



What shapes plant and animal diversity on urban golf courses?

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Abstract

Recent concern over increasing loss of biodiversity has prompted considerable interest in the role of urban green spaces as reservoirs of local biodiversity. This study assessed the diversity of three indicator taxa - plants, ants and birds - on golf courses spanning a wide range of environmental variation in terms of climate, elevation, course age, size and connectivity to native woodland. Species richness and community composition was further compared between contrasting on-course habitat types that reflect different management intensities. We identified a set of taxon-specific environmental correlates indicating an intricate interplay of landscape- and local-scale variables that affect local species diversity. Our results show that floristic diversity is positively associated with the amount of rainfall, whereas ant and bird diversity are related to local-scale factors, particularly the number of trees and the size of water features on a site. The amount of on-course native habitat was a strong predictor of plant and ant diversity and was also associated with the number of unique species at the site level; this reinforces the value of remnant habitat patches as local biodiversity reservoirs that represent mini hot-spots in an otherwise species-poor urban landscape. Community composition for all three taxa differed markedly between non-playing and playing areas, with boundary and remnant habitats generally having more diverse, species-rich communities. Our results suggest that local floral and faunal biodiversity on urban golf courses can be enhanced by creating woody non-playing areas and, especially, by preserving, restoring or expanding remnant habitats.

Keywords Biodiversity · Community composition · Climate · Environmental factors · Urban environment · Golf courses · Plants · Ants · Birds

Introduction

Human modification of the global environment has led to the rapid decline of biological diversity, driven mainly by

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land use changes, with climate change, nitrogen deposition and elevated atmospheric CO₂ concentrations also playing major roles (Sala et al. 2000; Chapin et al. 2000). High levels of biodiversity are considered important for a number of reasons, including the provision of ecosystem services such as primary production and local climate regulation, for its intrinsic and aesthetic value and, in particular, for providing ecosystem resistance and resilience in the face of disturbance (Chapin et al. 2000). A complex interplay of environmental and biotic factors governs biodiversity at different spatial scales. At the landscape scale, the main drivers of biodiversity variation are environmental factors such as temperature, precipitation and soil type (Sala et al. 2000). At the more local scale, biodiversity can be strongly influenced by air quality and adjacent land use (Bailey 2007; Gadsdon et al. 2010; Lee and Power 2013) as well as the type, relative size and connectivity of native habitat fragments (Bailey 2007; Pardini et al. 2010; Hagen et al. 2012; Beninde et al. 2015). Biotic factors such as vegetation structure and complexity also play an important role in mediating species interactions and movement through the landscape (e.g. Beninde et al. 2015). Concern over the impact of land use

change, particularly rapid urbanisation (e.g. Grimm et al. 2008), has led to recent interest in assessing the contribution of large recreational green spaces - i.e. parks, gardens and golf courses - to urban and peri-urban biodiversity (Lin and Fuller 2013; Aronson et al. 2014). Whilst golf courses typically have relatively low biodiversity when compared to native bush or forest areas (Terman 1997), they can compare well to other urban habitats (Colding and Folke 2009; Mata et al. 2017; Threlfall et al. 2016; Threlfall et al. 2017).

The benefits of green space in urban landscapes are increasingly being recognized, in terms of its importance for recreation and human health, including local climate regulation (Grimm et al. 2008; Vidrih and Medved 2013; Doick et al. 2014) and improved local air quality (Hartig et al. 2014; Hartig and Kahn 2016). Urban green spaces enhance human well-being by, for example, providing daily access to nature and reducing noise (Andersson et al. 2014; Hartig and Kahn 2016), factors that have tangible value, as evidenced by the frequently higher house prices where properties are close to green areas (Andersson et al. 2014). Larger vegetated areas typically support greater levels of biodiversity than smaller pockets of urban green space. Indeed, a recent study by Beninde et al. (2015) revealed positive relationships between the amount of green space and the diversity of a variety of taxonomic groups across 75 cities worldwide, while, at the more regional scale, Turrini and Knop (2015) found a positive association between the diversity of arthropods and the amount of vegetated area in several cities in Switzerland. Habitat connectivity also has an important influence on species movement and thus diversity in urban environments, as exemplified by Shanahan et al. (2011) for bird species richness in Brisbane. The value of golf courses as important reservoirs of biodiversity is often underestimated (Gange et al. 2003), despite the fact that they typically represent a considerable proportion of green space within the urban landscape, providing varied habitats that support a diverse range of flora and fauna (Colding and Folke 2009; Gange et al. 2003; Threlfall et al. 2016; Threlfall et al. 2017). Indeed, suburban golf courses have been shown to enhance local biodiversity for a range of taxa, including bird, beetle and bumblebee species in the UK (Tanner and Gange 2005), and plants, vertebrates and invertebrates in Japan (Yasuda and Koike 2006). Within Australia, golf courses have been identified as valuable refugia for threatened vertebrate species, including birds and mammals in suburban southeast Queensland (Hodgkison et al. 2007a, b), as well as a diverse fauna of birds and bats (Threlfall et al. 2016, 2017), ants (Ossola et al. 2015), bugs (Mata et al. 2017) and native bee communities (Threlfall et al. 2015) in Melbourne (southeast Victoria). Golf courses typically comprise both playing areas (intensively managed fairways, greens and tees) and non-playing areas (generally including boundary and between-fairway vegetation, water features such as lakes and ponds and areas of remnant native woodland). Non-playing areas are generally more structurally diverse and have been shown to support as

many species of plants, birds and vertebrates as areas of adjacent remnant native habitat outside of course boundaries (e.g. Yasuda et al. 2008; Hudson and Bird 2009; Hodgkison et al. 2007b).

