Spatial and temporal rates and patterns of mesquite (Prosopis species) invasion in Western Australia

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Abstract

Historical archives of aerial photography provide a rare data source for quantifying rates and characterising patterns of plant invasions. Canopies of a ca. 70-year-old exotic mesquite population in Western Australia were extracted from a temporal series of panchromatic aerial photography over an area of 450 ha using unsupervised classification. Non-mesquite trees and shrubs could not be differentiated from mesquite, and so were masked out using an image acquired prior to invasion. The accuracy of this technique was corroborated in the field and found to be high ($R^2 = 0.98, P < 0.001$); however, only shrubs $> 3$ m$^2$ could be reliably detected with the 1.4 m spatial resolution of the imagery used. Rates and patterns of invasion were compared to mesquite invasions where it is native. It was determined that: (i) the shift from grass to mesquite domination has been rapid, with rates of increase in canopy cover comparable to invasive populations in its native range; (ii) rate of patch recruitment was high in all land types, including stony flats, but patch expansion and coalescence primarily occurred in the riparian zone and red-loamy soils; (iii) sheep and macropods have been the main vectors of spread and (iv) early successional patterns, such as high patch initiation followed by coalescence of existing stands, are similar to those where mesquite is native, but patch mortality was not observed.

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1. Introduction

Plant invasions pose one of the greatest threats to the world’s ecosystems (Mack et al., 2000). A major challenge is to understand the processes underlying plant invasions, and thereby to identify opportunities for management intervention. Analysis of plant invasions at the landscape level has received considerable attention recently, because it is the scale at which spatial and temporal patterns of invasion can be linked to proximate causes, the rates and patterns of spread can be quantified and the efficacy of different management practices can be assessed (e.g. Ansley et al., 2001; Brown and Carter, 1998). Since invasion of woody shrubs
often occurs over decades, such studies have often utilised temporal sequences of historical aerial photography to quantify invasion rates and characterise spatial patterns through both space and time (e.g. Goslee et al., 2003; Scanlan and Archer, 1991; Sharp and Bowman, 2004a, b).

Historical archives of panchromatic aerial photography provide one of the few sources of long-term, temporal data at the resolution required to study historical invasion and its relationship with the landscape (Rango and Havstad, 2003). However, invasive plants rarely have spectral characteristics that enable their discrimination from coexisting species using panchromatic aerial photography and standard techniques such as thresholding (e.g. Hutchinson et al., 2000; Lahav-Ginott et al., 2001), unsupervised self-organising clustering algorithms (e.g. Manson et al., 2001) or supervised methods such as the maximum likelihood method (e.g. Kadmon and Harari-Kremer, 1999). At best, these methods have only been able to discriminate between trees and shrubs by, for example, introducing a size threshold post-classification. This limitation has often led to researchers examining only small areas (typically less than 80 ha), where the plant has formed a virtual monoculture (e.g. Goslee et al., 2003) or, where vegetation composition has been heterogenous, discrimination between species has been achieved using manual photo interpretation (e.g. Ansley et al., 2001; Fensham et al., 2002). However, the time-consuming nature of interpreting and manually delineating the canopies of a species of interest often limits analyses to only a small area, to sparsely vegetated areas, or to the interpretation of relatively coarse vegetation units (Kadmon and Harari-Kremer, 1999). In this paper, a combination of techniques is used to extract the canopies of an exotic mesquite (Leguminoseae: Prosopis spp.) population in the northwest Pilbara region of Western Australia, from a temporal series of aerial photography. Firstly, canopies of all woody vegetation types are extracted using a standard unsupervised classification approach. Secondly, in an effort to remove the subjectivity and high labour requirements of manual interpretation, an aerial photograph captured prior to mesquite introduction is then used to mask out non-mesquite vegetation by utilising editing tools available within most geographic information systems.

