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
Despite the threat to plant biodiversity posed by habitat loss, fragmentation and invasion by exotic species, quantification of their consequences for individual species are lacking. Since the 1950s, brigalow (*Acacia harpophylla*) forests in Australia have been extensively cleared and converted to pastures dominated by exotic grasses. Habitat requirements, population numbers and an assessment of the magnitude of threatening processes were undertaken for four poorly known bush tomato species, *Solanum adenophorum, S. dissectum, S. elachophyllum* and *S. johnsonianum*. Herbarium records and surveys demonstrated a strong association with brigalow habitat, although *S. elachophyllum* did occur in other habitat. Historical and current population estimates were derived from plant densities at current sites and the area of mapped brigalow habitat. Estimates of density are imprecise because of a high degree of variability in survey data, but the assessment indicates population declines greater than 93%. *S. dissectum* and *S. johnsonianum* did not persist in cleared brigalow habitat, while *S. adenophorum* and *S. elachophyllum* had some capacity to persist in clearings. None of the species occur where the exotic grass cover is greater than 40%. Between 27% and 57% of the records of the four species are located in high edge:area or open (<50% cover) brigalow remnants highly vulnerable to invasive grasses. The current study presents an example of accurate Red List assessment of poorly known plant species and recommends *S. dissectum* and *S. johnsonianum* as Critically Endangered; *S. adenophorum* as Vulnerable; and *S. elachophyllum*, as Near threatened.

Introduction

The most widely used and authoritative conservation assessment of the world's flora is represented by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (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 with the benefit of comprehensive surveys of their native populations (Brummitt et al., 2015). Habitat loss (Krauss et al., 2010) and the invasion of habitat by exotic species (Daehler & Strong, 1994) are widespread threats to plant species. While decline has been inferred from historical and current collecting records (Robbirt et al., 2006; Brummitt et al., 2015), and decline has been estimated from the results of disease (Schwartz et al., 2000), there has been no published attempts to quantify the response of individual plant species to past declines and future threats to habitat quality. This is a major omission given the importance of this process for assessing the threat status of the world's flora under the Red List criteria (Mace et al., 2008).

There is a general recognition that rarity alone does not determine extinction risk and the revised Red List criteria have very low thresholds for population size and Extent of occurrence (EOO, IUCN, 2012) for species that have not declined (IUCN, 2012). The species of greatest concern are those species that were once common but are subject to ongoing threatening processes (McIntyre & Lavorel, 1994; Burgman, 2002). However, the magnitude of historical and continuing declines is difficult to accurately assess and requires a clear understanding of species response to potentially threatening processes. To address this problem, it is necessary to design and implement systematic surveys and assessments that present a blue-print for a quantified evaluation under the IUCN guidelines.

The threat status of most plant species is not usually derived by a systematic assessment of population density across the area of occupancy (AOO) (i.e. Keith, 2000) and conservative extrapolations to available habitat (see Silcock et al., 2014). The current study provides a methodological standard for the assessment of the conservation status of plant species where habitat loss and decline of habitat quality can be assessed. The aim of this study is to generate adequate survey data to provide a quantitative assessment of the threat status of four species of *Solanum* associated with the brigalow (*Acacia harpophylla* F.Muell. ex Benth,)-dominated forest of eastern Australia. This forest type has been reduced to about 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 mapping of habitat loss as a surrogate for population decline. The study proceeds to demonstrate how the ongoing advance of invasive grasses impact on the target *Solanum* species. This information is integrated using transparent assumptions to determine historical and current population estimates. Threatening processes are quantified to evaluate the threat status of the species using IUCN Red List criteria and general management recommendations for the habitat of the *Solanum* species are provided.

Study area and study species

The Brigalow Belt consists of two biogeographic regions spanning a subcoastal area in the east of 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, experiencing summer-dominant rainfall with annual rainfall throughout the ranges of the *Solanum* species averaging 521-716 mm (modelled data from Jeffrey et al., 2001). The brigalow forest generally has a dense tree canopy resulting in a sparse ground layer of herbaceous vegetation which ensures that when 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 extensive brigalow forest were mostly converted to pastures and crops within a 50 year period during the latter half of the twentieth century (Seabrook et al., 2006; Fensham et al., 2017). Fragmented forest remnants surrounded by productive pastures for cattle farming, mostly dominated by the African species buffel grass (*Cenchrus ciliaris* L.) are all that remain. 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 canopies further facilitate buffel grass invasion as 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 (*Acacia harpophylla* dominant and co-dominant) ecological community has a threatened status under the Australian Government *Environment Protection and Biodiversity Conservation Act 1999* (EPBC).