Different habitat types within golf courses can harbour distinctly different floral and faunal communities, with marked turnover in species composition and abundance (e.g. Yasuda and Koike 2006). In Australia, communities have generally been investigated by comparing golf courses to other land use types, such as patches of remnant forests (Hodgkison et al. 2007b) or urban parks and gardens (Ossola et al. 2015; Threlfall et al. 2015; Threlfall et al. 2016), but there has so far been very little attention paid to differences in community assemblages between habitats within golf courses.

To date, the separate effects of local-scale factors such as habitat diversity and complexity, and landscape-scale factors such as climate on the biodiversity of urban golf courses have been studied in different parts of the world. However, it remains less clear how these affect biodiversity when acting together. Our study addresses this knowledge gap by asking: Are local-scale factors more important for local biodiversity than landscape-scale factors, or vice-versa? And, are the patterns similar for different groups of organisms? Answers to these questions are of direct relevance for biodiversity management and conservation efforts in urban green spaces since they can highlight the possibilities and limitations of such efforts and help inform golf course managers in their choice of management strategies.

In the present study, we focused on biodiversity surveys of three key taxa: plants, ants and birds. Plants, as structurally diverse primary producers, are of key importance in terrestrial habitats. Ants are being increasingly used in biodiversity surveys, as they are abundant in the environment, contribute significantly to ecological functioning within the landscape and are sensitive to disturbance (Underwood and Fisher 2006; Andersen et al. 2002; Andersen and Majer 2004). Birds are a charismatic taxon and are commonly used as a vertebrate indicator group for biodiversity studies in urban environments (e.g. Rottenborn 1999; Blair 1999; Shanahan et al. 2011) including on golf courses (Sorace and Visentin 2007; Hodgkison et al. 2007a, b).

The present study seeks to address the following key research questions: (1) Which landscape and local scale environmental factors are associated with high levels of biodiversity on golf courses? (2) Which on-course habitat types harbour more species? (3) Does the community composition of plant and animal taxa differ between habitat types? Based on previous studies investigating plant diversity across environmental gradients (e.g. Kreft and Jetz 2007; Beninde et al. 2015), we predict that plant diversity is closely associated with both landscape-scale variables (e.g. climate) and local scale variables (e.g. connectivity to native vegetation; Shanahan et al. 2011; Beninde et al. 2015). We further predict that bird and ant

diversity are more closely related to local scale variables that influence nesting and foraging space, as has been previously found for both taxa (Hodgkison et al. 2007a, b; Ossola et al. 2015). Finally, we predict that there will be large differences in the composition of species assemblages associated with different golf course habitats, with the greatest contrasts being between remnant vegetation and highly managed playing areas, for all three taxa.

Methods

Study area

The Greater Sydney Region is Australia's most densely populated metropolitan area, supporting approximately five million people in an area spanning ~12 thousand square kilometres (www.cityofsydney.nsw.gov.au). We selected 15 golf courses covering a range of temperatures, precipitation and course characteristics, such as age, size and degree of connectivity to surrounding native habitat. Selected courses spanned an area of ~88 km east-west and ~50 km north-south. Sites ranged longitudinally from coastal Dee Why (33° 44' 20.75"S, 151° 18' 22.06"E) to Wentworth Falls (33° 41' 48.18"S, 150° 21' 45.98"E) in the Blue Mountains, and latitudinally from Terrey Hills (33° 41' 19.56"S, 151° 15' 38.52"E) in the north, to Camden (34° 3' 1.19"S, 150° 43' 51.29"E) in the south (Fig. 1).

Landscape and local-scale environmental variables

The diversity of three focal taxa (plants, ants and birds) was assessed in relation to four landscape-scale and six local-scale (site-level) environmental variables: Landscape-scale factors include (1) elevation (range 2–947 m above sea level); (2) mean

max. Summer temperatures (16–25 °C); (3) annual precipitation amount (854–1510 mm), obtained from the nearest weather station for each golf course and calculated over the last 30 years, (<http://www.bom.gov.au/>); (4) connectivity to surrounding woodland, calculated as the percentage adjacent to the golf course perimeter (10–85%). Local-scale factors were course age (42–111 years), course size (32–92 ha), size of on-course remnant vegetation (0–31 ha), size of water features (0–33 ha), average tree density (110–456 trees ha⁻¹) and tree biomass (13–199 t ha⁻¹). All site-level data are included in Table S1.

Survey design

To capture as much within-course variation as possible, species richness and community composition were assessed on each golf course in different habitat types: three woody habitat types were selected for plants, ants and birds, and an additional two non-woody habitats for ants and birds only (Fig. 1): woody: on-course remnant or restored native habitat, between-fairway habitat and course boundary habitat; non-woody: fairway habitat and water feature habitat. On each course, four replicates per habitat type were selected using a stratified randomised approach: a grid with 50 × 50 m cells was placed on the golf course and four survey locations per habitat type were randomly drawn from available grid cells at each site.

Plant survey

Within each replicate area, plant species identity was recorded in rectangular plots of 10 × 40 m and abundance was estimated by assigning scores of 0–5, following a modified Braun-Blanquet scale (DECCW 2009; Tozer 2003). Vegetation surveys were carried out once on each course between January and April 2014.

