

Threatened species in a threatened ecosystem: the conservation status of four *Solanum* species in the face of ongoing habitat loss

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Abstract Plant biodiversity is threatened by habitat loss, fragmentation and invasion by exotic species, but the effects of these disturbances on individual plant species are rarely quantified. Since the 1950s, brigalow *Acacia harpophylla* forests in Australia have been extensively cleared and converted to pastures dominated by exotic grasses. Here we assess the habitat requirements, population numbers and threats for four poorly known bush tomato species, *Solanum adenophorum*, *Solanum dissectum*, *Solanum elachophyllum* and *Solanum johnsonianum*. Herbarium records and surveys demonstrated a strong association of all four species with brigalow habitat, although *S. elachophyllum* also occurred in other habitat. We derived historical and current population estimates from plant densities at current sites and the area of mapped brigalow habitat. Density estimates are imprecise because the survey data vary greatly, but the assessment indicates the populations of all four species have declined > 93%. *Solanum dissectum* and *S. johnsonianum* did not persist in cleared brigalow habitat, whereas *S. adenophorum* and *S. elachophyllum* had some capacity to persist in clearings. None of the species occur where the exotic grass cover is > 40%. Between 27% and 57% of the records of the four species are in brigalow remnants with a high edge-to-area ratio or open canopy (< 50% cover), making them highly vulnerable to invasive grasses. We recommend the categorization of *S. dissectum* and *S. johnsonianum* as Critically Endangered, *S. adenophorum* as Vulnerable and *S. elachophyllum* as Near Threatened.

Keywords Australia, brigalow, disturbance, invasive grasses, land clearing, threatened species, plant conservation, *Solanum*

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Introduction

The IUCN Red List is the most widely used and authoritative conservation assessment of the world's flora (Mace et al., 2008). However, the disparity between the available information and the magnitude of the task means that assessments will always be subject to improvement and few species are assessed based on comprehensive surveys of their native populations (Brummitt et al., 2015). Habitat loss (Krauss et al., 2010) and invasion of exotic species (Pyšek et al., 2012) are threats to plant species. Although the decline of some species has been inferred from historical and current collecting records (Robbirt et al., 2006; Brummitt et al., 2015), and decline from disease has been estimated (Schwartz et al., 2000), to our knowledge there have not been any published attempts to quantify the response of individual plant species to past declines, or to estimate future threats to habitat quality. This is a major omission, given the importance of this process for assessing the conservation status of the world's flora under the Red List criteria (Mace et al., 2008).

Conservation biologists recognize that rarity alone does not determine extinction risk and the Red List criteria have low thresholds for population size and extent of occurrence (EOO) for species that have not declined (IUCN, 2012). The species of greatest concern are those that were once common but are subject to ongoing threatening processes (McIntyre & Lavorel, 1994; Burgman, 2002). However, accurately assessing the magnitude of historical and continuing declines is difficult and requires a clear understanding of species' responses to potentially threatening processes. Systematic surveys and assessments are necessary to quantitatively evaluate species' conservation status using the IUCN Red List criteria.

The conservation status of most plant species is not usually derived by a systematic assessment of population density across the area of occupancy (AOO; Keith, 2000) and conservative extrapolations that take into account available habitat (see Silcock et al., 2014). This study provides a methodological standard for assessing the conservation status of plant species where habitat loss and decline of habitat quality can be evaluated. Our aim is to generate adequate survey

data to assess the conservation status of four *Solanum* species associated with the forest type of eastern Australia dominated by brigalow *Acacia harpophylla*. This forest has been reduced to c. 10% of its former area by clearing, and the remnants are being further degraded by the invasion of exotic grasses (Fensham et al., 2017). We employ herbarium specimen records to identify habitat associations and to direct field surveys, and use mapping of habitat loss as a surrogate for population decline. We demonstrate how the ongoing advance of invasive grasses affects *Solanum* species, and integrate this information to estimate the historical and current populations. We quantify threatening processes to evaluate the conservation status of the species using the IUCN Red List criteria, and provide management recommendations for the habitat of the *Solanum* species.

Study area and study species

The Brigalow Belt consists of two biogeographical regions spanning a subcoastal area in eastern Australia typified by brigalow-dominated forest on clay-rich substrates, but occurring with a range of other vegetation and soil types (Fig. 1; Fensham et al., 2017). The climate is semi-humid, with rain falling predominantly in the summer and a mean annual rainfall of 521–716 mm throughout the ranges of the *Solanum* species (modelled data from Jeffrey et al., 2001). The brigalow forest generally has a dense tree canopy and a sparse ground layer of herbaceous vegetation; where the canopy is intact it is only rarely subject to fire (Fensham et al., 2017). The overstorey is dominated by *Acacia harpophylla*, but other tree species also occur and the understorey consists of shrubs, grasses and herbs (Fensham et al., 2017).

The once extensive brigalow forest was mostly converted to pastures and crops in the latter half of the 20th century (Seabrook et al., 2006; Fensham et al., 2017). The remaining forest is fragmented and surrounded by productive pastures for cattle farming, which are mostly dominated by the African buffel grass *Cenchrus ciliaris* L. Exotic grasses also invade remnant brigalow forest, outcompeting native species (Fairfax & Fensham, 2000) and rendering the normally fire retardant brigalow ecosystems prone to fire. The resulting open canopy further facilitates buffel grass invasion, leading to a destructive grass–fire cycle (Butler & Fairfax, 2003). Roadside corridors provide important habitat for remnants of the brigalow ecosystem but are often heavily infested with exotic grasses (Butler, 2008; Butler et al., 2014). The brigalow ecological community (*Acacia harpophylla* dominant and co-dominant) has a threatened status under the Australian Government Environment Protection and Biodiversity Conservation Act 1999.

