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Habitat associations of the Southern Squatter Pigeon *Geophaps scripta scripta* in Queensland

Penn Lloyd[1]*, Elizabeth R. Williams[1], Chris Hansen[2], John M. van Osta[3], Lindsay Agnew[4], Mark Sanders[5], Edward A. Meyer[5], Steve Marston[6], Simon Danielsen[7] and Brad Dreis[3]

[1]Biodiversity Assessment and Management Pty Ltd, P.O. Box 1376, Cleveland QLD 4163, Australia
[2]Hansen Botanical Assessments Pty Ltd, P.O. Box 63, Coolum Beach QLD 4573, Australia
[3]E2M Pty Ltd, P.O. Box 1444, Milton QLD 4064, Australia
[4]Austecology, 5 Davina Street, Tarragindi QLD 4121, Australia
[5]EcoSmart Ecology, 48 Streeton Parade, Everton Park QLD 4053, Australia
[6]Eco Solutions and Management, P.O. Box 5385, Brendale QLD 4500, Australia
[7]Astrebla Ecological Services, P.O. Box 3110, Darra QLD 4076, Australia
*Corresponding author. Email: penn@baamecology.com

Abstract. The characteristics of habitats preferred by the southern subspecies of Squatter Pigeon *Geophaps scripta scripta* remain poorly understood. We intersected high-precision records of Southern Squatter Pigeon occurrences and nests with various environmental spatial datasets and measured ground vegetation cover in a subset of vegetation communities associated with records to characterise the habitat associations of this subspecies across its range in Queensland. Southern Squatter Pigeons showed a preference for alluvial plain landforms but also used a range of other landform types. Similarly, most nest records were on alluvial plains. Southern Squatter Pigeons were associated with gentle slopes averaging 0.64–2.36° in all land zones, with 95% of records on slopes <3.3°. They were mostly recorded in eucalypt woodlands, particularly those dominated by Reid River Box *Eucalyptus brownii* or Poplar Box *E. populnea*, Narrow-leaved Red Ironbark *E. crebra* or Queensland Grey Ironbark *E. drepanophylla,* Silver-leaved Ironbark *E. melanophloia,* and River Red Gum *E. camaldulensis* or Forest Red Gum *E. tereticornis.* The records were located an average distance of 496 ± 554 m from the nearest perennial water source and 95% were within 1.7 km of a perennial water source. Nests were located 245 ± 214 m from a perennial water source. Average ground vegetation cover in remnant or high-value regrowth communities inhabited by Southern Squatter Pigeons ranged between 24% and 73%.

Introduction

When assessing the environmental impacts of development proposals on threatened species and their habitats, ecological assessments under Australia's *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) must consider species-specific information contained within the conservation advice, listing advice, recovery plans and/or the Species Profile and Threats (SPRAT) Database that is maintained by the Australian Government's Department of Climate Change, Energy, the Environment and Water (DCCEEW). This information is used to characterise the habitat requirements of the relevant threatened species as well as the extent of the species' habitat that is predicted to be impacted by the development proposal. Habitat that meets the habitat requirement description may be identified as habitat supporting the species, whereas habitat that does not meet the habitat requirement description may be identified as unlikely to support the species. If habitat impacted by a development is assessed as not supporting a threatened species, a development proposal is unlikely to have a significant impact on the species' habitat and no offset is required to compensate for any significant residual impact (Department of Sustainability, Environment, Water, Population and Communities 2012). Thus, the accuracy of the information contained in the conservation advice, listing advice, recovery plan and/or the species profile and threats database has implications for the identification and conservation of threatened species' habitat.

The southern subspecies of the Squatter Pigeon *Geophaps scripta scripta* (herein Southern Squatter Pigeon) is listed under the EPBC Act as vulnerable to extinction (Threatened Species Scientific Committee 2015). Threats include habitat loss, fragmentation and degradation (particularly by intensive grazing) and predation by feral Cats *Felis catus* and Red Foxes *Vulpes vulpes* (Threatened Species Scientific Committee 2015; Ward *et al.* 2021), as well as being sensitive to extreme droughts (Woinarski & Catterall 2004) and climate change (Garnett & Franklin 2014). The species profile and threats database characterises habitat for the subspecies as open forests to sparse open woodlands and scrub that are (1) mostly dominated in the overstorey by *Eucalyptus, Corymbia, Acacia* or *Callitris* species; (2) remnant, regrowth or partly modified vegetation communities; and (3) within 3 km of waterbodies or watercourses because of the species' dependence on water for daily drinking (DCCEEW 2025). In its administration of the EPBC Act, DCCEEW distinguished between foraging, breeding and dispersal habitats. Breeding habitat for Southern Squatter Pigeon is specifically defined as stony rises occurring on sandy or gravelly soils, within 1 km of a suitable, permanent waterbody (DCCEEW 2025). Yet the ecological requirements of breeding habitat were identified as a significant knowledge gap by a panel of experts (Squatter Pigeon Workshop 2011), based on a paucity of data on nest records for both subspecies (Higgins & Davies 1996). The definition of foraging and breeding habitat is further clarified as occurring on well-draining, sandy or loamy soils on low, gently sloping, flat to undulating plains and foothills (i.e. Queensland Land zone 5: Wilson & Taylor 2012), and lateritic soils on low jump-ups and escarpments (i.e. Land zone 7: DCCEEW 2025).

DCCEEW (2025) asserted that waterbodies that are suitable for the subspecies occur on the lower, gentle slopes and plateaus of sandstone ranges (equivalent to Land zone 10), alluvial clay soils on river or creek flats (represented by Land zone 3) or non-alluvial clay soils on flats or plains that are not associated with current alluvial deposits (represented by Land zone 4). Hence, where natural foraging or breeding habitat occurs (i.e. on Land zones 5 and 7), the Southern Squatter Pigeon may be found in vegetation types growing on Land zones 3, 4 and 10 (DCCEEW 2025). These habitat definitions reflect that the Northern Squatter Pigeon *G. s. peninsulae* is described as preferring areas of sandy soil dissected by low gravelly ridges that have the most open and shortest cover of grasses, being less common on heavier soils with dense growth of grasses (Higgins & Davies 1996).

In this paper, we intersect a large dataset of high-precision records of Southern Squatter Pigeon occurrences and nests encountered during field surveys with a variety of environmental variables to provide a rigorous, records-based assessment of the foraging and nesting habitat associations of the Southern Squatter Pigeon across its range in Queensland.