Mesquite is recognised as a highly invasive plant in both its native and introduced range (Archer, 1995; van Klinken et al., 2006). It is a leguminous shrub that can form dense thorn-forests, resulting in serious economic, environmental and social costs (Gibbens et al., 1992; Goslee et al., 2003; Hennessy et al., 1983). Several studies have sought to describe the pattern of mesquite invasion in its native range using aerial photography, long-term demographic studies and modelling (e.g. Archer, 1995; Ansley et al., 2001; Goslee et al., 2003; Scanlan and Archer, 1991). The core observations of these studies can be summarised as follows: (i) the shift from grassland to mesquite shrubland has occurred relatively recently, typically in the past 50–100 years; (ii) mesquite invasion generally follows a process of high patch initiation, followed by coalescence; (iii) livestock, particularly cattle, are highly effective vectors of spread and (iv) rates of invasion have varied according to land type, with the greatest amount of recruitment and coalescence occurring in the most mesic parts of the landscape.

In this study, invasion rates and patterns are compared with those described at a smaller scale from its native range. Specifically, based on the abovementioned observations for mesquite in its native range, this study tested whether: (i) mesquite invasion has been as rapid as that observed in its native range; (ii) mesquite invasion follows a process of high patch initiation followed by coalescence; (iii) dispersion is widespread soon after introduction, providing evidence of long-distance dispersal vectors and (iv) certain land types are more resistant to mesquite invasion than others.

2. Study area description

The study site was located within a ca. 150,000 ha mesquite population in the semiarid Pilbara region of Western Australia. This population was initiated from intentional plantings in the 1930s to serve as a drought fodder plant (pods) as well as for shade for livestock. It is described as a hybrid swarm of P. pallida, P. velutina and P. glandulosa var glandulosa (van Klinken and Campbell, 2001). P. pallida belongs to the P. juliflora–P. pallida complex, which is native to southern Central America, while P. velutina and P. glandulosa are a complex native to the USA and Mexico (Pasiecznik et al., 2001). Approximately 30,000 ha have been identified as dense stands (van Klinken and Campbell, 2001).

The core of the invasion is located on the Mardie Pastoral Station, and is primarily to the north and east of the Mardie Station homestead, situated on the Fortescue River floodplain (Fig. 1). Sheep were the main
livestock on this pastoral lease from the late 1800s, but were replaced with cattle in 2000. Sheep and cattle have not been observed to browse on mesquite, although both consume mesquite pods and subsequently disperse seeds through their dung (Brown and Archer, 1987; Cox, et al., 1993). Mean annual temperatures are 26°C (CV = 18%, n = 3307), with a mean minimum of 12°C (CV = 18%, n = 263) in July and a mean maximum temperature of 36°C (CV = 6%, n = 125) in December. Long-term annual rainfall averages 290 mm (CV = 51%, n = 74), with a distinct wet season from December to March. The relatively high rainfall variation between years is caused, in part, by the irregularity, number and intensity of tropical cyclones over the area (van Vreeswyk et al., 2004; Fig. 2).

A test area of 450 ha (central point: 21°11’18"S, 115°56’57"E) was selected for this analysis within the main 30,000 ha dense infestation. The test area was located within a single, 3700 ha paddock ("home" paddock) in order to keep any disturbance and dispersal effects by livestock as consistent as possible. Anecdotal evidence suggests that mesquite was unlikely to have established over the test area prior to the wet season of 1945 (Meadly, 1962) with significant quantities of mesquite not observed north of the homestead on Mardie Station prior to 1949 (T. Patterson, personal communication, 2004). However, mesquite is the dominant shrub/tree species in the area today. Native woody vegetation is predominately *Eucalyptus* spp., *Acacia xiphophylla* E. Pritzel (snakewood) and *Hakea suberea* S. Moore (corkwood). The most abundant grasses in the area are *Triodia wisiana* C. Gardner and *Triodia pungens* R. Br. (Spinifex), *Cenchrus ciliaris* L. (buffel grass), *Cenchrus setiger* (birdwood grass) and the tussock grass *Eragrostis xerophila* Domin. (knottybutt neverfail grass) (Beard, 1975). Elevation over the test area slopes gently from around 15 m ASL in the east to around 11 m ASL in the west (based on four spot heights). The absence of detailed elevation measurements precluded analysing the effect that micro-topographic relief may exert on the mesquite distribution. The water table is at approximately 8 m (Department of Environment, Western Australia, unpublished records) and therefore well within the reach of mesquites’ taproot (Gibbens and Lenz, 2001; Gile et al., 1997; Stromberg et al., 1993).