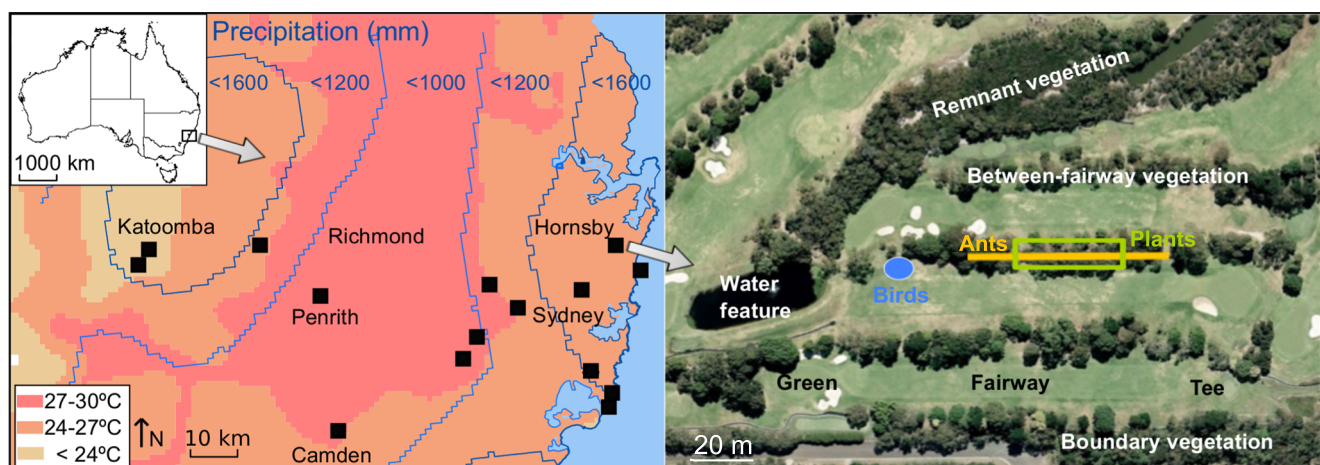


Fig. 1 Location of surveyed golf courses within the Greater Sydney area Left panel shows the study area, where filled squares show golf courses, ragged lines show annual precipitation isolines, shading indicates mean maximum summer temperature, averages based on

available data from the last 30 years (<http://www.bom.gov.au/>). Inset shows location of study area within Australia. Right panel shows habitat types within golf courses and exemplary survey setup for plants (rectangle), ants (transect) and birds (survey point)

Ant survey

Ants were collected between January and April 2014 using minced meat baits in five habitat types; these included the three woody habitats used for vegetation surveys (see above), and additionally around water features and on fairways. Four replicate areas were surveyed once per habitat type for each course. Following preliminary trials of different methods, five baits were deployed in 1.5 ml Eppendorf tubes along one 100 m transect per replicate and left out for three hours, during the morning (09.00–12.00 h). A total of 100 tubes per course (five habitats x four replicates x five tubes) were collected and samples preserved with 70% ethanol and stored in the freezer at -20°C . Ants were first sorted to genus and then to species level, using morphospecies, i.e. recognisable taxonomic units based on morphology, following procedures described in Oliver et al. (2012). Identification to subfamily/genus level was carried out using taxonomic keys (Shattuck 1999; Andersen 1991) and online identification resources (<http://www.antwiki.org/wiki/>). Final species identification was carried out in Darwin, Australia, under the expert guidance of Prof. Alan Andersen and the use of the CSIRO ant reference collection. Voucher specimens have been lodged there as a reference.

Bird survey

Bird surveys were carried out in the morning (06.00–10.30 h), using a modified point survey method (Gregory et al. 2002). Two sets of bird surveys were conducted, the first between September and December 2014 and the second in February–March 2015. For each golf course, 16 locations - in the vicinity of the vegetation/ant surveys - were selected. After approaching the survey point, a settling time of one minute was allowed before observations started. An observation consisted of a 5-min period during which all visible bird species were identified, individuals counted and the habitat noted. Only birds using the site, i.e. perching, resting or feeding were counted. Birds flying overhead or those that were heard, but not seen, were not included in the site counts.

Data analyses

Data were used to calculate plant, ant and bird species richness, diversity and community composition. Diversity was calculated as the Shannon-Wiener diversity index (H), which accounts for species richness and the proportional abundance of each species in the sample (Shannon 1948; Magurran 2004), using the program EstimateS

v9.1 (Colwell 2013). In addition, for two taxa, the diversity of a subset of species, i.e. native plants and non-water birds, was analysed in the same fashion as described above.

Multiple regression analysis was used to assess relationships between taxon-level diversity (H) and the four landscape-scale and six local-scale environmental variables. Analyses were carried out with untransformed variables, except for elevation, which was logged. Linear regression models (*lm*) were fitted using the least squares approach to calculate R^2 in the package *MASS* (Venables and Ripley 2002). A two-step process was used to select the best explanatory model. Firstly, co-linearity amongst environmental factors was assessed by calculating the variance inflation values (VIF) and factors with values >4 were omitted (O'Brien 2007). Secondly, the most parsimonious model was selected based on the lowest Bayesian Information Criterion (BIC) value in a combined step-down and step-up model selection process (MacNally 2000). A canonical correspondence analyses (CCA) ordination was used to visualise the community composition for each of the three taxa, in relation to the tested environmental factors (Fig. S1). All statistical analyses were conducted in R version 3.2.0 (R Development CoreTeam 2015). Initially, the effect of environmental variables on species richness was explored, revealing highly similar trends as for species diversity. Given this similarity we have focused our study on relationships between environmental drivers (landscape and local-scale) and biodiversity of the three taxa assessed on Sydney's urban golf courses.