Methods

We first prepared a dataset of high-precision records of Southern Squatter Pigeon that had been recorded using hand-held GPS devices within 30 m of bird observations. The records (n = 584) were derived from our field surveys over the period 2001–2024. These surveys typically involved searching for Southern Squatter Pigeons as part of general fauna surveys while we traversed a study area by vehicle or on foot, as well as incidental observations of the subspecies during general survey activities. Although these records were obtained from >100 study areas across the range of the Southern Squatter Pigeon, they reflect opportunistic records since the selection of study areas was not specifically designed to assess the habitat associations of the subspecies. The locations of nests (n = 11) were similarly recorded to precision of 10 m with hand-held GPS devices, and photographs were taken of both the nest contents and surrounding habitat. Nests were opportunistically encountered when flushing adults directly off the nest at close range while undertaking general survey activities on foot. Additional occurrence records (n = 318) with a precision of ≤100 m were sourced from Atlas of Living Australia, a database of similarly opportunistic records from throughout the range of the subspecies. These records were then intersected using QGIS (v3.42.0, QGIS.org 2025) with the following spatial datasets to determine habitat associations: (1) Regional Ecosystem (RE) and condition (remnant, high-value regrowth or non-remnant) (State of Queensland 2025a) to identify the vegetation community type and land zone; (2) pre-clearing RE mapping (State of Queensland 2025b) to identify land zone for non-remnant REs; (3) bioregions of Queensland (State of Queensland 2010); and (4) smoothed 3-second digital elevation model (State of Queensland 2013) to calculate slope using the Raster Terrain Analysis (Slope processing tool in QGIS).

In our analysis, remnant vegetation is defined as vegetation where the predominant tree canopy covers >50% of the undisturbed canopy, averages >70% of the vegetation's undisturbed height and is composed of species characteristic of the vegetation's undisturbed canopy (State of Queensland 2024). High-value regrowth is vegetation in an area that has not been cleared for at least 15 years (State of Queensland 2024), whereas non-remnant vegetation is typically vegetation that has been cleared within the past 15 years. Non-remnant vegetation includes all types of vegetation that may be present in areas cleared within the past 15 years, including regrowth of trees. Records in non-remnant vegetation were individually checked against historical aerial imagery to confirm the vegetation status at the time of the record in case vegetation clearing had occurred since then. In Queensland, vegetation communities are characterised as REs based on (1) bioregion; (2) land zone, a combination of landform, geology and soil type; and (3) composition of plant species (Neldner *et al*. 2022). The structural class (tussock grassland, open woodland, woodland, open forest) and dominant tree species for each RE were characterised using Queensland Herbarium (2024).

The distance from each record to the nearest waterpoint was determined manually for each record using aerial imagery (Queensland Globe: State of Queensland 2025c) to identify the closest likely perennial water source, which included livestock watering points (Figure 1), farm dams and rivers of Stream order 4 or greater. For records in non-remnant vegetation, distance from each record to the nearest scattered trees (consistent with a woodland to open woodland structure) was similarly measured manually using aerial imagery.

To test whether the association of Southern Squatter Pigeon records with distance from permanent water and slope differed from that expected from a random distribution, we quantified these two variables at 100 random points within the range of the subspecies (c.f. Manly *et al*. 2002). The coordinates for these random points were generated in QGIS by first buffering all the Southern Squatter Pigeon records in our dataset to a 10-km radius. The areas within these buffer polygons were then merged into a single layer, removing any overlapping areas. We assumed this layer to represent the approximate area encompassing

Figure 1. Southern Squatter Pigeons and a Crested Pigeon *Ocyphaps lophotes* drinking at a livestock watering trough. Photo: Penn Lloyd

all Southern Squatter Pigeon records in our dataset. The QGIS Random points in polygon tool was then used to generate 100 points within this merged polygon, with a minimum distance between points set to 1 km. We used a Welch's two-sample *t*-test on log-transformed data to test whether mean distance to water and mean slope differed between Southern Squatter Pigeon occurrences and random points.

To estimate groundcover in Southern Squatter Pigeon habitats, we sourced groundcover data from BioCondition plots that had been established in the same vegetation community types in which the Pigeons were recorded. Groundcover was not measured at precise Southern Squatter Pigeon locations; rather, it was measured in a stratified random manner in the same habitat types where Southern Squatter Pigeons were recorded at the same study site. The sites for BioCondition plots were selected to be representative of the extent of RE being assessed, with sites located at least 1 km apart (after Eyre *et al*. 2015). However, at three nest sites, groundcover was recorded adjacent to the nest site using either ten 1x1 m quadrats spaced at 5-m intervals along a 50-m tape (n = 2 nests) or a standard BioCondition plot (n = 1 nest). BioCondition plots were established using a 100-m tape, with groundcover measured in each of five 1 x 1 m quadrats on alternating sides of the tape at 10-m intervals between the 25-m and 75-m marks of the tape (after Eyre *et al*. 2015). In each 1 x 1-m groundcover plot, the projective foliage cover of the following categories was recorded (total cover 100%): native and non-native grass, native and non-native forbs and shrubs (<1 m height), litter, rock and bare ground. We summed the cover measures of all grass, forbs and shrubs as a single measure of ground vegetation cover.

Results

A total of 902 high-precision records of Southern Squatter Pigeon were used in the analysis, including 584 collected by us and 318 sourced from the Atlas of Living Australia, excluding duplicate records. These records covered a substantial portion of the range of this subspecies in Queensland (Figure 2). Of these records, 55% were in remnant vegetation communities, 6% in high-value regrowth and 39% in non-remnant vegetation (i.e. historically cleared areas with substantially reduced tree cover). For context, remnant vegetation comprised 60% of the total area of 7.2 million hectares within a 10-km buffer of all records, whereas high-value regrowth comprised 3% and non-remnant comprised 37%. Most records in remnant and high-value regrowth vegetation were in woodland (88% of records), with smaller percentages of records in open woodland (5%), open forest to woodland (5%) and tussock grassland (2%). Excluding records in tussock grassland, 93% of records were in communities dominated by at least one eucalypt (*Eucalyptus, Corymbia, Angophora*) tree species, whereas 4% were in communities dominated by *Melaleuca* species and 3% in communities dominated by *Acacia* species. Southern Squatter Pigeon records were disproportionately associated with communities dominated by Reid River Box *Eucalyptus brownii* or Poplar Box *E. populnea*, Narrow-leaved Red Ironbark *E. crebra* or Queensland Grey Ironbark *E. drepanophylla,* Silver-leaved Ironbark *E. melanophloia,* and River Red Gum *E. camaldulensis* or Forest Red Gum *E. tereticornis* (Table 1).