Control, using both herbicide and the mechanical removal of trees with heavy chains, began in the early 1950s in the vicinity of Mardie Station homestead. However, available records suggest no control work was...
conducted in our test area (Meadly, 1962). This is supported by anecdotal evidence from a local pastoralist (T. Patterson, personal communication, 2004) who has been in the area since before control work commenced and by assessment of the historical aerial photographs.

3. Methodology

All analyses were performed using ArcGIS v.9 (ESRI, 2004) except for two landscape metrics (distance to nearest neighbour patch and patch density), which were performed using FRAGSTATS v.3 (McGarigal et al., 2002).

3.1. Data sets

A series of aerial photographs and flight line diagrams were examined in order to ensure all flights were within the same season (to avoid seasonal fluctuations in mesquite’s appearance) and assist selection of photographs without cloud interference. There was no meta-data on the time the imagery was acquired, but visual inspection of hard copies showed them to be free from shadow effects. As the study area is predominantly flat, shadow effects resulting from topographic variation were minimal. The test area was located within the center of two individual panchromatic aerial photographs (August 1943, 1:30,000 and August 1970, 1:40,000) and a true colour digital orthophoto, captured on September 2001 (1:25,000).

On November 2004, digital multispectral imagery (DMSI) was acquired with a spatial resolution of 1 m to assist mapping land types and to validate the method used to extract mesquite canopies. This imagery was flown around noon, and in clear conditions. Four narrow band-pass interference filters were used to generate the imagery in blue (450 nm), green (550 nm), red (675 nm) and near-infrared (780 nm) portions of the spectrum. This imagery was delivered georectified and corrected for bidirectional effects using in-house developed software, based on inversion of the bidirectional reflectance model proposed by Roujean et al. (1992). This imagery could not be used as an additional temporal data point as mesquite control work had been conducted at the site since 2001.
3.2. Preprocessing of imagery

To enable digital processing, the two aerial photographs were scanned from film at a resolution of 1200 dots per inch (dpi) using a photogrammetric scanner. Each image was georeferenced to the 2001 orthophoto. Root-mean-square errors were recorded to be 1.4 m for the 1943 image and 1.3 m for the 1970 image. Because of the varying flight altitudes for each image, grain sizes ranged from 0.8 m (1943) to 0.86 m (1970). Both images were resampled to 1.4 m resolution, to coincide with the resolution of the 2001 orthophoto, using bilinear interpolation since an attempt to use the nearest neighbour method resulted in images that appeared blocky (Mather, 2004). All images were clipped to the extent of the test area, which excluded the vignetting effect that commonly occurs at the edges of aerial photographs.

As the DMSI imagery was acquired at 1 m resolution, it was first degraded to 1.4 m to more closely represent the detection ability of the aerial photography. Only the red band was used in image classification so that results would be similar to those found from the panchromatic aerial photographs.

3.3. Image classification and construction of vegetation layers

The high density of vegetation and relatively large test area demanded a semi-automated technique for mesquite classification. A two-step procedure was implemented to accomplish this. Firstly, all images were processed using an iterative self-organising clustering procedure (ISODATA). This method begins by assigning pixel values to a set of arbitrary cluster means, which are then recalculated at iteration and as the number of iterations increase, the mean class values gravitate towards natural breaks in the distribution of image pixels (Mather, 2004). The required parameters of the ISODATA routine were found heuristically (20 iterations, 5 clusters). As expected, discrimination between vegetation types was not achieved during this step, although it did adequately distinguish between woody vegetation and other background landcovers. The cluster representing woody vegetation was extracted to form four new raster layers; one for each of the time steps considered (1943, 1970, 2001 and 2004). A subsequent step was required to remove native vegetation from the 1970, 2001 and 2004 images. This was achieved by masking out all patches of vegetation present in the 1943 image, which were assumed to be native (Meadly, 1962; T. Patterson, personal communication) from all subsequent imagery using the editing tools in ArcGIS 9 (ESRI, 2004).