Species richness was compared between habitat types using linear mixed effects models (LMEs) in the package *lme4* (Bates et al. 2015) to account for the nested design of the study (habitats nested within golf courses) (Zuur et al. 2009). An appropriate function based on the distribution of the untransformed count data was selected: the full and native plant species data sets were analysed using the function “*glmer.nb*” based on a negative binomial distribution to account for overdispersion; birds were analysed using “*glmer*” based on a Poisson distribution; and ants and exotic plants were analysed using “*lme*” based on a Gaussian distribution (Zuur et al. 2009).

The community compositions of the three surveyed taxa were analysed using “*manyGLM*” in the package *mvabund* (Wang et al. 2015). The multivariate test statistic $\text{Wald-}X^2$ was used to evaluate compositional differences between habitats within individual golf courses. The “*block*” function was used to account for nesting of habitats within courses. Data were visualised using a model-based approach to unconstrained ordination based on latent variable models (LVMs) (Hui et al. 2015) in *boral* (Hui 2016).

Results

Comparisons between golf courses – species numbers & diversity

Overall, we identified 603 species across three taxa; of these 438 were plant species with an average of 62 ± 25 ($AV \pm SE$) species per site (equivalent to 75–230 species per ha) (Table S2). Across all sites, 62% ($n = 270$) of recorded plant species were native and 38% exotic ($n = 168$). Plant diversity was positively associated with site elevation and precipitation (Table 1, Fig. 2a, b), but there was no significant relationship with other environmental factors, such as course size or connectivity. In addition, the diversity of native plant species was higher on courses with larger areas of remnant habitats (Table 1, Fig. 2c).

Ant surveys involved the collection and identification of 13,149 individual ants, belonging to 68 species, with an average of 18 ± 0.80 (range 12–22) species per course (Table S2). At the overall course level, ant diversity was significantly ($P = 0.03$) positively related to tree biomass (Table 1, Fig. 2d) although relationships with other environmental factors were not significant.

A total of 8660 individual birds, representing 97 species, were recorded during morning surveys. Site level species counts ranged from 26 to 52, with an average of 34 ± 4.5 species identified per golf course (S1 Table). Bird species diversity was positively related ($P < 0.01$) to the area of water features on a site (Table 1, Fig. 2e). However, the diversity of non-water birds (77% of all bird species) was significantly higher ($P = 0.02$) on older courses (Table 1, Fig. 2f). Relationships with other environmental factors were not significant.

Comparisons between habitat types – numbers of species

We identified 350 species across three taxa in on-course remnant habitats, 393 in boundary and 280 in between-fairway habitats. At water features and fairways, where only ants and birds were recorded, we found a total of 86 and 55 species, respectively. On average, there was greater native plant richness in remnant (14 ± 1.13) compared to boundary habitats (8 ± 0.79), whereas species richness of exotic plants was greatest in boundary habitats (4 ± 0.41) (Fig. 3a, c). Fairways were associated with particularly low species richness for ants (1

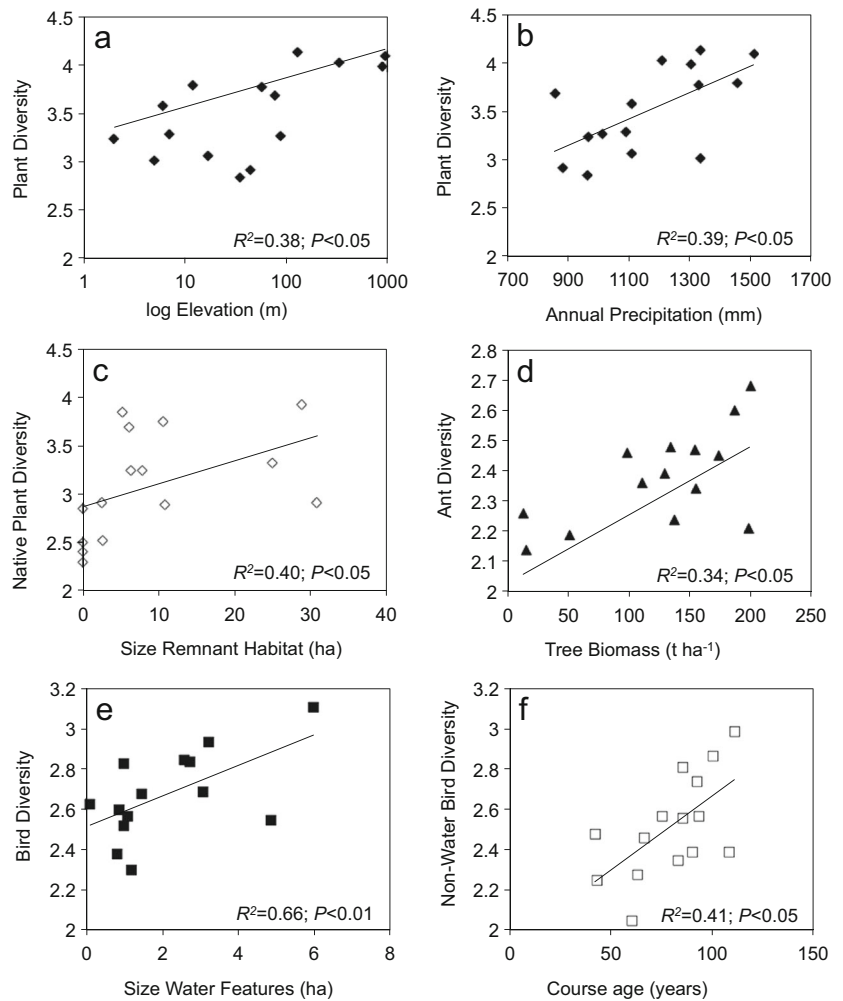
Table 1 Summary of final (minimal) multiple regression models for Shannon-Wiener diversity index (H) and associated environmental variables including the model coefficient (Estimate), standard error (SE), p -value, F- statistic (degrees of freedom) and R^2 -values