Southern Squatter Pigeons in non-remnant areas were an average of 67 ± 135 m (range 0–1290 m; n = 356) from the closest area of scattered trees consistent with an open

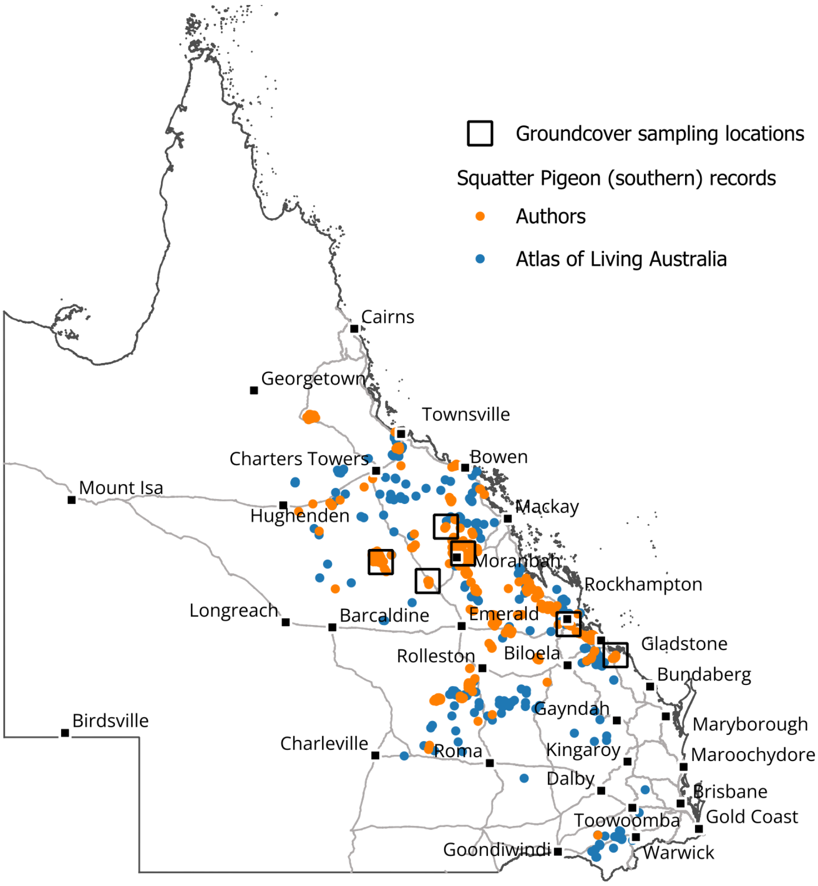

Figure 2. Map of Southern Squatter Pigeon records (distinguishing between our records and Atlas of Living Australia records) and ground vegetation cover sampling sites across Queensland.

Table 1. Association of Southern Squatter Pigeon records with tree species listed as the dominant or codominant species in wooded remnant and high-value regrowth vegetation communities: percentage and number (*n*) of records. Closely related tree species that replace one another biogeographically have been paired.

Dominant tree species		*Percentage of records*	*n*
Reid River Box/Poplar Box	*Eucalyptus brownii/E. populnea*	21.4	110
Narrow-leaved Red Ironbark/ Queensland Grey Ironbark	*Eucalyptus crebra/E. drepanophylla*	21.2	109
Silver-leaved Ironbark	*Eucalyptus melanophloia*	14.0	72
River Red Gum/Forest Red Gum	*Eucalyptus camaldulensis/E. tereticornis*	12.0	62
Gum-topped Box	*Eucalyptus moluccana*	4.9	25
Poplar Gum	*Eucalyptus platyphylla*	4.1	21
Dallachy's Ghost Gum	*Corymbia dallachiana*	3.9	20
Broad-leaved Paperbark	*Melaleuca viridiflora*	3.7	19
Spotted Gum	*Corymbia citriodora*	3.3	17
Long-fruited Bloodwood	*Corymbia clarksoniana*	3.3	17
Normanton Box	*Eucalyptus persistens*	3.3	17
Coolabah	*Eucalyptus coolabah*	2.9	15
White Cypress Pine	*Callitris glaucophylla*	1.9	10
Rusty Gum	*Angophora leiocarpa*	1.7	9
Moreton Bay Ash	*Corymbia tessellaris*	1.7	9
Brigalow	*Acacia harpophylla*	1.4	7
Bendee	*Acacia catenulata*	1.4	7
Lancewood	*Acacia shirleyi*	1.4	7
Mountain Coolibah	*Eucalyptus orgadophila*	1.4	7
Dawson Gum	*Eucalyptus cambageana*	1.2	6
Belah	*Casuarina cristata*	0.8	4
Pink Bloodwood	*Corymbia intermedia*	0.8	4
Broad-leaved Ironbark	*Eucalyptus fibrosa*	0.8	4
White's Ironbark	*Eucalyptus whitei*	0.8	4
Black Tea-tree	*Melaleuca bracteata*	0.8	4
Gidgee	*Acacia cambagei*	0.6	3
Desert Bloodwood	*Corymbia brachycarpa*	0.6	3
Rustyjacket	*Corymbia leichhardtii*	0.6	3
White Box	*Eucalyptus albens*	0.6	3
Sydney Blue Gum	*Eucalyptus saligna*	0.6	3
Gum-topped Ironbark	*Eucalyptus decorticans*	0.4	2
Inland Grey Box	*Eucalyptus woollsiana*	0.4	2
Swamp Box	*Lophostemon suaveolens*	0.4	2
Black Gidyea	*Acacia argyrodendron*	0.2	1
Rough-leaved Bloodwood	*Corymbia setosa*	0.2	1
Paperbark Gum	*Eucalyptus chartaboma*	0.2	1
Queensland Peppermint	*Eucalyptus exserta*	0.2	1
Grey Box	*Eucalyptus microcarpa*	0.2	1
Mugga Ironbark	*Eucalyptus sideroxylon*	0.2	1
Queensland Yellowjacket	*Eucalyptus similis*	0.2	1
Blackdown Stringybark	*Eucalyptus sphaerocarpa*	0.2	1

woodland to woodland structure, and 95% of records in non-remnant areas were within 300 m of scattered trees or woodland (Figure 3a). The average distance between records and the nearest perennial water source was 496 ± 554 m (range 0–3830 m), and 95% of records were within 1.7 km of a perennial water source (Figure 3b). The average distance to water was variable across different land zones (Table 2). The average distance to water at random points was 1584 ± 1460 m (range 0–8200 m). Southern Squatter Pigeon records were significantly closer to the nearest perennial water source (t = 9,35, P <0.001) than were random points within range of the subspecies (Figure 3c).