Plant species associated with brigalow forest are potentially threatened and the magnitude of this potential threat has been ranked (Fensham et al., 2018). The genus *Solanum*

exhibits substantial radiation in the brigalow ecosystem (Bean, 2004), and four species, namely *Solanum adenophorum* F. Muell., *Solanum dissectum* Symon, *Solanum elachophyllum* F. Muell. and *Solanum johnsonianum* A.R. Bean (Plate 1), were second, third, sixth and ninth on the ranked list of threatened species (Fensham et al. 2018).

Solanum is the largest genus in the family Solanaceae, with > 1250 species (Weese & Bohs, 2007). On the IUCN Red List *Solanum* is mostly represented by species from South and Central America, and Australian species are yet to be assessed (Table 1). The spiny *Solanum* clade (subgenus *Leptostemonum*) is the largest subgenus, with c. 450 species (Bohs, 2005) and includes all four target species. A significant share of this diversity occurs within the north-eastern Australian state of Queensland, with 88 indigenous (50 endemic) and two naturalized species (Bean, 2004). Several other species in the subgenus *Leptostemonum* also occur in brigalow forest within the geographic range of the target species, but they are not considered rare because they are more widely distributed or have broader habitat preferences (Fensham et al., 2018). All four target species are categorized as Endangered under the Queensland Government Nature Conservation Act 1992 (Table 1). *Solanum adenophorum*, *S. dissectum*, and *S. johnsonianum* are the only *Solanum* species categorized as Endangered under Australian Government legislation and *S. elachophyllum* is not categorized as threatened even though it has an Endangered status under Queensland state legislation (Table 1). As for the majority of plant species assessed using the Red List criteria (IUCN, 2012) for international, national or provincial listings, the assessment of these species has relied on expert opinion rather than on quantitative information. Discrepancies in the status of *Solanum* species between national and state jurisdictions (Table 1) provide an imperative to update categorizations with current information, such as the systematic surveys presented here, and to align categorizations, including an update of the IUCN Red List for *Solanum* from Australia.

Methods

Regional ecosystem mapping

This study establishes associations between *Solanum* species and native habitats delineated on regional ecosystem maps in Queensland, Australia (Queensland Herbarium, 2016). We use these maps to document habitat decline because they provide a complete coverage of regional ecosystems prior to extensive forest clearance (Queensland Herbarium, 2016). Regional ecosystems are defined by combinations of biogeographical region, geological substrate and dominant vegetation type that are then grouped into broad vegetation groups. Broad vegetation groups are a higher-level grouping