Potentially threatened plant species have been identified based on their association with brigalow forest and the region where the clearance of brigalow forest has occurred (Fensham et al., 2018). The genus *Solanum* exhibits substantial radiation in the brigalow ecosystem (Bean, 2004), and four species in that genus, namely *Solanum adenophorum* F. Muell., *S. dissectum* Symon, *S. elachophyllum* F.Muell. and *S. johnsonianum* A.R.Bean (Fig. 2), were second, third, sixth and ninth on this list respectively.

Solanum is by far the largest genus in the family Solanaceae, containing over 1250 species globally (Weese & Bohs, 2007). *Solanum* is mostly represented on the IUCN Red List by species from South and Central America and there are no Australian species currently listed (Table 1). The 'spiny *Solanum* clade' (subgenus *Leptostemonum*) is the largest subgenus, with ca. 450 species worldwide (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 of the four target species are listed as Endangered under Queensland Government *Nature Conservation Act 1992* (NCA) (Table 1). *Solanum adenophorum, S. dissectum,* and *S. johnsonianum* are the only *Solanum* species listed as Endangered under Australian Government legislation and *S. elachophyllum* is not listed under any threat category (Table 1). However, the assessment of these species and the majority of plant species assessed using Red List criteria (IUCN, 2012) for international, national or provincial listings relies heavily on expert opinion and only patchy information exists about plant populations across the geographic range of a species. Discrepancies in the status of *Solanum* species between national and state jurisdictions (Table 1) provides a clear imperative to upgrade listings with current information, such as the systematic surveys presented here, and to align lists including an update of the IUCN Red List for *Solanum* from Australia.

Materials and methods

Regional ecosystem mapping

This study establishes associations between Solanum species and native habitats from Regional Ecosystem maps in Queensland Australia (Queensland Herbarium, 2016). We use these maps to document habitat decline as they represent a complete coverage of Regional Ecosystems prior to extensive human modification by forest clearance (Queensland Herbarium, 2016). Regional Ecosystems are defined by combinations of biogeographic region, geological substrate and dominant vegetation type that are then grouped into Broad Vegetation Groups.

Broad Vegetation Groups (BVGs) are a higher-level grouping that combine Regional Ecosystems, and the brigalow forests are represented as unit 25: *Acacia harpophylla* (brigalow) sometimes with *Casuarina cristata* Miq. (belah) open forests to woodlands on heavy clay soils (Neldner et al., 2015). Another BVG dominated by species related to brigalow is unit 26: *Acacia cambagei* R.T.Baker (gidgee)/*A. georginae* F.M.Bailey (georgina gidgee)/*A. 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. Allocation of search effort is based on the Regional Ecosystem mapping.

Pre-existing models suggest that on average buffel grass cover reaches 30% when forest canopy is reduced to 50% of original canopy cover (Butler et al., 2014). In the current study it is assumed that areas with less than 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 the *Solanum* species in the long-term. Additional mapping was conducted to distinguish ‘intact’ (≥50% tree cover) and degraded remnant habitat (<50% tree cover) using visual assessment of DMC-3 imagery (2017). This information is used to assess the likely magnitude of ‘ongoing decline’ under IUCN Red list criteria.

Habitat association, distribution and density

Historical records from the Queensland Herbarium database were used to quantify previous search effort across the habitats within the EOO of the four species as it was known from collecting locations in 2012. Records with the same geographic coordinate and date of survey were aggregated as one single record. All records were assigned 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 evaluating the habitat specificity of the four Solanum species.

Field survey

Field surveys were conducted in February-October 2012, November 2013-May 2014 and May 2017. These surveys were undertaken to confirm historical records, to search for new populations within and up to 80 km from the geographic range as it was known from collecting locations in 2012, and to assess the habitat association of the species following the procedures of Keith (2000). Previous 6 months’ rainfall was above average for 2012 and 2017 and slightly lower than average, during other times. 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 pasture dominated by buffel grass) and other vegetation types were also surveyed (Table 3). A total of 741 locations were surveyed 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. Surveys were conducted in all designated conservation reserves within the EOO of the four species. To estimate population densities at each location, search distance was measured using GPS tracking along linear transects, the number of plants was counted within a width of either 4 m or 6 m, and the search area derived as the search distance multiplied by the width. Surveyed areas for individual species within remnant brigalow varied between 47.5 ha and 195.4 ha (Table 3). The life history and regeneration of the species was observed during the surveys. These observations indicated that vegetative shoots can be connected by underground suckers (forming a single genet), each emergent shoot (ramet) was treated as an individual plant.

Population assessment

Population sizes were estimated 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 a weighted average was used to calculate densities (in plants per hectare):

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

with *x* the count 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*) can also be generated:

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

The total pre-clearing, remnant and intact areas were multiplied by the proportion of the presences at surveyed sites (*P* in Table 2) and the respective densities of species to provide an estimate of the total population of each species. The historical population estimates assume that historical plant densities were the same as current densities. The proportion of remnant habitat relative to pre-clearing habitat was used to assess past decline, and the proportion of intact habitat relative to remnant habitat used to assess the magnitude of ongoing decline.