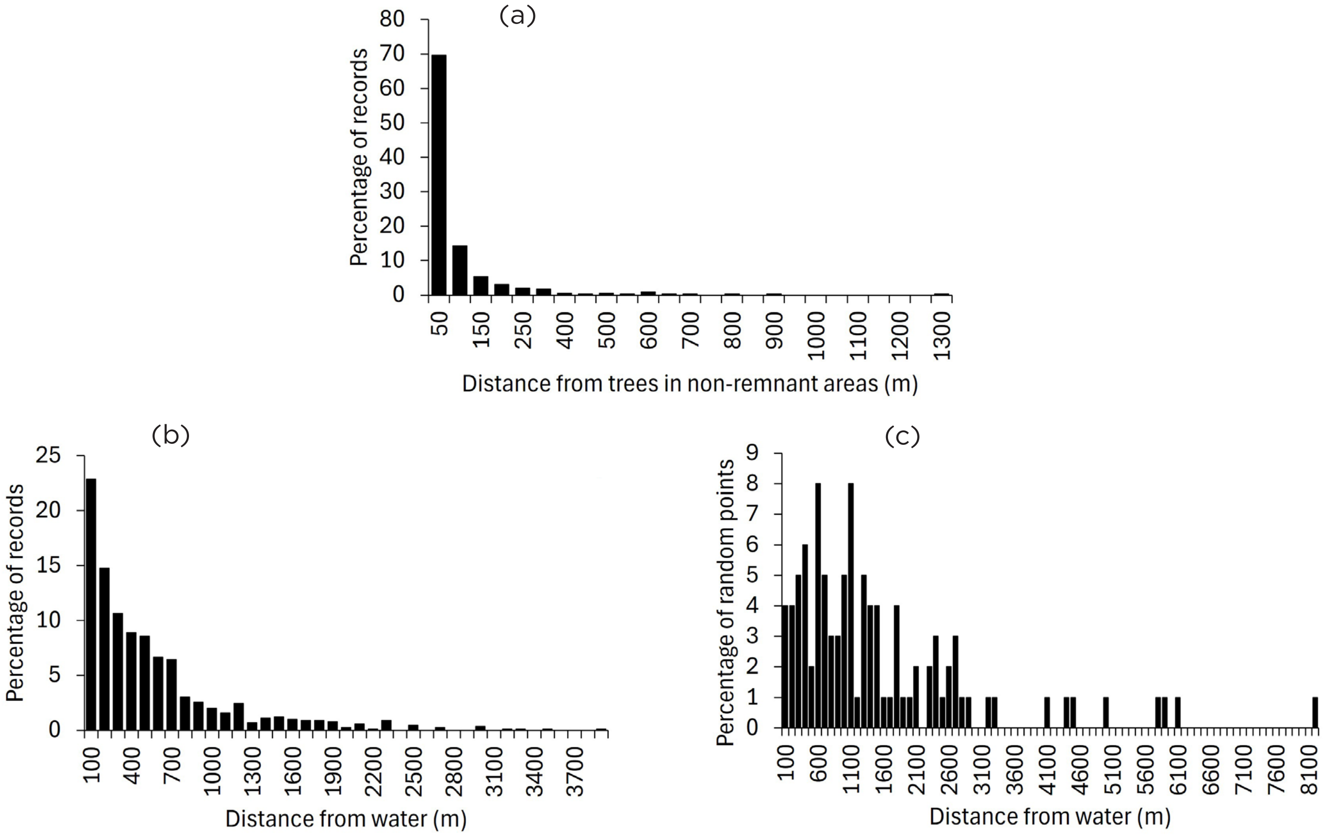

Figure 3. Frequency distribution of (a) distance between Southern Squatter Pigeon records in non-remnant vegetation (n = 385) and the closest scattered trees or woodland, (b) distance of all records (n = 902) from the closest perennial water source; and (c) distance of random points (n = 100), within the range of Southern Squatter Pigeon, from the closest perennial water source.

The Southern Squatter Pigeon was generally recorded in all relevant land zones in each bioregion within its Queensland range (Table 3). However, in all bioregions, the percentage of records on alluvial plains (Land zone 3) substantially exceeded the percentage of the area of the bioregion made up by alluvial plains (Table 3). The association with alluvial plains was particularly strong in the Brigalow Belt and Desert Uplands bioregions that form the core of the subspecies' range in Queensland. For example, in the Desert Uplands, 56% of records were on alluvial plains despite this land zone covering only 21% of the Desert Uplands. Nonetheless, in bioregions with a low proportion of alluvial plains, most records were associated with the land zones that dominate the bioregion. For example, in the Einasleigh Uplands, Southeast Queensland, and Central Queensland Coast bioregions, most records were on Land zone 12 (hills and lowlands on granitic rocks), which dominates these bioregions. Similarly, in the New England Tableland, most records were on Land zone 11 (hills and lowlands on metamorphic rocks) that dominates the bioregion (Table 3). Southern Squatter Pigeon records were associated with gentle slopes across all land zones, with the average slopes ranging from 0.64 to 2.36° (Table 2). The average slope across all

Table 2. Average distance to the nearest perennial water source and average slope (± 1 standard deviation) at Southern Squatter Pigeon record locations across different land zones (LZ), n = sample size of records.

LZ	*Land zone description*	*Distance to water (m)*	*Slope (degrees)*	*n*
3	Alluvial plains	374 ± 392	0.93 ± 0.97	404
4	Clay plains	454 ± 395	0.64 ± 0.91	51
5	Old loamy and sandy plains	692 ± 712	0.82 ± 0.59	130
7	Ironstone jump-ups	455 ± 434	1.27 ± 0.75	23
8	Basalt plains and hills	860 ± 850	1.63 ± 1.56	21
9	Undulating country on fine grained sedimentary rocks	624 ± 675	1.32 ± 1.05	42
10	Sandstone ranges	959 ± 845	2.36 ± 1.45	68
11	Hills and lowlands on metamorphic rocks	325 ± 339	1.81 ± 1.12	106
12	Hills and lowlands on granitic rocks	531 ± 466	1.90 ± 1.90	55
Overall		**496 ± 554**	**1.21 ± 1.19**	**900**

Table 3. Percentage of Southern Squatter Pigeon records in different land zones across different bioregions in Queensland, with percentage of the land area of the bioregion comprising each land zone in brackets. *n* = sample size of records; n/a = not applicable, land zone not present. One record in Land zone 2 and one record in each of the Mitchell Grass Downs and Mulga Lands bioregions were excluded because of small sample sizes. See Table 2 for descriptions of land zones.

Bioregion	*Land zone*										*n*
	3	*4*	*5*	*7*	*8*	*9*	*9–10*	*10*	*11*	*12*	
Brigalow Belt	46.0 (23.6)	7.2 (12.4)	12.4 (12.0)	1.4 (5.3)	1.8 (5.1)	5.8 (14.7)	0 (0.1)	9.5 (11.3)	12.0 (7.6)	3.8 (8.0)	708
Desert Uplands	56.1 (20.6)	1.9 (7.6)	32.7 (55.9)	9.3 (11.1)	0 (0.2)	0 (0.2)	n/a	0 (3.7)	0 (0.8)	0 (0.1)	107
Einasleigh Uplands	12.1 (7.5)	0 (<0.1)	9.1 (8.4)	9.1 (2.2)	21.2 (16.5)	0 (0.1)	n/a	3.0 (1.1)	6.1 (29.0)	39.4 (35.1)	33
Southeast Queensland & Central Queensland Coast	31.3 (17.6)	n/a	9.4 (9.4)	0 (<0.1)	3.1 (7.0)	0 (0.1)	3.1 (13.9)	n/a	6.3 (19.0)	46.9 (33.0)	32
New England Tableland	15.8 (6.8)	n/a	n/a	0 (0.1)	n/a	0 (0.6)	n/a	n/a	84.2 (71.7)	0 (20.9)	19
Overall	**44.8 (19.4)**	**5.9 (8.0)**	**14.3 (15.8)**	**2.6 (4.7)**	**2.3 (6.8)**	**4.6 (8.6)**	**0.1 (1.6)**	**7.6 (7.1)**	**11.7 (12.9)**	**6.1 (15.1)**	**899**

Table 4. Average ± 1 standard error (sample size of sites in brackets) percentage projective foliage groundcover in the late wet season (February–April) or late dry season (October–November) in different Regional Ecosystems (REs) inhabited by Southern Squatter Pigeons, including a separate sample (bottom four rows) comparing cover measured at the same sites in both the late wet and late dry seasons. All communities were in remnant condition unless specified as regrowth (high-value regrowth) or non-remnant. See Table 1 for common names of trees.