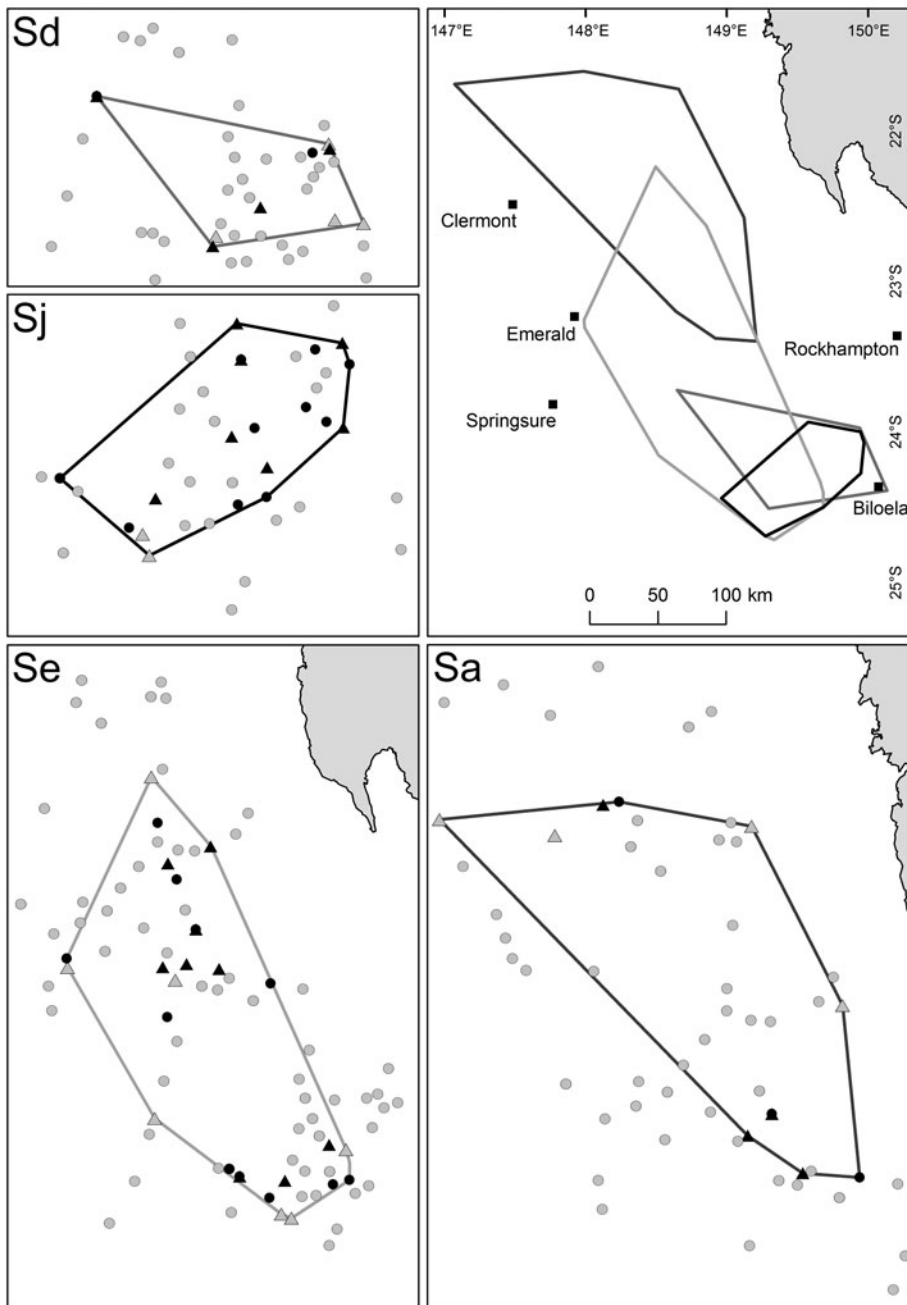


FIG. 1 The EOO (convex polygons) of the four *Solanum* species in relation to the north-east coast of Australia (top right); and the location of sites used to define the distribution of *Solanum adenophorum* (Sa), *Solanum dissectum* (Sd), *Solanum elachophyllum* (Se) and *Solanum johnsonianum* (Sj). Triangles represent historical herbarium records (grey, population not located during current surveys; black, population located during current surveys); circles represent survey searches for this study (grey, population not located; black, population located). Some absence records from the current study have been excluded for clarity.

that combine regional ecosystems, and the brigalow forests are unit 25: *Acacia harpophylla* (brigalow) sometimes with *Casuarina cristata* Miq. (belah) open forests to woodlands on heavy clay soils (Neldner et al., 2015). Another broad vegetation group dominated by species related to brigalow is unit 26: *Acacia cambagei* R.T. Baker (gidgee)/*Acacia georginae* F.M. Bailey (georgina gidgee)/*Acacia argyrodendron* Domin (blackwood) dominated associations, and occurs in similar edaphic environments to brigalow. This broad vegetation group has only small areas within the EOO of the target species and is combined here with unit 25, and the two broad vegetation groups are referred to as ‘brigalow’ hereafter.

Another mapping layer represents regional ecosystems as ‘remnant’ (uncleared) in 2017 (Queensland Herbarium, 2016) and the proportion of ‘remnant’ relative to ‘pre-clearing’ is used here as a measure of habitat loss. We allocated our search effort to different areas based on the regional ecosystem mapping. Previous models suggest that on average buffel grass cover reaches 30% when forest canopy is reduced to 50% of the original canopy cover (Butler et al., 2014). We assumed that areas with < 50% canopy cover will be subject to increased fire frequency and further invasion by exotic grasses (Butler & Fairfax, 2003), and will not provide habitat for *Solanum* species in the long term. We conducted

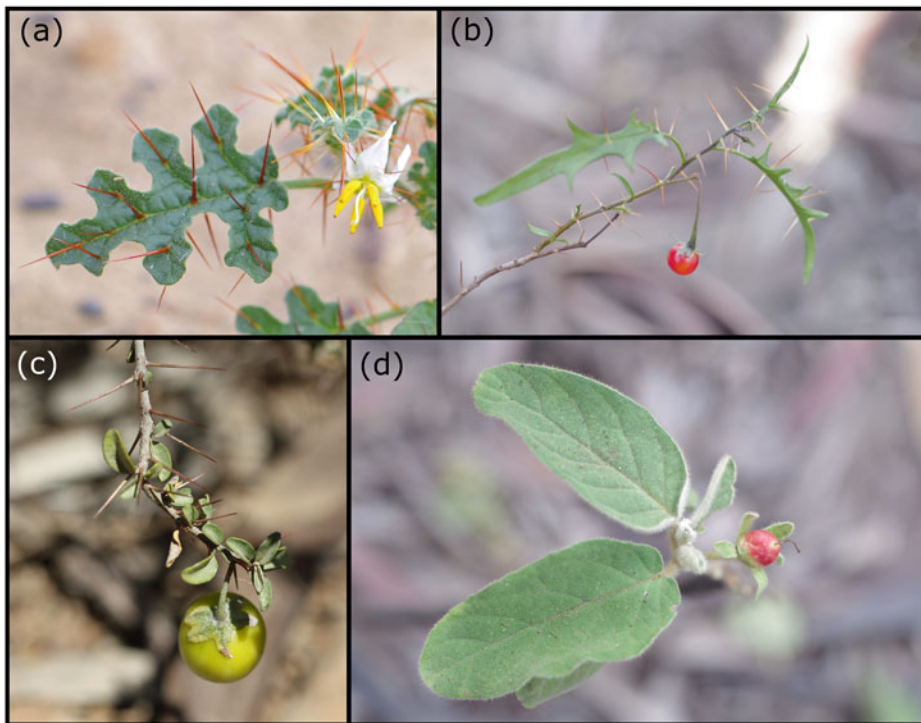


PLATE 1 The four species of *Solanum* forming the target of this study: (a) *S. adenophorum*, (b) *S. dissectum*, (c) *S. elachophyllum*, (d) *S. johnsonianum*.

TABLE 1 Red List status of *Solanum* species (*Sa*, *Solanum adenophorum*; *Sd*, *Solanum dissectum*; *Se*, *Solanum elachophyllum*; *Sj*, *Solanum johnsonianum*) in various countries and regions (with authorities in parentheses).