A visual assessment of average canopy cover using DMC-3 imagery (2017); and the edge to area ratio of remnant brigalow habitat was determined for the current localities of the target species. We use the proportion of populations where the remnant habitat has an edge (km):area (ha) ratio greater than 0.15 or with less than 50% canopy cover as inviable habitat and to further assess the magnitude of 'ongoing decline' under IUCN Red List criteria.

Association with tree canopy and exotic grass cover

The following data was collected to establish relationships between the occurrence of the four *Solanum* species and perennial grasses and tree cover. 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 meter along the tape the presence or absence of a tree canopy, a perennial grass tussock and a *Solanum* colony (a group of plants with distances between stems less than 1 m) was determined (i.e. 50 intercepts for each attribute)**.**

Assessment of threat status

An assessment of threat status according to IUCN Red List criteria (IUCN, 2012) was conducted following guidelines in IUCN Standards and Petitions Subcommittee (2017). 'Estimated' plant density is here based on a replicated sample of sub-populations. Population size and decline are 'inferred' in that they are indirectly derived from estimated plant density and comprehensively mapped areas of available habitat.

AOO was calculated using a 4 km^2 grid prescribed by IUCN Standards and Petitions Subcommittee (2017) but decline in population size used the regional ecosystem mapping as high resolution 'habitat maps'. This variation in procedure is justified because it represents a modelling of sub-populations occurring in past and present suitable habitat that has not been surveyed.

Reservation status and land tenure

The occurrence of populations of the four *Solanum* species in National Parks and other conservation reserves was collated, and the tenure of other large brigalow remnants within the EOO of the four species investigated.

Results

Life history and habit observations

No seedlings (cotyledons or small-statured plants without fertile parts) were observed for any of the *Solanum* species during the surveys. The stems of *Solanum adenophorum* are not woody and populations that are abundant in wet seasons disappear or dwindle dramatically during dry seasons. 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 (R. Fensham pers. obs.). Excavation of the other three species revealed lateral stems regenerating clonal shoots from rhizomes. These species are perennial sub-shrubs with woody stems, although rhizomes grow more or less aerial shoots depending on seasonal conditions and all shoots can flower and fruit rapidly in response to rain events.

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. It was also observed 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). *S. 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 more than 93% reductions in population size, and decline is even greater if remnants with <50% canopy are considered inviable habitat (see above). Assuming future decline in inviable habitat *Solanum dissectum* and *S. johnsonianum* will undergo more than 98% contraction, and *Solanum adenophorum* and *S. elachophyllum* will undergo more than 95% contraction. *S. elachophyllum* occurs in eight non-brigalow habitat sites of a total of 65 sites and five sites of cleared brigalow (Table 3) and the assumptions of decline for this species are least valid.

Of the confirmed locations, five sites (28%) for *S. adenophorum,* ten sites (53%) for *S. dissectum,* 28 sites (48%) for *S. elachophyllum* and 30 sites (58%) for *S. johnsonianum* are in high edge:area remnants (<0.15) with low tree canopy cover (<50%)(Fig. 3). The habitat (i.e. less than 50% canopy cover) of *S. dissectum* and *S. johnsonianum,* both of which occur in the southern portion of the study area, is generally less degraded than for the other two species (Fig. 1).

S. elachophyllum occurred in 17% (8/48), *S. adenophorum* in 9% (3/32), and *S. johnsonianum* and *S. dissectum* in 0% (0/21, 0/19 respectively) of the searches in cleared brigalow (Table 3). *S. elachophyllum* occurred in 49% of the total searched area of cleared brigalow. *Solanum adenophorum* occurred 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 habitat of the target species but green panic (*Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.L.Jacobs) was also predominant. 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*. From 49 line-intercepts only three (one for *S. elachophyllum*, two for *S. johnsonianum*) had more than 40% exotic grass cover and none had more than 50% exotic grass cover. Mean tree canopy cover varied between 52.4% for *S. adenophorum*, 53.6% for *S. dissectum*, 44.6% for *S. elachophyllum* and 59.6% for *S. johnsonianum*.

Assessment of threat status

The categorisation of *Solanum adenophorum* as Vulnerable under Category B2,b,c is predicated on decline in association with an AOO less than 500 km^2 (Table 5). Based on current records the AOO calculated using the prescribed methodology is 12×4 km^2 = 48 km^2, but 94 km^2 based on the area of intact brigalow forest, and the proportion occupied by the species (Table 3). Decline for this species is justified based on b) continuing decline; and c) extreme fluctuations (Table 5). *Solanum adenophorum* is regarded here as a short-lived ephemeral (less than three 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.