RE	*Vegetation community description*	*Vegetation cover (%)*
10.3.14a	*Eucalyptus coolabah* woodland to open forest on sandy to clayey floodplain alluvium	24 ± 9 (4) wet
10.7.4	*Eucalyptus persistens* low woodland on laterite	25 ± 11 (9) wet
11.3.2	*Eucalyptus populnea* woodland on alluvial plains	28 ± 17 (3) wet
10.3.13a	*Eucalyptus camaldulensis* woodland to open forest on sandy alluvium fringing major watercourses	43 ± 16 (12) wet
10.5.4	*Eucalyptus drepanophylla* woodland on sand plains	43 ± 6 (4) wet
11.11.1 regrowth	*Eucalyptus crebra* woodland on subcoastal hills formed on moderately to strongly deformed and metamorphosed sediments and interbedded volcanics	44 (1) dry
12.12.28	*Eucalyptus moluccana* woodland on broad ridges and lower slopes on igneous rocks	44 (1) wet
10.3.12a	*Corymbia plena*–*Corymbia dallachiana* woodland on sandy alluvium	45 ± 21 (12) wet
10.5.5a	*Eucalyptus melanophloia* woodland on plains	51 ± 14 (36) wet
10.3.6	*Eucalyptus brownii* woodland on alluvial floodplains	54 ± 15 (13) wet
10.3.9	*Eucalyptus whitei* woodland on sandy alluvial fans	56 ± 7 (6) wet
12.12.5	*Corymbia citriodora*–*Eucalyptus crebra* woodland on hills and ranges on igneous rocks	60 (1) wet
11.11.15	*Eucalyptus crebra* woodland on metamorphosed sediments and interbedded volcanics on low hills	61 ± 33 (5) wet
12.12.12 regrowth	*Eucalyptus tereticornis*–*Corymbia intermedia*–*E. crebra* woodland on igneous rocks on lower slopes, especially granite lowlands and basins	73 (1) wet
None	Non-remnant	87 ± 0 (2) wet
10.3.6	*Eucalyptus brownii* woodland on alluvial floodplains	58 ± 22 (6) wet
10.3.6	*Eucalyptus brownii* woodland on alluvial floodplains	46 ± 29 (6) dry
10.5.5a	*Eucalyptus melanophloia* woodland on plains	54 ± 16 (22) wet
10.5.5a	*Eucalyptus melanophloia* woodland on plains	39 ± 16 (22) dry

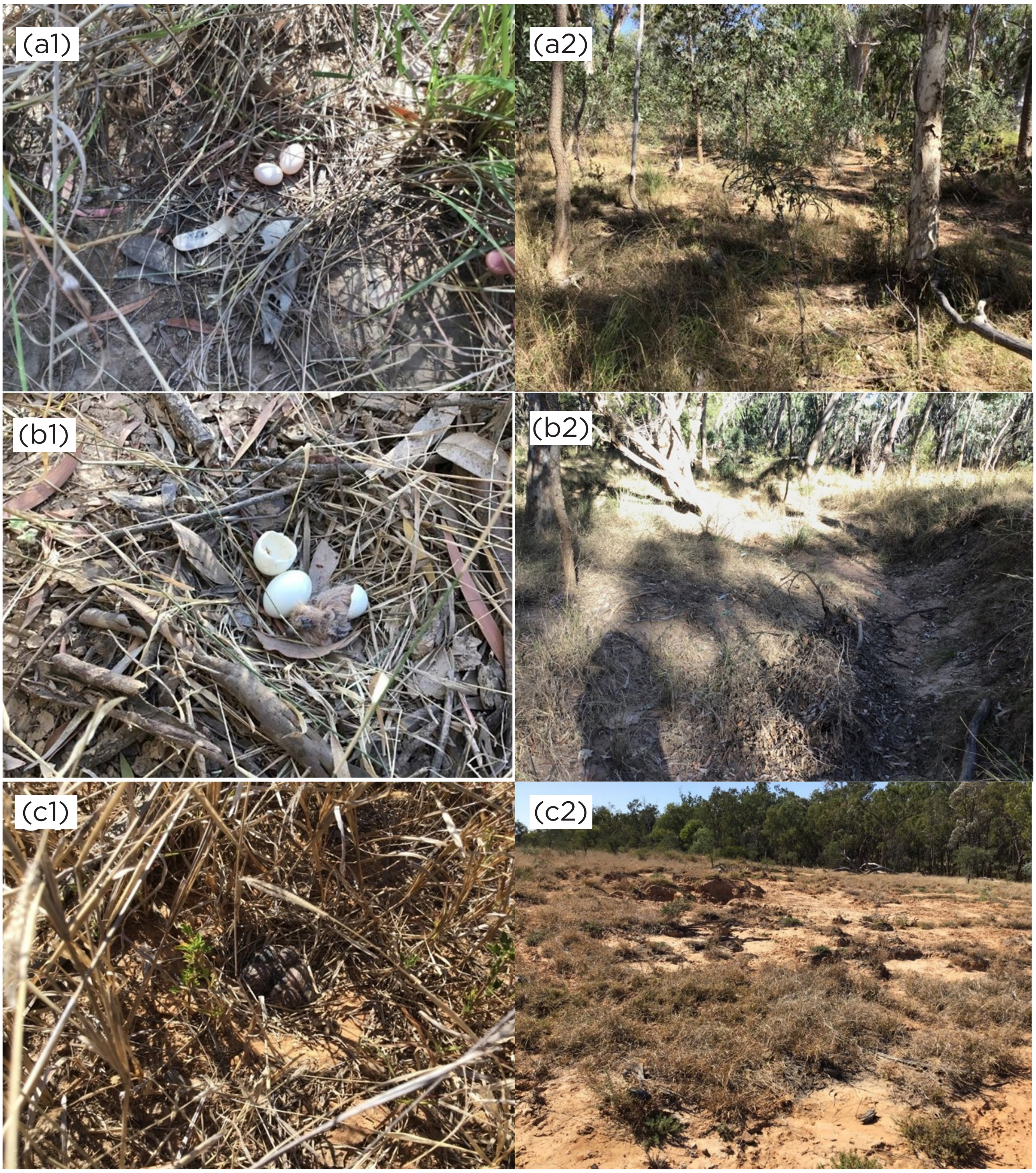

Figure 4. Nest and nesting habitat of Southern Squatter Pigeon. (a1–2) Nest with two eggs in alluvial soil (Land zone 3) on the bank of a seasonal drainage channel in remnant River Red Gum–Weeping Paperbark *Melaleuca leucadendra* woodland (RE 10.3.13a); (b1–2) nest with one egg and one newly hatched squab in alluvial soil on the bank of an incised seasonal drainage channel in remnant River Red Gum–Weeping Paperbark woodland; (c1–2) nest with two squabs in a cleared livestock grazing paddock dominated by Buffel Grass on eroded alluvial plain, 45 m from remnant River Red Gum–Weeping Paperbark open forest. Photos: Penn Lloyd