Jurisdiction ¹	Vulnerable	Endangered	Critically endangered	Extinct
South & Central America (IUCN Red List)	11	7	3	0
Australia (IUCN Red List)	0	0	0	0
Other (IUCN Red List)	2	1	3	0
Australian Government (EPBC listing)	2	3 (<i>Sa</i> , <i>Sd</i> , <i>Sj</i>)	0	1
Queensland (NCA listing)	5	12 (<i>Sa</i> , <i>Sd</i> , <i>Se</i> , <i>Sj</i>)	0	0
Other Australian states (relevant state legislation)	2	7	0	1

¹EPBC, Environment Protection and Biodiversity Conservation Act 1999; NCA, Nature Conservation Act 1992.

additional mapping to distinguish intact ($\geq 50\%$ tree cover) and degraded remnant habitat ($< 50\%$ tree cover) by visually assessing high-resolution imagery (Department of Environment and Science, 2017). We used this to assess the likely magnitude of ongoing decline according to the IUCN Red List criteria.

Habitat association, distribution and density

We used historical records from the Queensland Herbarium database to quantify previous search effort within the EOO of the four species from collecting locations in 2012. Records with the same geographical coordinates and survey date were aggregated as a single record. We assigned all records to a broad habitat category (see Table 1) using search terms from the habitat notes (Supplementary Table 1), and, where the habitat notes were inadequate, by intersecting the collecting localities with the regional ecosystem mapping

(Queensland Herbarium, 2016). This data collation also contributes to the evaluation of the habitat specificity of the four *Solanum* species.

Field surveys

We conducted field surveys in February–October 2012, November 2013–May 2014 and May 2017. These surveys aimed to confirm historical records, search for new populations within and up to 80 km from the geographic range as it was known from collecting locations in 2012, and assess the habitat association of the species following the procedures of Keith (2000). Rainfall during the 6 months prior to the survey was above average for 2012 and 2017, and slightly below average in 2013 and 2014. Historical records suggested that the target species have a strong association with brigalow (Table 2), directing most of the survey effort to remnants of this ecosystem. However, non-remnant brigalow (cleared

TABLE 2 Number of specimen records of the four target *Solanum* species within their respective EOO (records of other vascular plants in parentheses), by broad vegetation group (Neldner et al., 2015). Numbers include all records from the Queensland Herbarium with a unique location and date.

Broad vegetation group(s)	No. of records in EOO			
	<i>S. adenophorum</i>	<i>S. dissectum</i>	<i>S. elachophyllum</i>	<i>S. johnsonianum</i>
Brigalow/gidgee	13 (196)	17 (152)	28 (412)	23 (170)
Cleared brigalow/gidgee	1 (41)	1 (25)	4 (76)	0 (19)
Alluvial woodland	0 (54)	0 (91)	0 (130)	0 (56)
Dry rainforest	0 (77)	0 (22)	0 (49)	0 (16)
Grassland	0 (96)	0 (7)	0 (49)	0 (11)
Eucalypt	0 (443)	0 (261)	3 (1,266)	0 (129)
Other <i>Acacia</i>	0 (47)	0 (22)	0 (95)	0 (16)
Cleared and disturbed, other than brigalow/gidgee	0 (10)	0 (11)	0 (28)	0 (6)

pasture dominated by buffel grass) and other vegetation types were also included (Table 3). We surveyed 741 locations to determine the EOO, habitat requirements and population density of the *Solanum* species. Of these locations 645 were within the EOO of the four species. We conducted surveys in all designated conservation reserves within the species' EOO. To estimate population densities at each location, we measured search distance using GPS tracking along linear transects, counted the number of plants within a width of either 4 or 6 m around the transect line, and calculated the search area by multiplying the search distance by the transect width. Surveyed areas for individual species within remnant brigalow were 47.5–195.4 ha (Table 3). We also observed the life history and regeneration of the species during the surveys and found that vegetative shoots can be connected by underground suckers (forming a single genet); we treated each emergent shoot (ramet) as an individual plant.

Population assessment

We estimated population sizes using the regional ecosystem mapping and population densities from field surveys. The EOO of each species was calculated from a minimum convex polygon containing all historical and current records. Within the EOO of each species, where plants were present in remnant brigalow, we used a weighted average to calculate densities (in plants per ha):

$$\bar{x} = \sum_{i=1}^n w'_i x_i$$

where x is the number of plants recorded at each search plot where $x > 0$, n is the sample size and w' is the proportion of the total search areas represented by each search plot where $x > 0$. A measure of the standard error of the weighted mean (SEM) is given by:

$$SEM_w = \sqrt{\frac{n}{(n-1)w^2} \sum w_i^2 (x_i - \bar{x})^2}$$

To provide an estimate of the total population of each species, we multiplied the total pre-clearing, remnant and intact areas by the proportion of the presences at surveyed sites (P in Table 3) and the respective densities of species. The historical population estimates assume that historical plant densities were the same as current densities. We used the proportion of remnant habitat relative to pre-clearing habitat to assess past decline, and the proportion of intact habitat relative to remnant habitat to assess the magnitude of ongoing decline. We visually assessed the average canopy cover using DMC-3 imagery (2017) and determined the edge-to-area ratio of remnant brigalow habitat for the current localities of the target species. Remnant habitat with an edge-to-area ratio > 0.15 km/ha or a canopy cover $< 50\%$ was considered inviable in the long term, and we used the proportion of populations occurring in these areas to assess the magnitude of ongoing decline under the IUCN Red List criteria.

Association with tree canopy and exotic grass cover

We collected data to establish relationships between tree cover and the occurrence of the four *Solanum* species and perennial grasses. Within populations (*S. adenophorum*, $n = 5$; *S. dissectum*, $n = 5$; *S. elachophyllum*, $n = 23$; *S. johnsonianum*, $n = 16$), a 50 m tape was laid out within representative habitat. At every metre along the tape we recorded the presence or absence of a tree canopy and/or a perennial grass tussock and a *Solanum* colony (i.e. a group of plants whose stems were less than 1 m apart).