Taxon group	Environmental variable	Estimate	SE	P-value	F ^a	R^2 -values ^b
Plants			0.296	0.0061	7.17 (3,11)	0.57
	Intercept	1.492	0.519	0.0152		
	Precipitation	0.001	0.001	0.0250		0.39
	Elevation (log)	0.289	0.105	0.0185		0.38
Native plants	Size	0.007	0.005	0.1626		
			0.261	0.0002	16.34 (3,11)	0.77
	Intercept	0.977	0.397	0.0318		
	Precipitation	0.001	0.001	0.0066		0.48
Ants	Elevation (log)	0.332	0.091	0.0038		0.44
	Size of remnant habitat	0.019	0.007	0.0158		0.40
			0.129	0.0171	7.645 (1,13)	0.34
	Intercept	2.177	0.079	0.0001		
Birds	Tree biomass	0.002	0.001	0.0171		0.34
			0.141	0.0028	9.545 (3,10)	0.66
	Intercept	2.607	0.147	0.0001		
	Size water features	0.331	0.101	0.0080		0.66
Non-water birds	Elevation (log)	-0.097	0.056	0.1168		
	Connectivity	0.0027	0.001	0.0683		
			0.196	0.0176	5.764 (2,12)	0.41
	Intercept	1.818	0.214	0.0001		
	Course age	0.007	0.003	0.0153		0.41
	Connectivity	0.003	0.002	0.1343		

^a Numbers in parentheses show degrees of freedom

^b Adjusted R^2 -values shown for the final model, partial R^2 -values for associated environmental variables are shown in *italics*

Fig. 2 Relationships between Shannon-Wiener diversity index (H) and environmental factors for (a) Plant diversity and course elevation (log), (b) plant diversity and annual precipitation amount, (c) native plant diversity and area of remnant habitat, (d) ant diversity and tree biomass, (e) bird diversity and the area of water features and (f) diversity of non-water birds and course age. Only significant relationships are shown



± 0.49) (Fig. 3b) and birds (12 ± 0.82), the latter otherwise having very similar species richness between the remaining habitat types (Fig. 3d). Overall, significant differences were

found between habitat types for the species richness, for all plants, native plants, ants and birds, but not for exotic plant species (Table 2; Fig. 3). These differences were mainly

Fig. 3 Number of species, by habitat type, across 15 golf courses (a) Native plants, (b) ants, (c) exotic plants and (d) birds. Boxes show median and upper and lower quartile, whiskers extend to 10th and 90th percentile

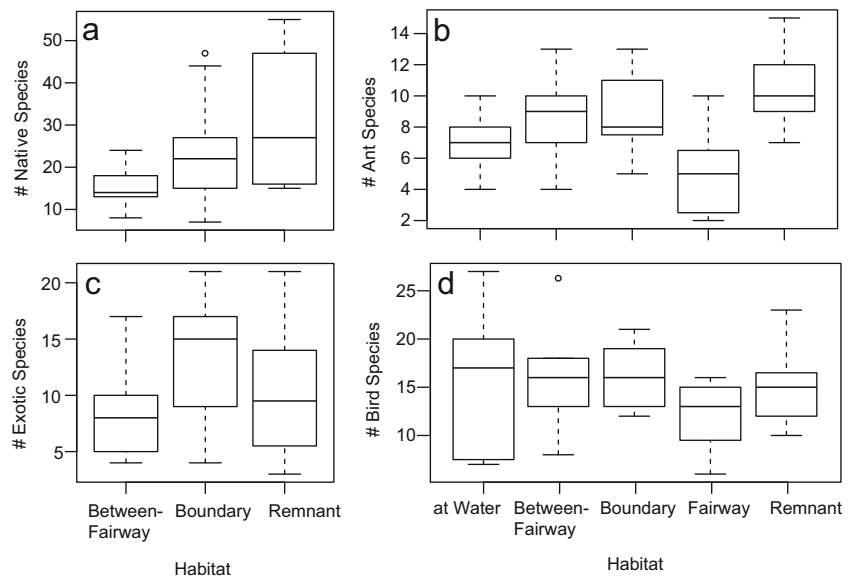


Table 2 Summary LMEs for species richness by habitat type including the model coefficient (Estimate), standard error (SE) and *p*-value

Taxon ^a	Habitat type	Estimate	SE	<i>P</i> -value
Plants	Intercept	2.135	0.094	0.0001
	Between-Fairway	−0.350	0.100	0.0004
	Boundary	0.350	0.099	0.0004
	Remnant	0.612	0.110	0.0001
Native plants	Intercept	1.667	0.119	0.0001
	Between-Fairway	−0.337	0.146	0.0207
	Boundary	0.337	0.146	0.0207
	Remnant	0.818	0.154	0.0001
Exotic plants	Intercept	3.217	0.600	0.0001
Ants	Intercept	2.417	0.213	0.0001
	Between-Fairway	0.533	0.275	0.0581
	Boundary	0.617	0.275	0.0294
	Fairway	−0.917	0.275	0.0016
Birds	Intercept	3.903	0.155	0.0585