3.4. Mapping land types

GIS overlays of hydrography showed an obvious association between thick vegetation (both native shrubs and trees and mesquite) and drainage lines. For this study, the riparian zone was defined as an area within 50 m of hydrography (Bowman et al., 2001; Grice et al., 2000). The remainder was defined as uplands. The riparian zone was not subclassified by soil type, but it was primarily red loamy soil.

Uplands were differentiated based on their edaphic characteristics, into two categories: stony flats (which comprised all crusted soils, including hard pans and clay pans) and red-loamy soils. These land types were mapped using a false colour composite (near infrared, red, green) of the DMSI and corroborated in the field. Stony flats were easily differentiated from red-loamy soils using this band combination. Stony flats appeared as dark green areas often associated with Spinifex (*Triodia wiseana* C. Gardner and *Triodia pungens* R. Br.), which appeared blue under this combination. Red-loamy soils appeared as light green under this combination.

3.5. Analysis of mesquite cover and temporal change

Three methods of comparison were used to assess the relationship between mesquite canopy cover and the three land types (riparian zone, red-loamy soils and stony flats).

3.5.1. Patch dynamics

Four processes have been reported to influence changes in mesquite cover: recruitment of new mesquite plants or patches; coalescence of expanding mesquite patches; a combination of recruitment and coalescence of mesquite patches; and mortality of mesquite plants (Ansley et al., 2001). To assist identification of the
process that was dominant for each time-frame studied, over the entire test area or for each land type, two landscape metrics were computed: (i) mean distance to the nearest patch (m), calculated as the average Euclidean distance to the nearest neighbouring patch, from cell center to cell center and (ii) patch density, calculated as the average number of patches per unit area (ha) (McGarigal et al., 2002). In addition, histograms were prepared showing the size class distribution of mesquite patches in 1970 and 2001 for each land type.

3.5.2. Change detection

A 20 × 20 m lattice of 11,250 quadrats was placed over the 1970 and 2001 images representing mesquite canopy cover, and the percentage of cover for each quadrat was calculated within the GIS. The appropriate quadrat size for change detection was determined by plotting the variance of estimated mesquite cover (%) against a range of quadrat sizes and identifying the point at which it became stable (Fig. 3; Greig-Smith, 1983; Papanastasis, 1977). Image differencing was used to detect change in mesquite cover for all coincident quadrats between years. To visualise significant change throughout the test area, a threshold value was derived (using all quadrats) from the mean difference between images plus one standard deviation (Jensen, 1996).

3.5.3. Analysis of cover

Two tests were performed on both the 1970 and 2001 images to determine if certain land types are more resistant to mesquite invasion than others. The first test aimed to determine if mesquite presence was dependent on land type. Quadrats were converted to presence/absence and a random sample (N = 200) was taken for each of the three land types. The interaction of mesquite presence/absence within the different land types was tested using one-way between subjects ANOVA, followed by Tukey’s Honestly Significantly Different (HSD) test. A second test was carried out to determine if canopy cover was higher over certain land types, where it was present. To this end, a random sample of 200 quadrats from each land type was tested using one-way between subjects ANOVA on quadrats that had more than 0% cover. Tukey’s HSD test was used to assess the differences in canopy cover between land types.

3.6. Field verification of image processing

To substantiate the accuracy of the semi-automated technique used to extract mesquite canopies from the aerial photographs, field verification was undertaken in September 2005. As shrubs may have grown between the last aerial photograph acquisition and the time of ground truthing, we chose to use the DMSI (acquired in November 2004) to support ground verification.