Assessment of conservation status

We assessed conservation status using the IUCN Red List criteria (IUCN, 2012), following the guidelines in IUCN Standards & Petitions Subcommittee (2017). Estimated plant density is here based on a replicated sample of subpopulations. Population size and decline are inferred in that

TABLE 3 Summary of survey, habitat and population characteristics within the EOO of the four target species including assessment of decline. The combined search area is provided in brackets after the number of searches. Habitat references are pre-clearing (prior to clearing), remnant (uncleared in 2017), non-remnant (cleared in 2017) and intact (remnant brigalow with $\geq 50\%$ canopy cover).

	<i>S. adenophorum</i>	<i>S. dissectum</i>	<i>S. elachophyllum</i>	<i>S. johnsonianum</i>
EOO (km ²)	21,612	7,172	23,836	4,962
Mean annual rainfall range (mm)	521–679	612–716	570–691	640–716
Pre-clearing brigalow (km ²); area of habitat where species present assuming <i>P</i> below	8,677; 2,231	2,213; 699	9,762; 5,458	2,503; 1,947
Remnant brigalow (km ²); area of habitat where species present assuming <i>P</i> below	566; 146	45; 14	442; 247	49; 38
Intact brigalow (km ²); area of habitat where species present assuming <i>P</i> below	367; 94	44; 14	345; 193	48; 37
Current presence records, within 4 km ² grid cells (km ²) (AOO)	48	36	172	124
Presences/searches in remnant brigalow (<i>P</i>) (search area, ha)	18/70 (25.4/104.8)	18/57 (21.3/47.5)	52/93 (154.8/195.4)	56/72 (99.5/109.1)
Presences/searches in non-remnant brigalow (search area, ha)	3/32 (1.9/88.9)	0/21 (0.0/77.3)	8/48 (163.0/333.8)	0/19 (0.0/65.3)
Presences/searches in remnant non-brigalow (search area, ha)	0/32 (0.0/149.4)	0/20 (0.0/17.0)	5/39 (1.7/75.9)	0/12 (0.0/8.4)
Presences/searches in non-remnant non-brigalow (search area, ha)	0/11 (0.0/89.4)	0/34 (0.0/54.4)	0/34 (0.0/78.3)	0/23 (0.0/43.6)
Density in remnant brigalow where species present (individuals/ha) \pm SE	26.4 \pm 31.0	81.8 \pm 33.5	86.2 \pm 59.5	151.9 \pm 65.5
Estimated historical population in brigalow, 1,000s \pm SE	5,900 \pm 6,917	5,721 \pm 2,339	47,047 \pm 32,459	29,570 \pm 12,752
Estimated current population in remnant brigalow, 1,000s \pm SE (decline, %)	385 \pm 452 (93.5)	117 \pm 48 (98.0)	2,131 \pm 1,470 (95.5)	580 \pm 250 (98.0)
Estimated current population in intact brigalow, 1,000s \pm SE (decline, %)	250 \pm 293 (95.8)	115 \pm 47 (98.0)	1,662 \pm 1146 (96.5)	565 \pm 244 (98.1)

they are indirectly derived from estimated plant density and mapped areas of available habitat. We calculated AOO using a 4 km² grid (IUCN Standards & Petitions Subcommittee, 2017), but used the regional ecosystem mapping as high resolution habitat maps to determine decline in population size. This variation in procedure is justified because it represents a modelling of subpopulations occurring in past and present suitable habitat that has not been surveyed.

Reservation status and land tenure

We collated the occurrence of populations of the four *Solanum* species in conservation reserves and investigated the tenure of other large brigalow remnants within the EOO of the four species.

Results

Life history and habit observations

During our surveys we did not observe seedlings (cotyledons or small-statured plants without fertile parts) of any of the *Solanum* species. The stems of *S. adenophorum* are not woody and populations that are abundant in the wet season disappear or dwindle dramatically during the dry season. Excavation of *S. adenophorum* plants revealed no robust underground structures, suggesting the species regenerates only from seed and is short-lived but is not an annual (RF, pers. obs.). Excavation of the other three species revealed lateral stems regenerating clonal shoots from rhizomes. These species are perennial subshrubs with woody stems, although the number of aerial shoots growing from rhizomes varies depending on seasonal conditions, and all shoots can flower and fruit rapidly in response to rain.

Habitat association, distribution and density

Herbarium records indicate considerable botanical collections within the EOO of the four target species and confirm the strong association of all species with brigalow forest (Table 2). The targeted surveys also confirm the association of the four species with brigalow forest. However, 8% of *S. elachophyllum* historical records are from eucalypt-dominated vegetation. We also observed it in eucalypt forest during the surveys, but always near brigalow forest (Table 3).

Solanum adenophorum had the largest EOO and *S. johnsonianum* the smallest (Table 3, Fig. 1). *Solanum adenophorum* occurred in 26% (18/70), *S. dissectum* 32% (18/57), *S. elachophyllum* 56% (52/93) and *S. johnsonianum* 78% (56/78) of sites in remnant brigalow. For the sites where the species were present, population densities in remnant brigalow have high standard error estimates, and in the case of *S. adenophorum* this is higher than the weighted

average. The weighted average is relatively low for *S. adenophorum*, moderate for *S. dissectum* and *S. elachophyllum* and high for *S. johnsonianum* (Table 3). Estimates for pre-clearing population sizes are in the millions and tens of millions (Table 3). Within remnant brigalow habitat all species have undergone > 93% reductions in population size, and decline is even greater if remnants with < 50% canopy are considered inviable habitat. Assuming future decline in inviable habitat, the decrease in population size will be > 98% for *S. dissectum* and *S. johnsonianum*, and > 95% for *S. adenophorum* and *S. elachophyllum*. *Solanum elachophyllum* occurs in eight non-brigalow habitat sites of a total of 65 sites and five sites of cleared brigalow (Table 3), thus the assumption that persistence requires remnant brigalow forest is least valid for this species.