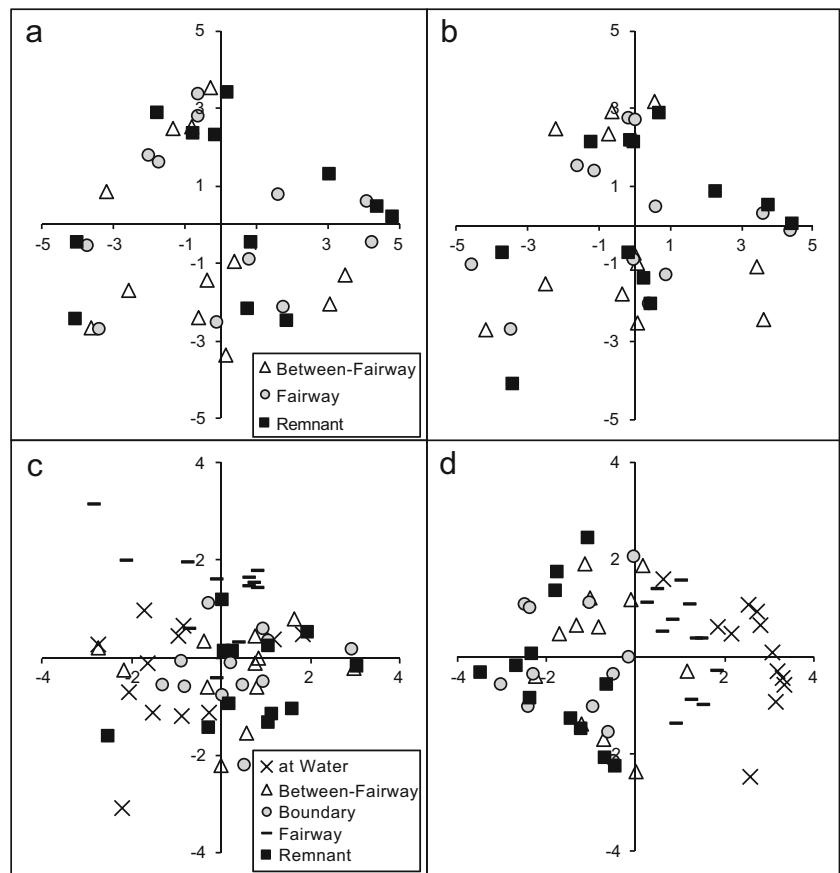
^a Plants & native plants: Number of observations (*n* = 168); Habitat:Course (*n* = 42); Course (*n* = 15). Birds & ants: Number of observations (*n* = 288); Habitat:Course (*n* = 72); Course (*n* = 15)

driven by significantly more plant species (all and native; *P* < 0.01) in remnant habitats and significantly less ant (*P* < 0.001) and bird (*P* < 0.05) species on fairways.

Comparisons between habitat types – community composition

Plant species composition varied by habitat type with remnant habitats having the highest proportion of native (compared to exotic) plant species (75%; average of 30.7 ± 4.4 species), followed by between-fairway (65%; 15.7 ± 1.2) and then boundary (61%; 22.5 ± 3.1) habitats. Species composition for the three surveyed taxa combined differed significantly between habitat types (Wald-*X*² = 18.09; *P* < 0.05; *df* 2,33) (Fig. 4a). Pairwise comparisons showed that the combined community composition in remnant habitats was distinctly different to that in between-fairway habitats (*P* < 0.01), and also when compared with boundary and between-fairway habitats (*P* < 0.05). On its own, plant community composition was not significantly different between habitats (Wald-*X*² = 13.64; *P* = 0.102; *df* 2,33), but pairwise comparisons showed that it did differ between remnant and between-fairway areas (*P* < 0.05), as well as between

Fig. 4 Unconstrained ordination based on latent variable models (LVMs) showing community composition by habitat type across 15 golf courses (a) All three taxa combined, (b) native plants, (c) ants and (d) birds



boundary and between-fairway habitats ($P < 0.05$). These differences were largely driven by a greater abundance of native species such as old man Banksia (*Banksia serrata*), coastal wattle (*Acacia longifolia* ssp. *sophorae*), spiny-head mat-rush (*Lomandra longifolia*) and sweet Pittosporum (*Pittosporum undulatum*) in remnant habitats, and by high abundances of tallowwood (*Eucalyptus microcorys*), Queensland Brush Box (*Lophostemon confertus*) and the non-native Kikuyu grass (*Pennisetum clandestinum*) in between-fairway habitats. The overall composition of native plant species was similarly unaffected by habitat type (Wald- $\chi^2 = 11.50$; $P = 0.164$; df 2,33) (Fig. 4b), although pairwise comparisons revealed significant differences between remnant and between-fairway habitats ($P < 0.01$), with the same species mentioned above driving observed pair-wise differences.

Unlike the plant community, ant community composition did differ significantly between habitat types (Wald- $\chi^2 = 9.833$; $P < 0.05$; df 4,55) (Fig. 4c). Pairwise comparisons showed that fairways harboured a distinctly different ant community ($P < 0.05$) compared to all other habitat types. Of particular note were higher abundances of *Nylanderia nana* and *Pheidole* spp., and lower abundances of *Rhytidoponera* spp. and *Iridomyrmex* spp. on fairways. Habitats around water features were significantly different to remnant habitats ($P < 0.001$) with differences mainly driven by the particularly high occurrence of *Iridomyrmex* nr. *septentrionalis* around water features and the occurrence of species from the genera *Anonychomyrma*, *Camponotus* and *Monomorium*, and *Crematogaster laeviceps* in remnant habitats.