S. dissectum and *S. johnsonianum* are categorised as Critically Endangered under criterion A2c (Table 5). 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 is the period coinciding with the decimation of the brigalow ecosystem between 1950 and 2010, with this habitat having declined over that period by more than 80% (Table 3).

S. elachophyllum persists in cleared and degraded brigalow habitat and also persists in non-brigalow habitat providing exotic grass cover is low (Table 5). 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 species and an estimated population of more than 23 million plants (Table 3). *S. elachophyllum* qualifies for a Near Threatened status (Table 5).

Reservation status and land tenure

All species have less than 1.0% of their habitat in conservation reserve assuming *Solanum adenophorum* is no longer present in Dipperu National Park (Table 4). It is also known from Taunton National Park and these two reserves include the largest areas of brigalow forest in the region (Table 4). *S. elachophyllum* is known from five reserves and three of these have more than 1000 ha of habitat. *S. dissectum* and *S. johnsonianum* are both only reserved in Roundstone Conservation Park and Overdeen State Forest (Table 4).

The largest known populations of *S. dissectum* and *S. johnsonianum* occur in a 264 ha remnant of brigalow forest on freehold land (-24.04, 150.34). Mining leases contain considerable areas of remnant brigalow forest within the geographic range of the four *Solanum* species, but particularly within the range of *Solanum adenophorum* and *S. elachophyllum* (Supplementary Table 2).

Discussion

Ours study supports the assumption 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. *S. adenophorum* has been recorded in gidgee (*Acacia cambagei*) forest, an ecological analogue of brigalow forest in drier environments.

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

The current population estimates are generated by multiplying plant densities from extensive surveys with available habitat area. This is not the conventional method for estimating populations size, which usually assumes that known populations represent total populations and generate much lower population estimates (e.g. Shapcott et al., 2017). Search effort is 0.19%, 1.06%, 0.44%, 2.22% respectively for *S. adenophorum*, *S. dissectum*, *S. elachophyllum*, *S. johnsonianum* of the available remnant brigalow within their respective EOOs. The predicted population sizes in remnant brigalow representing viable habitat have declined to estimates in the order of 10^5 and 10^6 (Table 3). However, the high standard errors presented here (Table 3) indicate large variation in density. Despite surveying only a limited proportion of available habitat and approximate population estimates, the method presented here is more realistic for Red Listing purposes than assuming population based on observations and counts in situations where there are large portions of un-surveyed habitat. It is recommended that this method be adopted more widely in threat status assessments.

Perennial forb richness declines sharply when brigalow forest is cleared (Fairfax & Fensham, 2000). The four target *Solanum* species were not recorded in areas with greater than 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 (R. Fensham, C. Hansen pers. obs.). The populations that persist in cleared areas are unlikely to persist in the long-term without intensive management to restore canopy cover so that exotic grasses can be suppressed. 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 predicted loss of these remnants as viable habitat will result in further decline, *S. adenophorum* and *S. elachophyllum* are likely to be more impacted than the other two species (Table 3). A high proportion of the known locations of the four *Solanum* species demonstrate this state of degradation (presence in habitat with edge: area ratio >0.15 or canopy <50%) (Fig. 3). These habitats are unlikely to be viable in the long-term because of the destructive feedback between invasive grasses and fire. Reducing fuel loads with exotic grasses can be most readily achieved by livestock grazing (Melzer, 2015), although the impacts of grazing on *Solanum* are yet to be evaluated. The propagation of the species is unexplored and translocation under the variable climate occupied by brigalow (Fensham et al., 2017) appears to be difficult and should be a lower priority than preserving the natural sub-populations.

Some historical populations were not confirmed by the current 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 3.8 ha of searching in 2014 and 1.8 ha in 2017. However, populations of *S. adenophorum* were relocated at Taunton National Park while it had not been recorded for over 15 years despite substantial search effort (R. Melzer pers. comm.). *S. adenophorum* is almost certainly ephemeral and was abundant at Taunton a month after 120 mm of rain in March 2017. Population estimates of *S. adenophorum* (Table 3) are probably underestimated as most field surveys were conducted during conditions when antecedent rainfall is slightly lower than average and the ephemeral populations have not realized their potential.

Security of existing remnants

The current Queensland state legislation prohibits the clearance of existing remnants on freehold land. Illegal clearing is still an ongoing problem (Queensland Department of Science, 2016) and no protection is provided against mining and gas developments. Furthermore 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).

