differences in density were found among feeding guilds (Kruskal–Wallis χ² = 6800 d.f. = 6, P < 0.0001, Fig. 2). Mixed feeders (3.98 ± 0.009 birds ha⁻¹) were the most abundant feeding guild, followed by insectivores (3.01 ± 0.01 birds ha⁻¹) and granivores (1.03 ± 0.004 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 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 χ² = 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 χ² = 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 = −0.01.19, t-value = −2.44, P = 0.0403).

Avian density showed a significant positive relationship with EVI (coefficient = 0.000132, 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 χ² = 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.
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 (Proches 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

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 | (Intercept) | Coefficient | Standard error | $t$-value | $P$ |
|-------------------|--------------------|--------------------|-------------|-------------|---------------|----------|----|
| Species richness  | Poisson*           | 7.02/8.98 (78.11%)| 2.43 0.270  | 9 1.85E-05  |               |          |    |
|                    |                    |                    | Site 0.0344 | 2.55 0.0341 |               |          |    |
|                    |                    |                    | EVI 0.000375| 3.53 0.00778|               |          |    |
|                    |                    |                    | Mean vegetation height -0.00136 | -4.15 0.00321|               |          |    |
|                    |                    |                    | Season (spring) -0.191 | -2.44 0.0403 |               |          |    |
|                    |                    |                    | Season (winter) -0.0676 | -0.883 0.403 |               |          |    |
| Density            | Poisson*           | 23/28.69 (80.16%)  | 1.09 0.796  | -1.37 0.203 |               |          |    |
|                    |                    |                    | EVI 0.00132  | 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%) | 2.145 1.04  | 2.065 0.0778|               |          |    |
|                    |                    |                    | Site -0.153 0.042  | -3.64 0.00831|               |          |    |
|                    |                    |                    | EVI 0.00154  | 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.
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 (Proches 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\(^{-1}\) 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, Swee 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 BSFD was not marked. Indeed, from this perspective, the *Acacia*-dominated sites resemble BSFDs that are typically found at local scales across the continent (Coetzee 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; Proches et al., 2008). In this respect, they resemble both the extant novel ecosystems found on other continents.

### Table 4

| Reference | Habitat                      | Species richness | Density (birds ha\(^{-1}\)) | Biomass (g ha\(^{-1}\)) |
|-----------|------------------------------|------------------|----------------------------|--------------------------|
| Fraser & Crowe (1990) | Mountain Fynbos | 9 | 3.3 | 64.9 |
|            | Restionaceous tussock marsh | 9 | 2.2 | 37.6 |
| Armstrong & Van Hensbergen (1994) | *Acacia* thicket | 23 (13–19) | (3.4–5.0) | (101.6–161.1) |
|            | Mixed alien trees | 22 (10–17) | (2.6–5.7) | (56.9–709.9) |
| Mangnall & Crowe (2003) | Pine forest | 32 (6–19) | NA | NA |
|            | Riparian vegetation | 23 (15–23) | NA | NA |
| Fox & Hockey (2007) | Agricultural land | 83 (16–81) | NA | NA |
|            | Fynbos | 49 | NA | NA |
|            | Strandveld | 40 (8–16) | 95.9 (24.6–145.5) | NA |
|            | Golf estate | 34 (5–16) | 80.2 (29–143) | NA |
| Dures & Cumming (2010) | Cape Flats Sand Fynbos fragments | 79 | NA | NA |
| Greve et al. (2011) | Mountain Fynbos | 33 (9) | 42 | NA |
|            | Pine forest | 25 (8) | 28 | NA |
(Lindenmayer et al., 2008), and those forecast to develop as landscapes continue to be transformed in various ways (Stralburg 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 ± 1.11 birds ha$^{-1}$ or 224 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; Pyke & 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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