The complement of bird species recorded during site surveys also differed between habitat types (Wald- $\chi^2 = 21.10$; $P < 0.001$; df 4,55) (Fig. 4d). Pairwise comparisons revealed that remnant habitats had a distinctly different bird assemblage compared to fairway and water features ($P < 0.001$), and also between-fairway areas ($P < 0.01$), but not compared to boundary habitats ($P = 0.962$). Differences were chiefly driven by greater numbers of noisy miners (*Manorina melanocephala*), Australian magpies (*Gymnorhina tibicen*) and red wattlebirds (*Anthochaera carunculata*) on fairways, and more Eurasian coots (*Fulica atra*) and little black cormorants (*Phalacrocorax sulcirostris*) at water features.

Species restricted to a single habitat type

Each habitat type added a suite of unique species to the total species count, most of which were singletons, occurring only once across all surveyed sites (for a complete list of these unique species, refer to Tables S3–S5). Of the five habitat types surveyed, remnant habitats harboured more unique species of native plants and ants than any other habitat type (Table 3). Water features had the most unique bird species ($n = 15$), and fairways the least ($n = 1$) at the site level.

Discussion

This study surveyed biodiversity on urban golf courses at two spatial scales, assessing the influence of habitat type within courses, and the role of environmental drivers between courses. Like many studies of its kind, the lack of repeat surveys over time may limit the generalisability of our findings. As hypothesised, we have clear evidence that floristic diversity was particularly associated with landscape-scale environmental variables including climate and elevation, whereas faunal diversity was more closely associated with local-scale variables such as the area of water features or overall biomass of trees. At the community level, the composition of all three taxa differed markedly between playing and non-playing (woody) areas, indicating that the presence of a heterogeneous mix of habitat types can enhance levels of biodiversity within the wider metropolitan landscape.

Environmental drivers of biodiversity differ between taxa

Environmental correlates of biodiversity differed for plants, birds and ants. Floristic and faunal diversity has been related to a wide range of environmental variables in previous studies with, for example, plant diversity positively related to precipitation and temperature, and negatively related to altitude (Gaston and Blackburn 2000). Similar trends have been reported for both ants (Dunn et al. 2009) and birds (Gaston and Blackburn 2000) in earlier studies.

The role of climate (in particular precipitation) and altitude as drivers of plant diversity is clear from our study, as evidenced by greater diversity on golf courses located in wetter locations and at higher elevations - principally in the area of the Blue Mountains to the west of the Sydney Basin. Although the average number of plant species in Blue Mountains golf courses (~220 spp. per hectare, see Table S2, supporting information) was lower than that in the surrounding native dry sclerophyll forests (360 spp. per hectare; Rice and Westoby 1983), these are particularly high values for on-course species richness compared to similar studies (e.g. Yasuda and Koike 2006). Other courses in the Sydney suburban area that had similar values for plant species richness and diversity to sites in the Blue Mountains were also located adjacent to large areas of native woodland, suggesting that the nature of the surrounding landscape plays an important role in course-level biodiversity. Indeed, golf courses can be considered important at the landscape-scale by providing connections between isolated areas of native habitats, and by adding structural diversity - such as water features and open spaces - to otherwise woodland-dominated areas (Hodgkison et al. 2007b; Gange et al. 2003). The importance of landscape-scale connectivity of remnant native habitats and corridors for species movement has previously been shown for semi-

Table 3 Unique species occurring within a single habitat type

Taxon	Remnant # (%)	Boundary # (%)	Between- fairway # (%)	Water feature # (%)	Fairway # (%)
All plants ^a	68 (16)	90 (21)	61 (23)	–	–
Native plants ^a	51 (19)	34 (13)	33 (12)	–	–
Exotic plants ^a	17 (10)	56 (33)	30 (18)	–	–
Ants	12 (17)	7 (10)	3 (4)	2 (3)	3 (4)
Birds	10 (10)	10 (9)	1 (1)	15 (16)	1 (1)

^a Plants were surveyed in woody habitats only; # shows number of species, percentage shown in parentheses

natural grasslands (Lindborg and Eriksson 2004), longleaf pine savannahs (Brudvig et al. 2009) and also for urban green spaces (Kong et al. 2010).

Local-scale features correlate with faunal diversity

Our study revealed a positive relationship between ant diversity and site-level tree biomass, which is in line with findings elsewhere of the greatest abundance and diversity of ants being associated with wooded, rather than other habitat types, such as heath (Andersen 1986). However, this contrasts with the lower ant diversity reported for more complex habitats in urban green spaces in the Melbourne area (Ossola et al. 2015) and in Sydney sandstone ridge-top woodlands (Lassau and Hochuli 2004). Differences in findings between these geographically close studies are likely associated with the contrasting settings of these studies (native habitat in Lassau and Hochuli (2004) versus metropolitan landscape in our study).

Birds featured prominently on the courses surveyed. We found higher bird diversity on courses with a greater area of water features, reflecting the dominance of water birds (e.g. cormorant, Australasian grebe, white-faced heron, and many ducks such as chestnut teal and hardhead) in our study – species that are attracted to well-maintained water features within courses. The importance of the size of suitable habitat patches for both species richness and abundance is well known for many taxa (e.g. MacArthur and Wilson 1967; Collinge 1996), including birds. Other studies investigating bird fauna on golf courses have also found species richness to be positively associated with the area of native on-course vegetation (Hodgkison et al. 2007b) and forest habitat (Sorace and Visentin 2007), indicating that structural heterogeneity within sites may be particularly important for birds.