The large remnants of brigalow forest provide little economic value for meat or grain production unless they are cleared. The acquisition for off-setting of large remnants would redress the financial inequity of large remnants of brigalow forest on freehold land and engender a sense of value in an important conservation asset. Securing the single large remnant of brigalow forest on freehold land (-24.04, 150.34) that contains the largest known populations of *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 overly extractable coal have great potential for perpetual security as conservation reserves. Negotiated agreements over remnant vegetation within mining leases are an important priority for brigalow conservation and particularly for the preservation of *Solanum adenophorum* and *S. elachophyllum* (Supplementary Table 2).

Assessment of threat status

The comprehensive dataset accumulated by this study (Table 3; IUCN, 2012) allowed for quantitative assessment of the *Solanum* species under the IUCN Red Book criteria. It is well known that the determination of AOO is contingent on scale (Willis et al., 2003; Keith et al., 2017) and determining AOO under the recommended guidelines of a 2 km^2 grid (IUCN Standards and Petitions Subcommittee, 2017) generates results that vary from those determined from fine-scale mapping (Table 3). If the grid method is applied to current known records it underestimates the AOO of *S. adenophorum, S. dissectum, S. elachophyllum* and overestimates the AOO 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 sub-populations in un-surveyed habitat, and overestimation using the 2 km^2 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 less than 500 km^2 and result in a Vulnerable categorization. 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 (geographic range size, and fragmentation, decline, or fluctuations) because they only satisfy one of the sub-criteria (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 and Petitions Subcommittee, 2017), all of which are poorly defined for semi-woody clonal plant species.Therefore,we have assumed that generation time is more than 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 in the past 60 years. These species and *S. elachophyllum* will decline further because they are extirpated where the cover of exotic grasses is high, and many remnants of brigalow are already degraded by fire and exotic grasses invasions. 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 the 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.

The current study presents an example of accurate Red List assessment of poorly known plant species by 1) supplementing historical records with systematic survey to accurately determine EOO; 2) the identification of the habitat association of target species; 3) establishing persistence in transformed habitat; 4) identification of factors limiting the distribution in transformed habitat; 5) inferring population size from density and available habitat; and 6) employing habitat mapping to define past declines and predict future ongoing threats.

Author contributions

RF designed the study, conducted some of the fieldwork and wrote the manuscript. JH and CH contributed data from their fieldwork. BL conducted some of the fieldwork and the analysis. BW conducted fieldwork and completed a first draft of the analysis and report.

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Conflicts of interest

None.

Ethical standards

All research presented here complies with the Code of Conduct for authors contributing articles to *Oryx.*

References

Biographical sketches

Rod Fensham seeks to build an understanding of the ecological issues required to manage and conserve the natural environment of the north-eastern quarter of the Australian continent. Jason Halford is interested in the ecology and conservation of threatened plants and manages an extensive seedbank. Chris Hansen is an environmental consultant who works to maximize plant conservation in the face of development. Boris Laffineur manages and analyses spatial and ecological data to enhance the conservation of vegetation. Billie Williams worked on this study as a student and has since become a school teacher.

Supplementary Material

Supplementary Table 1. Broad habitat categories assigned to the collecting records within the extent of occurrence of the four target species.

Supplementary Table 2. Mining leases and the areas (>200ha) of remnant brigalow habitat within the geographic range of the four *Solanum* species (Sa: *S. adenophorum*; Sd: *S. dissectum*; Se: *S. elachophyllum*; Sj: *S. johnsonianum*).

Table 1. Threat status of *Solanum* species in various countries and regions with authorities in brackets (IUCN; EPBC; NCA). The target species in this analysis are indicated as *Sa*, *S. adenophorum; Sd, S. dissectum; Se Solanum elachophyllum; Sj S. johnsonianum.*

Jurisdiction	Vulnerable	Endangered	Critically endangered	Extinct
South-Central America (IUCN)	11	7	3	0
Australia (IUCN)	0	0	0	0
Other (IUCN)	2	1	3	0
Australian Government (EPBC listing)	2	3 (*Sa, Sd, Sj*)	0	1
Queensland (NCA)	5	12 (*Sa, Sd, Se, Sj*)	NA	0
Other Australian states (Relevant state legislation)	2	7	0	1

Table 2. Number of specimen records from the Queensland Herbarium with a unique location and date, classified by Broad Vegetation Groups (numbers in brackets after Neldner et al., 2015) within the Extent of Occurrence of the four target *Solanum* species. The records for the four target species are excluded but are included in brackets.