Of the confirmed locations, five sites (28%) for *S. adenophorum*, 10 sites (53%) for *S. dissectum*, 28 sites (48%) for *S. elachophyllum* and 30 sites (58%) for *S. johnsonianum* are in remnants with a high edge-to-area ratio (> 0.15 km/ha) and low tree canopy cover (< 50%) (Fig. 2). The proportion of degraded habitat (< 50% canopy cover) of *S. dissectum* and *S. johnsonianum*, both of which occur in the southern portion of the study area, is generally lower than for the other two species (Fig. 1).

Solanum elachophyllum occurred in 17% (8/48) and *S. adenophorum* in 9% (3/32) of the searches in cleared brigalow, whereas *S. johnsonianum* and *S. dissectum* did not occur in these searches (0/21, 0/19 respectively; Table 3). *Solanum elachophyllum* occurred in 49% and *Solanum adenophorum* in only 2% of the surveyed cleared brigalow area (Table 3).

Association with tree canopy and exotic grass cover

Buffel grass was the main invasive species in the target species' habitat but green panic *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs was also common. At the line-intercept level mean exotic grass cover was 14.8% for *S. adenophorum*, 9.2% for *S. dissectum*, 8.9% for *S. elachophyllum* and 16.4% for *S. johnsonianum*. Out of 49 line-intercepts only three (one for *S. elachophyllum*, two for *S. johnsonianum*) had > 40%, and none had > 50% exotic grass cover. Mean tree canopy cover was 44.6% for *S. elachophyllum*, 52.4% for *S. adenophorum*, 53.6% for *S. dissectum* and 59.6% for *S. johnsonianum*.

Assessment of conservation status

The categorization of *S. adenophorum* as Vulnerable under criteria B2,b,c is predicated on a decline in association with an AOO of < 500 km² (Table 4). Based on current records the AOO calculated using the prescribed methodology is 12 × 4 km² = 48 km², but 94 km² based on the area of intact brigalow forest and the proportion of this occupied by the

species (Table 3). This species is subject to continuing decline (B2b), and extreme fluctuations (B2c; Table 4). *Solanum adenophorum* is regarded here as a short-lived ephemeral (< 3 years), and therefore assessment of decline defers to an estimated 10-year period, and it does not qualify as Vulnerable (population decline by > 50% over 10 years) under category A2.

Solanum dissectum and *S. johnsonianum* qualify for categorization as Critically Endangered under criterion A2c (Table 4). It is assumed here that the generation time of the clonal colonies of *S. dissectum*, *S. elachophyllum* and *S. johnsonianum* is at least 20 years (see below), and thus the assessment period is at least 60 years. This period coincides with the decimation of the brigalow ecosystem during 1950–2010, when this habitat declined by > 80% (Table 3).

Solanum elachophyllum persists in cleared and degraded brigalow habitat and also in non-brigalow habitat with low exotic grass cover (Table 4). Thus, it is not accurate to assume that the decline of brigalow habitat is a direct reflection of population reduction. Furthermore, the species has the largest EOO of all target species and an estimated population of > 23 million plants (Table 3). *Solanum elachophyllum* is categorized here as Near Threatened (Table 4).

Reservation status and land tenure

All species have < 1% of their habitat in conservation reserves, assuming *S. adenophorum* is no longer present in Dipperu National Park (Table 5). It is also known from Taunton National Park and these two reserves include the largest areas of brigalow forest in the region (Table 5). *Solanum elachophyllum* is known from five reserves and three of these have > 1,000 ha of habitat. *Solanum dissectum* and *S. johnsonianum* are both only reserved in Roundstone Conservation Park and Overdeen State Forest (Table 5).

The largest known populations of *S. dissectum* and *S. johnsonianum* occur in a 264 ha remnant of brigalow forest on freehold land (24°2'S, 150°20'E). Mining leases contain considerable areas of remnant brigalow forest within the geographical range of the four *Solanum* species, particularly within the range of *S. adenophorum* and *S. elachophyllum* (Supplementary Table 2).

Discussion

Our study supports the presumption that *S. adenophorum*, *S. dissectum*, *S. elachophyllum* and *S. johnsonianum* have a strong association with brigalow forest. However, *S. elachophyllum* also occurs in *Eucalyptus* forest, where brigalow and eucalypts co-occur in narrow banded zones on mixed sediments. *Solanum adenophorum* has been recorded in gidgee *Acacia cambagei* forest, an ecological analogue of brigalow forest in drier environments.

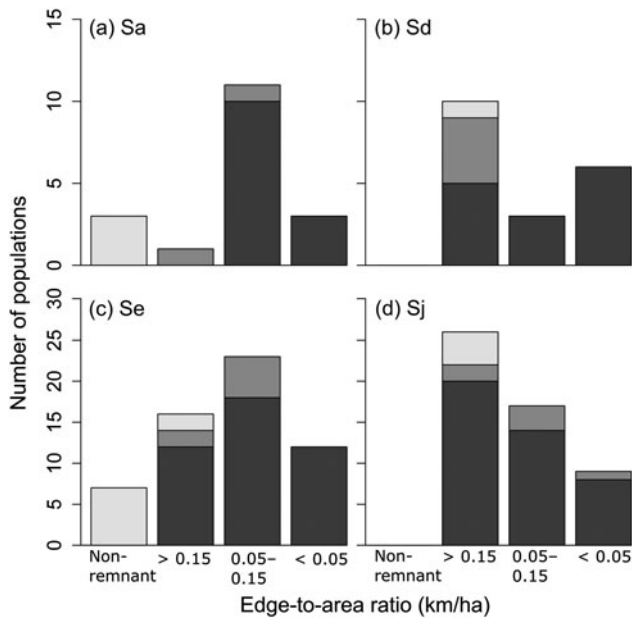


FIG. 2 Histogram of habitat condition for the current populations of (a) *S. adenophorum*, Sa; (b) *S. dissectum*, Sd; (c) *S. elachophyllum*, Se; and (d) *S. johnsonianum*, Sj. The x-axis categories are the edge-to-area ratio of habitat remnants and the bars are shaded according to tree canopy cover (light grey, 0–20%; medium grey, 21–50%; dark grey, ≥ 50%). Viable remnants are those with edge-to-area ratio < 0.15 km/ha and ≥ 50% canopy cover.