We did not find a significant relationship between the area of remnant vegetation and bird species richness, although the diversity of non-water birds was higher on older courses. Again, this relationship may be due to the fact that the oldest courses - with the highest bird diversity - are located in the Blue Mountains area, where the surrounding area has large tracts of continuous native woodland. Some of the woodland specialists were also associated with older courses, for

example the brown tree creeper (*Climacteris picumnus*), the white-winged triller (*Lalage tricolor*) and the lyrebird (*Menura novaehollandiae*), supporting the notion that older habitats are particularly valuable for more specialist species (Southwood et al. 1983), which are generally less frequent in a community (Gaston 1996). A similar pattern of higher faunal diversity on older golf courses has also been identified in the Greater Helsinki area in Finland (Saarikivi et al. 2010).

Remnant habitats add biodiversity value

Species richness and community composition were compared between different habitat types, which represent different management intensities in terms of mowing frequency, clearing of dead plant matter and supplementary inputs of water or agrochemicals. We found that remnant habitats consistently harboured more species than other habitat types (Fig. 3), a large proportion of which were unique at the site level. Furthermore, up to 90% of the recorded plant species in these habitats were native, the diversity of which was positively associated with the size of remnant patches, thus highlighting the importance of good-sized native remnants for preserving local flora. Similarly, in Japan, plant species composition in non-playing forest areas within golf courses was found to differ distinctly from between-fairway habitats, the former more closely resembling communities of native remnant forests (Yasuda and Koike 2006). All wooded habitats were associated with significantly higher numbers of bird species compared to fairways, suggesting that the former play an important role in supporting landscape-scale bird diversity, perhaps by providing refuges for species that are displaced as surrounding areas become increasingly urbanised (Sorace and Visentin 2007; Hodgkison et al. 2007a, b).

Golf courses can offer a great variety of habitats for ants, which are valuable ecosystem engineers as they scavenge for dead insects, predate on potential insect pests, pollinate plants and aerate the soil. Overall, significantly fewer ant species were found on fairway habitats compared to the more structurally complex wooded habitat types that are known to provide suitable habitat for foraging and nesting (Andersen 1986).

Community composition markedly different between playing and non-playing areas

The overall community composition for all three taxa differed between playing and non-playing areas (Fig. 4). For example, between-fairway habitats had simplified plant communities compared to boundary and remnant habitats; this trend was most likely driven by the more frequent occurrence of native shrubby understorey plants, including members of the *Banksia*, *Acacia* and *Leptospermum* genera in the latter habitats. Similar differences in plant species composition between habitats have been found on golf courses in Japan, with non-playing forest areas within courses more closely resembling communities of native remnant forests than, for example, between-fairway habitat (Yasuda and Koike 2006). The presence of multi-layered, remnant native vegetation has been found to be beneficial for local floral and faunal biodiversity in other urban studies (McKinnley 2002; Garden et al. 2007).

Between-habitat differences in bird community composition were driven by the occurrence of habitat specialists, particularly woodland birds in remnant and boundary habitats and wetland birds around water features. Similar distinctions between woodland versus wetland bird communities have also been reported for golf courses in suburban areas in southern Queensland (Hodgkison et al. 2007a). Of note here is that we frequently found that fairways were predominantly associated with typical grassland birds, including the masked lapwing (*Vanellus miles*) and the crested pigeon (*Ocyphaps lophotes*), as well as urban-adapted habitat generalists, such as the welcome swallow (*Hirundo neoxena*), magpie lark (*Grallina cyanoleuca*) and the noisy miner (*Manorina melanoccephala*). There were fewer bird species recorded on fairways than in other on-course habitats despite the more open nature of fairways making it easier to record a sighting. The noisy miners, in particular, drive other birds away and are particularly associated with eucalypt trees with little understorey i.e. fairway and between-fairway areas (Maron et al. 2013).

The unique ant composition in fairway habitats was largely driven by small yellow or brown ants of the genus *Pheidole*, which nest and live in the soil. This type of nesting behaviour can enhance topsoil condition and nutrient cycling by creating tunnels, mixing plant and animal litter and reducing soil compaction (Lopez and Potter 2003). Underground foraging behaviour can also provide great on-course benefits by removal of dead insects and predation on potential pest species (Lopez and Potter 2003). Urban generalist species, such as *Iridomyrmex* meat ants were the most abundant group of ants collected in this study. These ants are the most frequently encountered group in Australia, and can occur in such large numbers that they often outcompete other ants in the area (Andersen 1995). The second most common group of ants recorded was the green-headed ants (genus *Rhytidoponera*). These large green metallic ants are common in urban parks

and gardens; they prefer open habitats and are usually seen on the ground or on low vegetation (Shattuck 1999). This opportunistic genus is associated with disturbed habitats (Yates and Andrew 2011) and has also been reported to be abundant in urban woodland remnants and parks in southeast Melbourne (Ossola et al. 2015).

Conclusions

The key relationships between species diversity and environmental variables differed between taxonomic groups; plant diversity was closely associated with landscape-scale factors (precipitation), whereas ants and birds were more closely related to local (site-level) factors, notably tree biomass (ants) and the size of water features (birds). Overall, our results indicate that large areas of open, park-like fairways, water features and patches of remnant woodland on golf courses provide a habitat matrix that can support a wide range of plant and animal species. On-course remnant habitats in particular harboured a greater diversity of the less mobile species (i.e. plants and ants), highlighting their role as refugia for local flora and fauna and thus representing mini hot spots of diversity in an otherwise species-poor urban landscape. Our results suggest that the floristic and faunal diversity of urban golf courses can be enhanced by management practices aimed at increasing the extent of woody non-playing areas, especially by preserving and/or enhancing remnant native habitats.

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