Habitat	*S. adenophorum*	*S. dissectum*	*S. elachophyllum*	*S. johnsonianum*
Brigalow/gidgee (25,26)	196 (13)	152 (17)	412 (28)	170 (23)
Cleared Brigalow/gidgee (25, 26)	41 (1)	25 (1)	76 (4)	19
Alluvial woodland (16, 21, 34)	54	91	130	56
Dry rainforest (5, 6, 7)	77	22	49	16
Grassland (30)	96	7	49	11
Eucalypt (10, 11, 12, 13, 17, 18, 20)	443	261	1266 (3)	129
Other Acacia (24)	47	22	95	16
Cleared and disturbed (All except 25, 26)	10	11	28	6

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 ≥50% canopy cover). Summary of characteristics, habitat, survey, population and decline within the EOO of the four target species. Pre-clearing refer to habitat prior to clearing, remnant to non-cleared habitat in 2017 and intact to remnant brigalow with ≥50% canopy cover.

	S. adenophorum	*S. dissectum*	*S. elachophyllum*	*S. johnsonianum*
Extent of occurrence, km^2	21612	7172	23836	4962
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 *P* below	8677; 2231	2213; 699	9762; 5458	2503; 1947
Remnant brigalow, km^2; Area of habitat where species present assuming *P* below	566; 146	45; 14	442; 247	49; 38
Intact brigalow, km^2; Area of habitat where species present assuming *P* 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 (*P*)(area of search, 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 (area of search, 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 (area of search, 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 (area of search, 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.ha^{-1}±SE	26.4±31.0	81.8±33.5	86.2±59.5	151.9±65.5
Estimated historical population in brigalow, 1000s ±SE	5900±6917	5721±2339	47047±32459	29570±12752
Estimated current population in remnant brigalow, 1000s±SE (Decline, %)	385±452 (93.5)	117±48 (98.0)	2131±1470 (95.5)	580±250 (98.0)
Estimated current population in intact brigalow, 1000s±SE (Decline, %)	250±293 (95.8)	115±47 (98.0)	1662±1146 (96.5)	565±244 (98.1)

Table 4. Conservation reserves containing known populations of four *Solanum* species and the area of remnant brigalow in each reserve. *S. adenophorum* was collected in Dipperu National Park in 1971 but has not been located since despite considerable survey and the proportion of reserved habitat assuming it occurs in this reserve is indicated in brackets.

Reserve	Brigalow area (ha)	*S. adenophorum*	*S. dissectum*	*S. elachophyllum*	*S. johnsonianum*
Dipperu National Park (-21.937, 148.714)	6273.4	Possibly			
Junee National Park and State Forest (-22.821, 149.039)	4703.2			Present	
Taunton National Park (-23.533, 149.212)	3430.1	Present		Present	
Belmah Environmental Park (-23.54, 148.257)	1196.4			Present	
Overdeen State Forest (-24.264, 150.241)	384.83		Present		Present
Roundstone Regional Park and State Forest (-24.629, 149.751)	257.8		Present	Present	Present
Blackwater Conservation Park (-23.584, 148.811)	25.4			Present	
Percentage habitat in reserve		0.4 (1.1)	0.3	1.0	0.3

Table 5. Species assessment against IUCN criteria 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	Threat code	IUCN criteria	Threat status	Relevant evidence
S. adenophorum	B2	AOO estimated to be less than 2000 km$^{2-,}$ and estimates indicating…b. Continuing decline, observed, inferred or projected, in….(iii) area, extent and/or quality of habitat…c. Extreme fluctuations in (iv) number of mature individuals.	Vulnerable	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 within these areas the populations were restricted to the limited areas not invaded by exotic grasses (R. Fensham, C. Hansen pers. obs.). The species is restricted to areas with low cover of exotic grasses in brigalow habitat, and has only 21 known populations, 28% of which are probably not viable habitat (Fig. 3). Of the remaining brigalow habitat within the range of the species, only 64.8% is intact with ≥50% canopy cover the remainder mostly being inviable habitat because of invasion by exotic grasses. The species is short-lived and its population densities are known to fluctuate dramatically in relation to seasonal conditions. An historical population at Dipperu National Park has not been relocated despite extensive searching.
S. dissectum, S. johnsonianum	A2	An observed, estimated, inferred or suspected population size reduction of ≥80% over … three generations … where the reduction or its causes may not have ceased … based on (and specifying) …c. a decline in AOO, EOO and/or quality of habitat,…e. the effects of introduced taxa, …	Critically Endangered	Restricted to brigalow habitat (Table 2) that has been reduced by more than 90% over 60 years; the species do not occur in cleared habitat; the species are restricted to areas with low cover of exotic grasses in brigalow habitat, more than 53% of which are probably not viable habitat (Fig. 3)

S. elachophyllum	A2	An observed, estimated, inferred or suspected population size reduction of ≥50% over … three generations … where the reduction or its causes may not have ceased … based on (and specifying) …c. a decline in AOO, EOO and/or quality of habitat,…e. the effects of introduced taxa, …	Near threatened	Mostly restricted to brigalow habitat (Table 2) that has been reduced by more than 90% over 60 years; however the species also occurs in eight (17%) of surveyed sites in non-remnant brigalow and also in other habitats including eucalypt woodland that has been less extensively cleared than brigalow (Queensland Herbarium, 2016). The species is restricted to areas with low cover of exotic grasses in brigalow habitat, 48% of which are probably not viable habitat (Fig. 3). Of the remaining brigalow habitat within the range of the species, 21.9% has less than 50% canopy cover and is likely to be inviable habitat because of invasion by exotic grasses. There are an estimated 1.6 million plants remaining intact habitat over an area of 23836 km^2.