records was 1.21 ± 1.19° (range 0.02–10.49°). Ninety-five percent of records were associated with slopes <3.3° (5.8% slope). The average slope at 100 random points across the range of the Southern Squatter Pigeon was 2.95 ± 4.54° (range 0.06–26.66°). Average slope differed significantly between Southern Squatter Pigeon records and random points within range of the subspecies (t = 3.70, P <0.001).

The average projective foliage cover of groundcover vegetation in the late wet season, when vegetation cover is expected to be at its greatest, ranged between 24% and 73% in different remnant or high-value regrowth vegetation communities in which Southern Squatter Pigeons were present, but 87% at two sites in non-remnant vegetation (Table 4). At a different set of sites, ground vegetation cover in two different REs was 22–27% lower in the late dry season than in the late wet season (Table 4).

Eleven Southern Squatter Pigeon nests with two eggs or young in each (Figures 4–6) were found in February (2 nests), March (2), April (1), May (1), September (4) and December (1). Eight of these nests were on alluvial soils (Land zone 3), including two on the banks or bed of seasonal drainage lines, one on old sand plains (Land zone 5), one on hills and lowlands on metamorphic rocks (Land zone 11) and one on basalt plain soils derived from

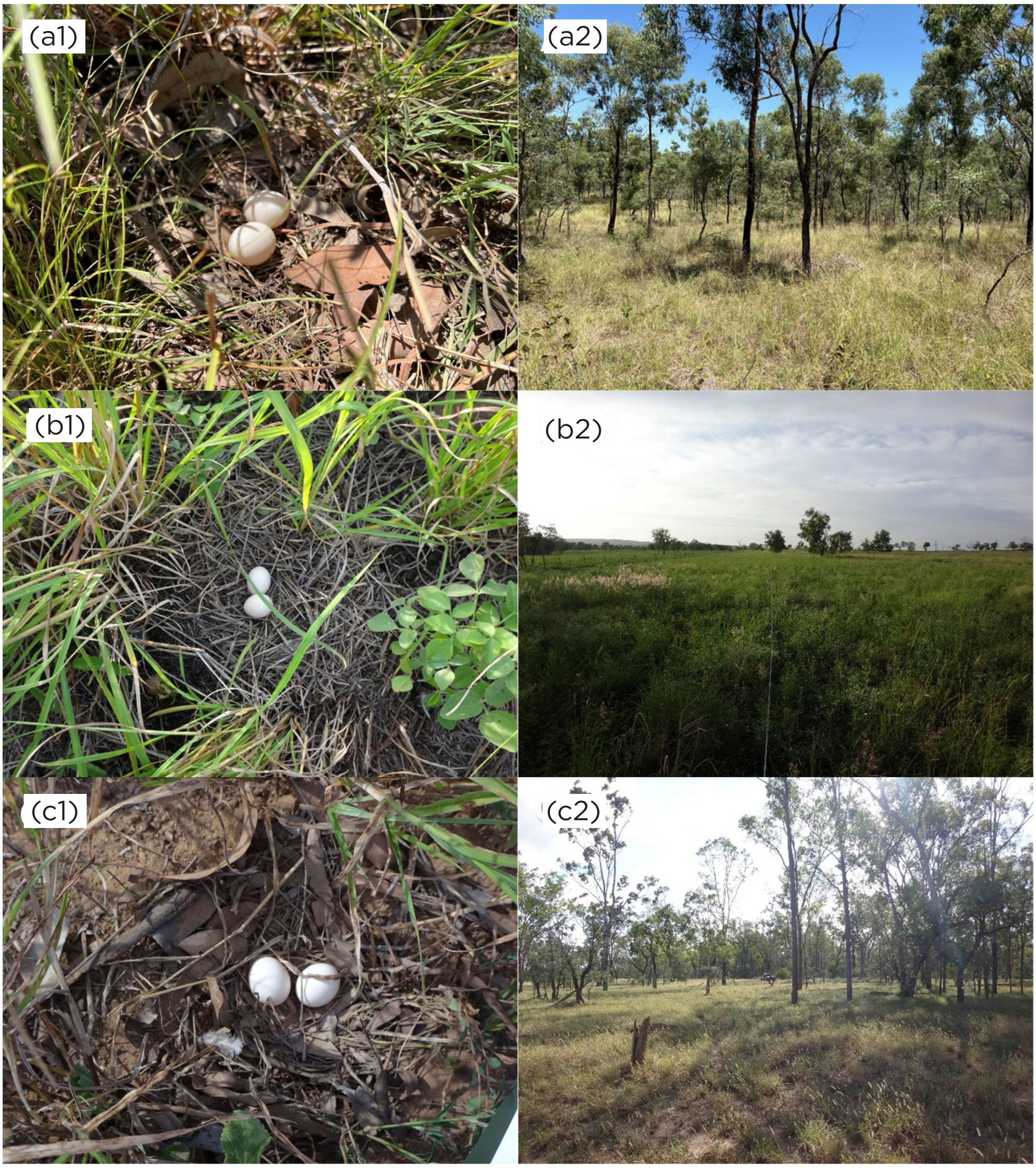

Figure 5. Nest and nesting habitat of Southern Squatter Pigeon. (a1–2) Nest with two eggs on top of a low hill in remnant Narrow-leaved Red Ironbark woodland on metamorphosed sediments and interbedded volcanics (RE 11.11.15); (b1–2) nest with two eggs in open remnant Queensland Bluegrass *Dichanthium sericeum* grassland on a basalt plain (RE 11.8.11), 100 m from nearest woodland; (c1–2) nest with two eggs in regrowth Poplar Box woodland on alluvial plain (RE 11.3.2). Photos: Penn Lloyd (a), Chris Hansen (b–c).

igneous rocks (Land zone 8). Each nest was in a space between grass tufts and comprised a shallow scrape in the soil surface, sparsely lined with dry leaves and grass stems (Figures 4–6). Nests were in eucalypt woodland to open woodland, except for two in open grassland (45 m and 100 m from the closest woodland). Ground vegetation cover was 15% adjacent to a nest in remnant RE 11.3.30 (Queensland Grey Ironbark *Eucalyptus drepanophylla*–Dallachy's Ghost Gum *Corymbia dallachiana* woodland on alluvial plains), 19% adjacent to a nest in RE 11.3.2 (Figure 5c) and 62% adjacent to a nest in RE 11.8.11 (Figure 5b). Although native grass species dominated the ground vegetation cover around nine nest sites, the introduced pasture grass Buffel Grass *Cenchrus ciliaris* dominated the groundcover at two nest sites. Nests were located at an average distance of 245 ± 214 m (range 80–780 m) from a perennial water source.