![Fig. 3. Relationship between the variance of estimated mesquite cover (%) and quadrat size.](image-url)
Fifteen quadrats were randomly selected for each of the following cover classes: zero cover (0%); low cover (>0% and ≤30%); moderate cover (>30% and ≤90%) and high cover (>90%). To assist accessibility, only quadrats within 200 m of existing tracks were candidates for random selection. The 15 quadrats within the zero cover class were incorporated into the validation scheme to estimate the size of shrubs that were not reliably detectable from the spatial resolution (1.4 m) of the aerial imagery.

Each of the 60 quadrats was located in the field with the aid of a Magellan eXplorist (100) global positioning system (GPS) and delineated with measuring tape. Canopy cover of mesquite was estimated for each quadrat using Simpson’s Rule of approximate integration (Stewart, 1995). All mesquite shrubs that were less than 1.4 m in length were ignored since they were technically not detectable using 1.4 m resolution imagery. Additionally, for the same reason, shrub clumps closer than 1.4 m were measured as one unit (Goslee et al., 2003). Quadrats containing clustered stands of mesquite, which were common in the moderate and high cover classes, were divided into 1 m intervals and the area of bare earth was measured. All field calculations were summed and converted to a percentage of mesquite canopy cover per quadrat and compared to the percentage of mesquite cover per quadrat calculated within the GIS.

4. Results

4.1. Analysis of mesquite cover and temporal change

Table 1 shows the relative proportions of the test area attributed to each of the three land types. Native vegetation in 1943 was highest in the riparian zone and was low in the stony flats. By 2001 there was considerably more mesquite over all land types when compared with native vegetation found in the 1943 image.

4.1.1. Patch dynamics

The total number of mesquite patches over the test area increased from 13,950 to 31,704 over the 31-year period from 1970 to 2001. Stony flats had a relatively low-patch density, and a relatively high-mean distance to nearest neighbour, compared to the riparian zone and red-loamy soils in 1970, which were roughly comparable (Table 1). Mesquite patches larger than 6 m² were uncommon on stony flats in 1970 suggesting that coalescence was rare (Fig. 4a). The number of patches increased substantially between 1970 and 2001 in all size classes in all land types, demonstrating continued patch recruitment (Fig. 4; Table 1). The distance between patches was similar in each land type. However, stony flats had a higher density of patches overall (Table 1) as well as in each of the smaller size classes, especially patches less than 6 m² in size (Fig. 4a). Patch density was slightly higher in red-loamy soils than in the riparian zone, although the size distribution was similar in both land types. Patches were up to 4.7 ha in size (Table 2). Patches larger than 100 m² were relatively common in both the riparian zone and red-loamy soils in 2001 (Fig. 4b,c; Table 2) and would have

<table>
<thead>
<tr>
<th>Land type</th>
<th>1943</th>
<th>1970</th>
<th>2001</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Area (ha)</td>
<td>Non-mesquite cover (%)</td>
<td>Mesquite cover (%)</td>
</tr>
<tr>
<td>Riparian</td>
<td>70</td>
<td>15.7</td>
<td>3.0</td>
</tr>
<tr>
<td>Red-loamy soils</td>
<td>324</td>
<td>10.2</td>
<td>2.6</td>
</tr>
<tr>
<td>Stony flats</td>
<td>56</td>
<td>2.7</td>
<td>0.4</td>
</tr>
<tr>
<td>Total</td>
<td>450</td>
<td>10.1</td>
<td>2.4</td>
</tr>
</tbody>
</table>

1Calculated as linear increase in canopy cover from 1943 (0% cover) and 1973, respectively.
2Different letters within a column represent differences in rates of change.
been partly the result of smaller patches coalescing to form dense thickets. Average and median patch size was largest in the riparian zone (Table 2), and is likely to be the main factor responsible for mesquite cover (%) being higher over this land type than over red-loamy soils (Table 1).