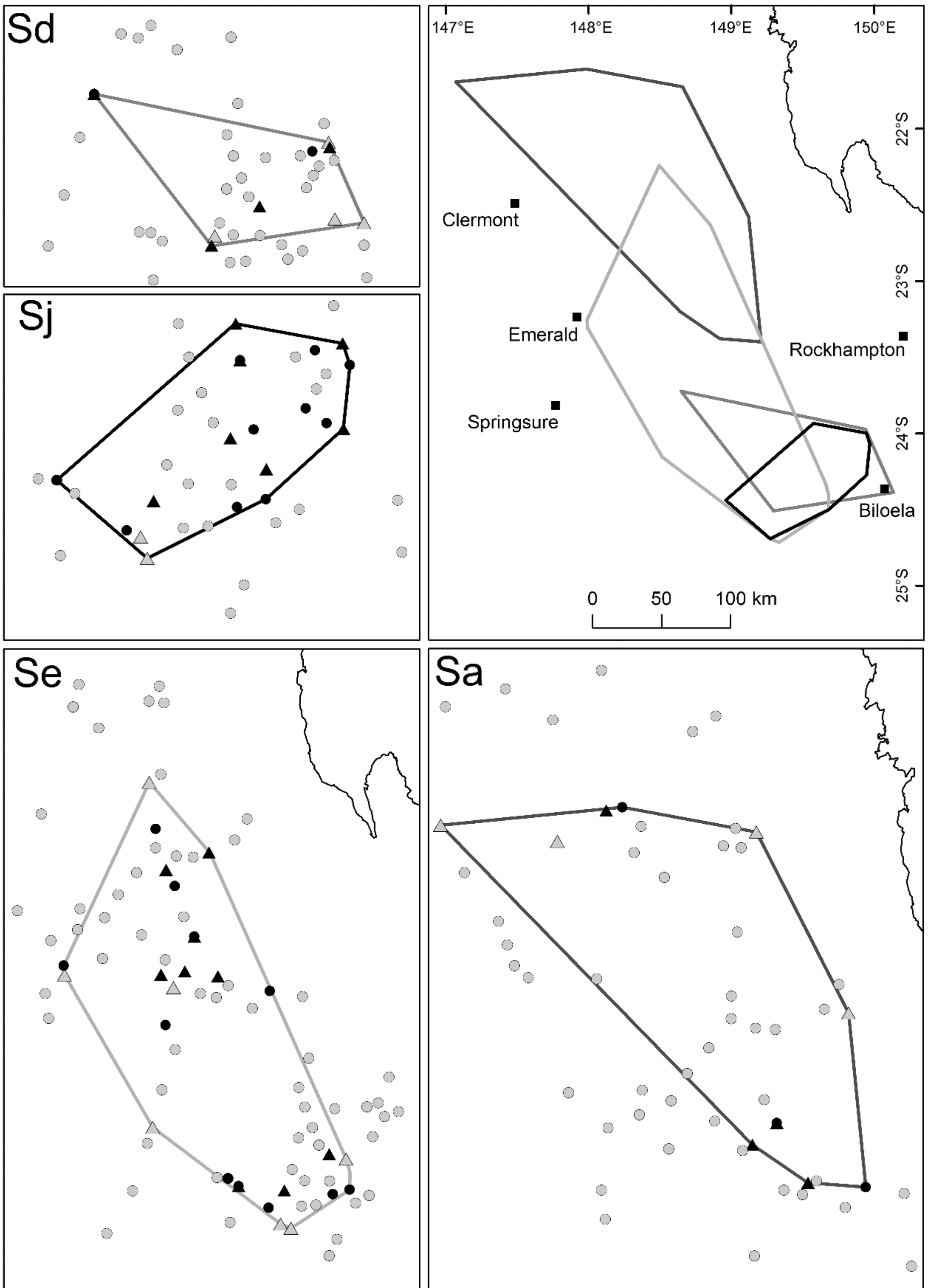

Figure 1. The EOO (convex polygons) of the four *Solanum* species in relation to the north-east coast of Australia (top right); and the location of sites used to define the distribution of *S. adenophorum* (Sa), *S. dissectum* (Sd), *S. elachophyllum* (Se) and *S. johnsonianum* (Sj). Triangles represent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

Figure 2. The four species of *Solanum* forming the target of this study; *S. adenophorum* (top left), *S. dissectum* (top right), *S. elachophyllum* (bottom left), *S. johnsonianum* (bottom right).