Discussion

Our results confirm that Southern Squatter Pigeons are predominantly associated with eucalypt woodland and open woodland vegetation communities. The Northern Squatter Pigeon is described as preferring areas of sandy soil dissected by low gravelly ridges that have the most open and shortest cover of grasses, being less common on heavier soils with dense growth of grasses (Higgins &

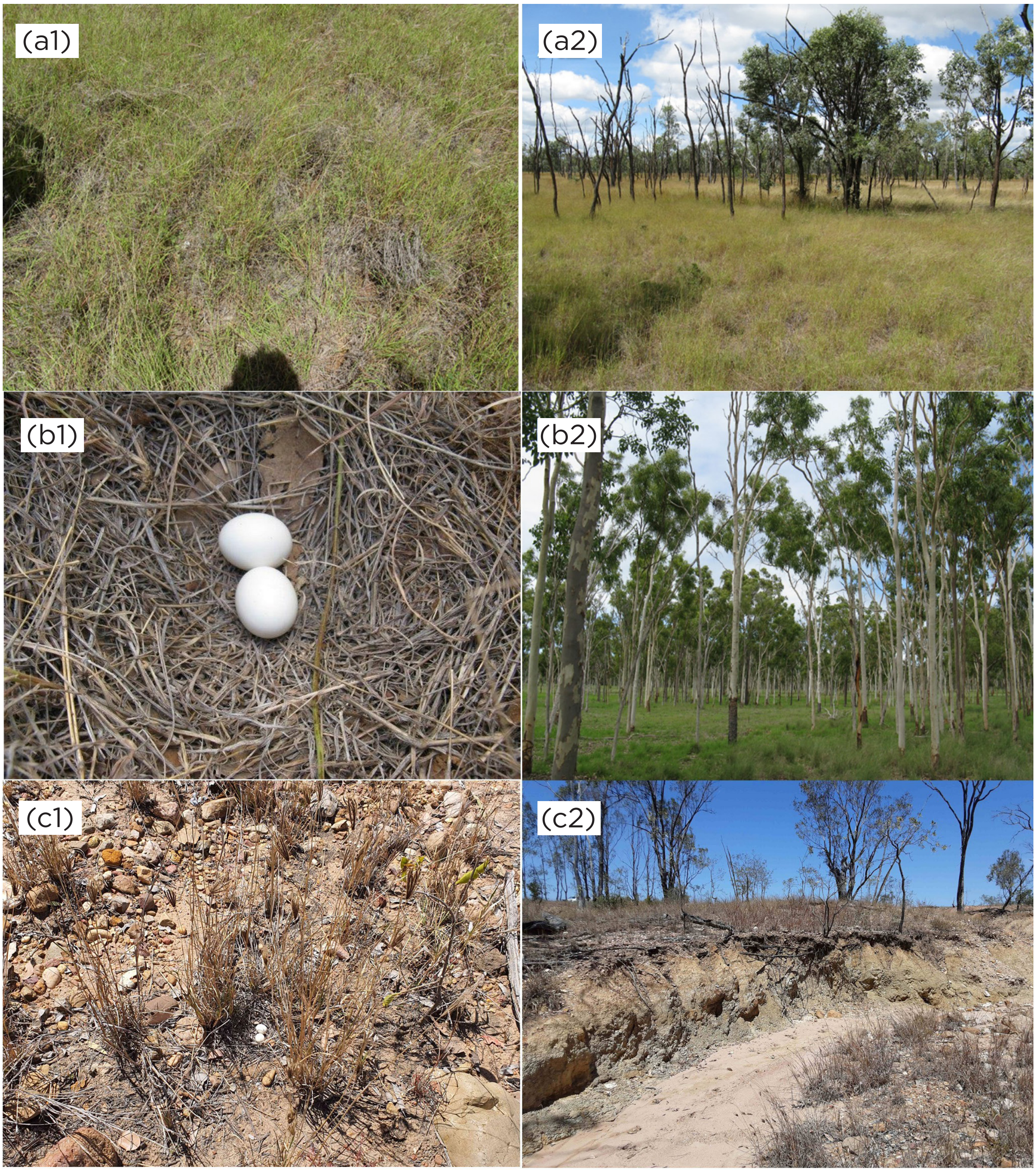

Figure 6. Nest and nesting habitat of Southern Squatter Pigeon. (a1–2) nest with two eggs in dense grass cover in non-remnant Poplar Box–Silver-leaved Ironbark *E. melanophloia* open woodland on sand plain (RE 11.5.3); (b1–2) nest with two eggs in Forest Red Gum–Moreton Bay Ash woodland on alluvial plain (RE 11.3.4); (c1–2) nest with two eggs on a sparsely vegetated, pebbly bar in the bed of an eroded seasonal watercourse in non-remnant Coolabah open woodland on alluvial plain (RE 11.3.3). Photos: Lindsay Agnew (a–b), Simon Danielsen (c)

Davies 1996). Yet we found that the Southern Squatter Pigeon was strongly associated with alluvial plains across all bioregions (Table 3). Using a largely independent set of 111 records from a portion of the Brigalow Belt bioregion, an unpublished study by Agnew (2006) similarly found that 53% of records were associated with alluvial plains (Land zone 3), whereas 25% of records were associated with old loamy and sandy plains (Land zone 5). Natural perennial water sources are predominantly found in alluvial areas, and many of the field records in our study were of birds visiting both natural and artificial water sources to drink. Consequently, the association of Southern Squatter Pigeons with alluvial plains could be an artefact of their drinking habits. Yet, we observed that birds visiting water points commonly spend considerable time feeding in the vicinity of watering points before or after drinking. Furthermore, 73% of our nest records were on alluvial plains, suggesting that the pigeons also have a strong affinity for alluvial areas for breeding. The apparent association with alluvial plains could also occur if survey effort were strongly biased towards alluvial areas compared with other land zones. Unfortunately, the nature of our data means that we were unable to control for survey effort across different land zones. Most of our records were obtained during ecological assessments that generally aimed to survey different vegetation communities in proportion to their occurrence across a site; therefore, a bias in survey effort towards any one land zone is not expected. Also, at one site in the Desert Uplands bioregion, despite greater survey effort on Land zone 5 (sand plains), including within 1 km of permanent water, than Land zone 3 (alluvial plains), all of the three nests found were on Land zone 3, suggesting a preference for alluvial plains.