Extent of occurrence and population estimates varied substantially between species (Table 3). *Solanum elachophyllum* and *S. adenophorum* both had broad distributions and historical populations estimated as c. 6 and 50 million individuals, respectively (Table 3). *Solanum dissectum* and *S. johnsonianum* have relatively small EOOs but the latter is estimated to have had a much higher historical population than the former because it occurs more often within its EOO and at twice the density (Table 3). The brigalow forest has been extensively cleared during the last 60 years, having diminished in area by 93.5–98.0% for the four species (Table 3).

The current population estimates are generated by multiplying plant densities from extensive surveys by available habitat area. This is not the conventional method for estimating population size, which is usually done by direct survey (e.g. Shapcott et al., 2017). Our search effort was 0.19, 1.06, 0.44 and 2.22% of the available remnant brigalow within their EOOs for *S. adenophorum*, *S. dissectum*, *S. elachophyllum* and *S. johnsonianum*, respectively. The population sizes in remnant brigalow forest have declined to an estimated 100,000–2,000,000 (Table 3). However, the high standard errors (Table 3) indicate large variations in density. Although we surveyed only a limited proportion of available habitat and generated approximate population estimates, the method presented here is more realistic for Red List assessments than assuming population size based on direct

TABLE 4 Species assessment using the IUCN Red List criteria (IUCN, 2012) with justification using evidence from the current study. Only the criteria for the most threatened status are included. Unless otherwise indicated statistics are presented from Table 3.

Species	Red List status	Criteria	Relevant evidence
<i>S. adenophorum</i>	Vulnerable	B2b(iii),c(iv): AOO estimated to be < 2,000 km ² (2) & estimates indicating continuing decline, observed, inferred or projected (b), in area, extent and/or quality of habitat (iii), & extreme fluctuations (c) in number of mature individuals (iv)	Restricted to brigalow habitat (Table 2) that has been reduced to 566 km ² . The species was also recorded in 2.1% of the surveyed cleared brigalow habitat, although restricted to the limited areas not invaded by exotic grasses (RF & CH, pers. obs.). The species is restricted to areas with low cover of exotic grasses in brigalow habitat & has only 21 known populations, 28% of which are probably in inviable habitat (Fig. 2). Of the remaining brigalow habitat within the range of the species, only 64.8% is intact with ≥ 50% canopy cover; the remainder is mostly inviable because of invasion by exotic grasses. The species is short-lived & its population densities fluctuate dramatically depending on seasonal conditions. A historical population at Dipperu National Park was not relocated despite extensive searching.
<i>S. dissectum</i> , <i>S. johnsonianum</i>	Critically Endangered	A2ce: an observed, estimated, inferred or suspected population size reduction of ≥ 80% over three generations where the reduction or its causes may not have ceased (2), based on a decline in AOO, EOO and/or quality of habitat (c), and the effects of introduced taxa (e)	Restricted to brigalow habitat (Table 2) that has been reduced by > 90% over 60 years; species do not occur in cleared habitat & are restricted to areas with low cover of exotic grasses in brigalow habitat, > 53% of which is probably not viable (Fig. 2).

TABLE 5 Conservation reserves containing known populations of the four *Solanum* species and the area of remnant brigalow habitat in each reserve. *Solanum adenophorum* was collected in Dipperu National Park in 1971 but has not been located there since, despite considerable survey effort.

Reserve	Brigalow area (ha)	<i>S. adenophorum</i>	<i>S. dissectum</i>	<i>S. elachophyllum</i>	<i>S. johnsonianum</i>
Dipperu National Park (21°56'S, 148°43'E)	6273.4	Possibly			
Junee National Park and State Forest (22°49'S, 149° 2'E)	4703.2			Present	
Taunton National Park (23°32'S, 149°13'E)	3430.1	Present		Present	
Belmah Environmental Park (23°32'S, 148°15'E)	1196.4			Present	
Overdeen State Forest (24°16'S, 150°14'E)	384.8		Present		Present
Roundstone Regional Park and State Forest (24°38'S, 149°45'E)	257.8		Present	Present	Present
Blackwater Conservation Park (23°35'S, 148°49'E)	25.4			Present	
Per cent habitat in reserve		0.4 (1.1) ¹	0.3	1.0	0.3

¹The proportion of reserved habitat assuming *S. adenophorum* is still present at Dipperu is indicated in parentheses.

observations and counts in situations where there are large areas of un-surveyed habitat. We recommend that this method be adopted more widely in conservation status assessments.