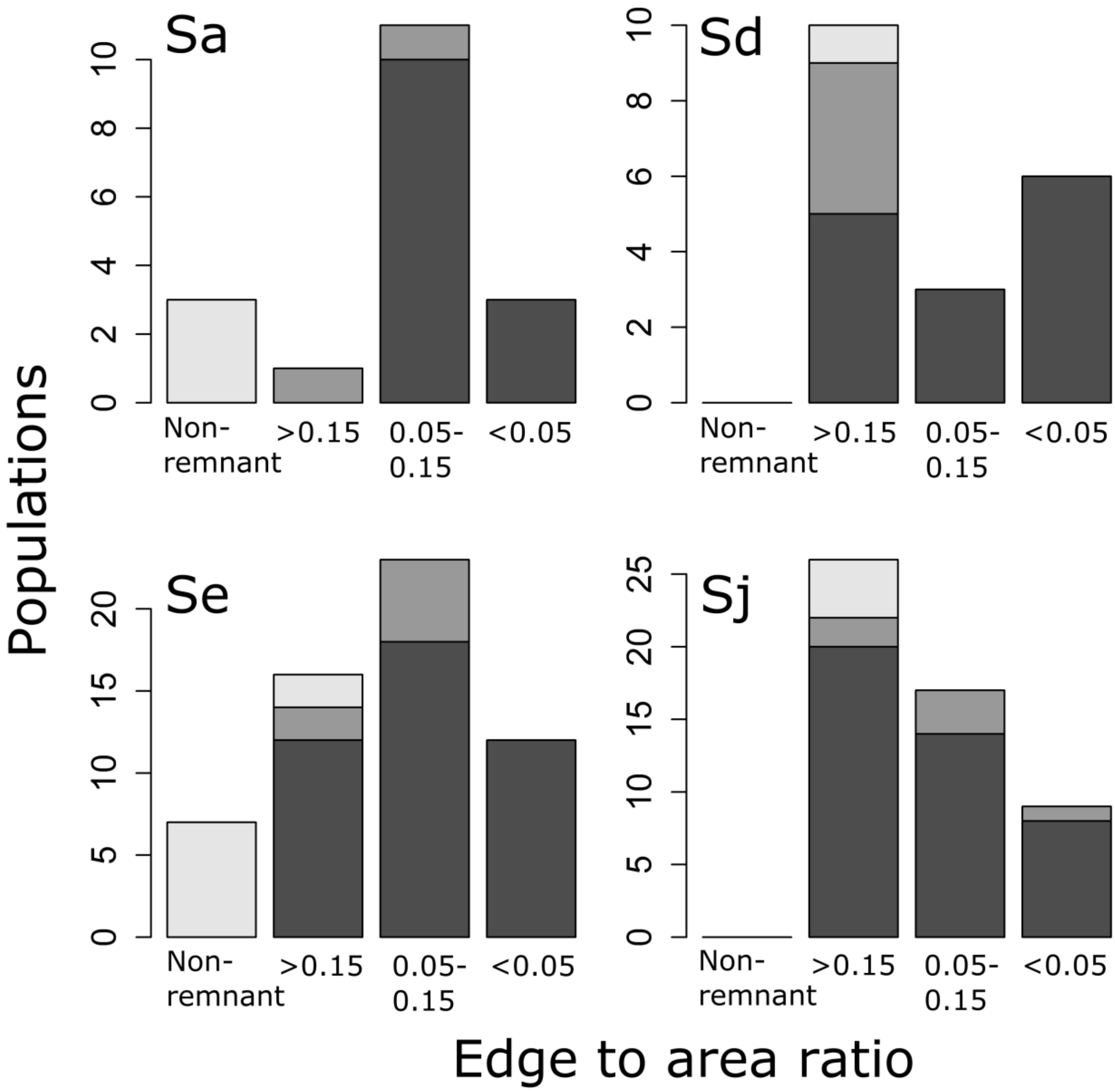

Figure 3. Histogram of habitat condition for the current populations of the four *Solanum* species (Sa, *S. adenophorum*; Sd, *S. dissectum*; Se, *S. elachophyllum*; Sj, *S. johnsonianum*). The x-axis categories are the edge (km) to area (ha) of remnants and the bars are shaded according to tree canopy cover (light grey, 0-20%; medium grey, 21-50%; dark grey, ≥50%). Viable remnants are assessed as those with edge:area ratio less than 0.15 and with ≥50% canopy cover.

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