DCCEEW (2025) considered natural foraging habitat to be restricted to Land zones 5 and 7, and the pigeons visited vegetation types growing on Land zones 3, 4 and 10 when visiting water points. Our results do not support such a narrow habitat definition, and particularly not across all bioregions. Land zone 5 accounted for >10% of Southern Squatter Pigeon records only in the Desert Uplands and Brigalow Belt bioregions, whereas Land zone 7 did not account for >10% of records in any bioregion (Table 3). By contrast, between 12% and 56% of records were associated with Land zone 3 across different bioregions. Consistent with their apparent preference for flat to gently undulating landforms, Southern Squatter Pigeon were associated with gentle slopes across all land zones (Table 2).

Southern Squatter Pigeons were disproportionately recorded in eucalypt communities dominated by Reid River Box or Poplar Box, Narrow-leaved Red Ironbark or Queensland Grey Ironbark, Silver-leaved Ironbark, and River Red Gum or Forest Red Gum, which are among the most common and widely distributed eucalypt species within the subspecies' range. Nonetheless, they also occupied communities dominated by a wide range of other eucalypt species (Table 1). Nearly all eucalypt-dominated communities where Southern Squatter Pigeon were recorded are characterised as having a grassy ground layer (Queensland Herbarium 2024). Relatively few records were from communities dominated by *Acacia, Callitris* and *Melaleuca* species or tussock grassland (Table 1). Where Southern Squatter Pigeons were recorded in non-remnant or grassland communities, most records were within 300 m of scattered trees or woodland, suggesting that in open areas they do not move far from trees.

Like other granivorous birds (MacMillen 1990; Smit *et al*. 2019), Squatter Pigeons must drink regularly, possibly daily, and are described as being found nearly always near permanent water (Higgins & Davies 1996). The results of our analysis confirm that they are closely associated with perennial water sources, with 95% of records located within 1.7 km of a perennial water source (Figure 3b), including larger water courses (Stream order 4 or greater), farm dams, permanent wetlands or livestock drinking troughs. Using a largely independent set of 58 records, Agnew (2006) similarly found that 83% of records were within 500 m of surface water. Most nests that we found were located within 500 m of a perennial water source, with one found within 1 km of permanent water, suggesting an increased importance of proximity to water when breeding.

Whereas DCCEEW (2025) considered the breeding habitat of Southern Squatter Pigeon to be restricted to Land zones 5 (old loamy and sandy plains) and 7 (ironstone jump-ups), the nests that we found were on Land zones 3 (alluvial plains), 5 (sand plains), 8 (basalt plains and hills) and 11 (hills and lowlands on metamorphic rocks). Consequently, it is likely that Southern Squatter Pigeons can nest on any land zone located close to suitable foraging habitat and a suitable water source. However, their known preference for sandy soils (Higgins & Davies 1996) suggests that they are less likely to use Land zone 4 (clay plains) for foraging and nesting. The only previously published information on the habitat associations of Squatter Pigeon nests is a nest of the northern subspecies found "in short dry grass on bank of creek" (White 1922, p. 106). Our observations of nesting by Southern Squatter Pigeon in February–May and September–December are similar to the observed pattern of egg production by Northern Squatter Pigeon in March–July and September in north-eastern Queensland (Crome 1976).

DCCEEW (2025) asserted that the ground-covering vegetation layer in foraging and breeding habitat is considerably patchy, consisting of native, perennial tussock grasses or a mix of perennial tussock grasses and low shrubs or forbs, with the ground layer of vegetation rarely exceeding 33% of the ground area. Yet we found that the average projective foliage cover of ground-layer vegetation in remnant and high-value regrowth vegetation communities where the Southern Squatter Pigeon was present ranged between 24% and 73%, frequently exceeding 33% ground-vegetation cover (Table 4). Furthermore, the average projective foliage cover of ground-layer vegetation was as high as 62% in the vicinity of a Southern Squatter Pigeon nest. However, within areas with relatively high average groundcover, it is quite possible that the Pigeons were using patches where the extent of groundcover was lower than the average groundcover for the broader habitat. Habitat assessments for development proposals are required to identify and map habitat at broad landscape scales. In this context, measures of average ground vegetation cover are more useful for defining habitat than the fine-scale definition that Southern Squatter Pigeons use patches with <33% ground vegetation cover. For example, it is impractical to map the fine-scale distribution of patches where groundcover is <33% at landscape scales of thousands of hectares. A more practical alternative is to measure average groundcover per vegetation community type and relate that to measures of average groundcover in vegetation communities associated with Southern Squatter Pigeons. Our data suggest that Southern Squatter Pigeons generally inhabit vegetation communities with average ground vegetation cover ranging between approximately 20% and 60% but were occasionally recorded in areas with higher average ground vegetation cover (Table 4).

Our study provides new information on the habitat associations of the Southern Squatter Pigeon across its range in Queensland, revealing that these are more complex than previously appreciated. Although our analysis is based on an extensive dataset of records, these opportunistic, presence-only records do not sample Southern Squatter Pigeon habitat randomly across their range. They are likely to be spatially biased towards project-specific surveys, easily accessed areas or areas with a greater density of observers (Phillips *et al.* 2009). Therefore, site-specific assessments of Southern Squatter Pigeon habitats should also be informed by site-specific occurrence data for the taxon. A better understanding of how the Southern Squatter Pigeon uses different land zones and the broader landscape, and how this might vary between wet and dry seasons, could be derived from radio-tracking or satellite-tracking studies (e.g. Rechetelo *et al*. 2016; Lilleyman *et al*. 2024; van Osta *et al*. 2024).

Conclusions

The results of our study suggest the following conclusions to inform the characterisation of habitat for the Southern Squatter Pigeon for ecological assessments in Queensland. First, although the pigeons have a strong preference for alluvial areas (Land zone 3), they also occur in a range of other land zones. Their use of other land zones varies across bioregions, largely related to the makeup of land zones of each bioregion. Second, they generally occupy areas with gentle slopes, with 95% of records on slopes <3.3°(5.8% slope). Third, they are primarily associated with eucalypt woodlands and open woodlands with a grassy ground layer, but they can occur in tussock grasslands (within 300 m of scattered trees or woodland) and, to a much lesser extent, communities dominated by *Acacia, Callitris* and *Melaleuca* tree species. Fourth, suitable habitats within 1.7 km of a perennial water source are important for foraging and those within 1 km of a perennial water source are important for nesting. Fifth, in remnant and high-value regrowth habitats, Southern Squatter Pigeons occur in vegetation communities with patchy groundcover and average ground vegetation cover ranging between 24% and 73%.

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