Perennial forb species richness declines sharply when brigalow forest is cleared (Fairfax & Fensham, 2000). The four target *Solanum* species were not recorded in areas with > 50% exotic grass cover, and this level of cover is typically exceeded in cleared brigalow pastures. Both *S. elachophyllum* and *S. adenophorum* occur in cleared areas (Table 3), although the latter occurs only in areas where exotic grasses are sparse (RF & CH, pers. obs.). The populations that persist in cleared areas are unlikely to do so in the long term without intensive management to restore canopy cover for suppression of exotic grasses. Much of the remnant brigalow has been disturbed by clearing, drought or fire, and tree cover has been reduced, allowing exotic grasses to invade (Butler et al., 2014). The loss of these remnants as viable habitat will result in further decline. *Solanum adenophorum* and *S. elachophyllum* are likely to be more affected than the other two species (Table 3). A high proportion of the known locations of the four *Solanum* species is degraded, with an edge-to-area ratio > 0.15 km/ha or canopy cover < 50% (Fig. 2). These habitats are unlikely to be viable in the long term because of the destructive feedback between invasive grasses and fire. Reducing fuel loads resulting from exotic grasses can be most readily achieved by livestock grazing (Melzer, 2015), but the impact of grazing on *Solanum* is yet to be evaluated.

Some historical populations could not be relocated in our survey despite the brigalow habitat remaining intact since they were originally located. A population of *Solanum adenophorum* known from a specimen collected at Dipperu National Park in 1971 was not located after searching of 3.8 ha in 2014 and 1.8 ha in 2017. However, populations

of *S. adenophorum* were relocated at Taunton National Park where it had not been recorded for > 15 years despite substantial search effort (R. Melzer, pers. comm.). *Solanum adenophorum* is almost certainly ephemeral and was abundant at Taunton 1 month after 120 mm of rain in March 2017. The population sizes of *S. adenophorum* (Table 3) have probably been underestimated because most field surveys were conducted when antecedent rainfall had been slightly below average and the ephemeral populations had not reached their full potential because of dry conditions.

Security of existing remnants

Current Queensland state legislation prohibits the clearance of existing brigalow remnants on freehold land, but illegal clearing is an ongoing problem (Queensland Department of Science, 2016) and no protection is provided against mining and gas developments. There is an ongoing threat of exotic grass invasion accompanied by the incursion of fire, which degrades tree canopies and results in further exotic grass invasion (Butler & Fairfax, 2003).

Securing the single large remnant of brigalow forest on freehold land (24°02'S, 150°20'E) that contains the largest known populations of the Critically Endangered *S. dissectum* and *S. johnsonianum* would make a major contribution to their conservation.

Remnant brigalow forest on mining leases (Supplementary Table 2) are under threat as coal mines expand, but remnants that do not overlie extractable coal have potential for perpetual security as conservation reserves. Negotiated agreements over remnant vegetation within mining leases are an important priority for brigalow conservation, particularly for the preservation of *S. adenophorum* and *S. elachophyllum* (Supplementary Table 2).

Assessment of conservation status

The dataset accumulated in this study (Table 3; IUCN, 2012) facilitated quantitative assessment of the *Solanum* species using the IUCN Red List criteria. Determination of AOO is contingent on scale (Willis et al., 2003; Keith et al., 2017) and determining AOO with the recommended 2 km² grid (IUCN Standards & Petitions Subcommittee, 2017) generates results that differ from those determined by fine-scale mapping (Table 3). If the grid method is applied to current known records, it underestimates the AOO of *S. adenophorum*, *S. dissectum* and *S. elachophyllum*, and overestimates that of *S. johnsonianum* relative to the mapping of remnant or intact brigalow habitat (Table 3). Underestimation will result from methods that fail to model undetected subpopulations in un-surveyed habitat, and overestimation using the 2 km² grid will occur when habitat occupies only a portion of the grid cells. Both the grid-based and mapped habitat method of determining AOO for *Solanum adenophorum* result in estimates < 500 km² and justify a categorization as Vulnerable. The difference between the grid-based and mapped habitat assessment of AOO does not affect the categorization of *S. dissectum*, *S. elachophyllum* and *S. johnsonianum*, which do not qualify under category B (geographical range size, and fragmentation, decline or fluctuations) because they only satisfy one of the subcriteria (b, continuing decline). Assigning *S. dissectum* and *S. johnsonianum* under criterion A (declining population, past, present and/or projected) requires an estimation of time frame based on the generation time of the species. Calculations of generation time can be derived from survival and fecundity rates of different aged individuals (IUCN Standards & Petitions Subcommittee, 2017), all of which are poorly defined for semi-woody clonal plant species. Therefore, we have assumed that generation time is > 20 years based on apparently low rates of germination and the potential for survival by regeneration of ephemeral ramets from perennial rootstocks. Additional tools for determining the generation time of plant lifeforms would be of considerable assistance for assessing species under categories A and C of the IUCN Red List criteria.

Conclusion

Solanum adenophorum, *S. dissectum* and *S. johnsonianum* are threatened because of their close association with an ecosystem that has been decimated over the past 60 years. These species and *S. elachophyllum* will decline further because they are extirpated where exotic grass cover is high, and many remnants of brigalow are already degraded by fire and invasion of exotic grasses. Many existing populations of the *Solanum* species will probably become extinct because they occur in inviable remnants, such as roadsides, that will be degraded by the same processes. The highest priority for conservation of these threatened *Solanum* species is the

preservation of the last large remnants of brigalow forest and the management of exotic grasses around these remnants to avoid the destructive effects of the grass–fire cycle.

This study presents an example of a Red List assessment of poorly known plant species by (1) supplementing historical records with systematic surveys to accurately determine EOO, (2) identifying the habitat association of the target species, (3) establishing persistence in transformed habitat, (4) identifying the factors that limit distribution in transformed habitat, (5) inferring population size from density and available habitat, and (6) employing habitat mapping to define past declines and predict ongoing threats.

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Author contributions Study design: RF; fieldwork: RF, JH and CH and BW; analysis: BW; writing: RF, BW.

Conflicts of interest None.

Ethical standards This research complies with the *Oryx* Code of Conduct.

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