4.1.2. Change detection

Mesquite canopy cover occupied 2.4% (10.7 ha) of the test area by 1970 (Table 1), and was already highly dispersed by this time (Fig. 5a). Canopy cover was not uniform throughout the test area, being much higher in the riparian zone and red-loamy soils (Table 1). Furthermore, the percentage of quadrats where canopy cover increased faster than the change threshold (>6.3% increase in canopy cover) was similar over both the

Fig. 4. Density of mesquite patches by size class for 1970 (black bars) and 2001 (open bars): (a) stony flats, (b) red-loamy soils and (c) riparian zone.

Table 2
Summary statistics for patches greater than 100 m² in 2001, broken down by land type

<table>
<thead>
<tr>
<th>Land type</th>
<th>Number of patches</th>
<th>Patches (ha⁻¹)</th>
<th>Median (m²)</th>
<th>Average (m²)a</th>
<th>Standard deviation (m²)</th>
<th>Maximum (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Riparian</td>
<td>280</td>
<td>4.0</td>
<td>194</td>
<td>789 (216)</td>
<td>3614</td>
<td>47,717</td>
</tr>
<tr>
<td>Red-loamy soils</td>
<td>1168</td>
<td>3.6</td>
<td>180</td>
<td>432 (37)</td>
<td>1270</td>
<td>29,572</td>
</tr>
<tr>
<td>Stony flats</td>
<td>55</td>
<td>1.0</td>
<td>158</td>
<td>180 (12)</td>
<td>91</td>
<td>619</td>
</tr>
</tbody>
</table>

aValues given in brackets represent the standard error.
Fig. 5. The distribution of land type and mesquite across the test area showing presence of mesquite (circles and triangles) and increase in mesquite cover within a quadrat above the change threshold (circles) in (a) 1970 and (b) 2001.
riparian zone and the red-loamy soils in 1970 (15% and 13%, respectively). In contrast, few quadrats showed a significant amount of change over the stony flats (0.3%).

Total mesquite canopy cover in 2001 was 24.4% (109.9 ha); representing an increase in canopy cover of approximately 0.71% year\(^{-1}\), assuming a linear increase from 1970. This was almost eight times the rate of increase observed prior to 1970. Again, rates of increase in canopy cover varied with land type over this period (Table 1). The most rapid change was over the riparian zone (Fig. 5b), with approximately 40% of quadrats increasing faster than the change threshold (>40.1% increase in canopy cover). This was followed by the red-loamy soils (18.1%) and stony flats (1.8%).

4.1.3. Analysis of cover

The interaction between the presence of mesquite and each of the three land types was highly significant in both 1970 \((F(2,597) = 70.9, P<0.01)\) and 2001 \((F(2,597) = 33.4, P<0.01)\). In 1970, quadrats over the riparian zone were more likely to be occupied by mesquite than those over red-loamy soils \((Q = 4.7, P<0.01)\) or stony flats \((Q = 16.4, P<0.01)\) and more likely to be occupied over red-loamy soils than stony flats \((Q = 11.6, P<0.01)\). In 2001, there was no statistical difference between quadrats occupied by mesquite over the riparian zone or red-loamy soils \((Q = 2.5, P>0.01)\); however, there were fewer quadrats occupied over stony flats than over the riparian zone \((Q = 11.0, P<0.01)\) or red-loamy soils \((Q = 8.5, P<0.01)\).

As might be expected from both the change analysis (Fig. 5) and total canopy cover in each land type (Table 1), the interaction between mesquite canopy cover in quadrats in which mesquite occurred and the three land types was highly significant in both 1970 \((F(2,597) = 33.0, P<0.01)\) and 2001 \((F(2,597) = 110.9, P<0.01)\). In 1970, Tukey’s HSD test showed that, when compared to the stony flats, there was significantly higher mesquite cover in the riparian zone \((Q = 10.3, P<0.01)\) and red-loamy soils \((Q = 9.2, P<0.01)\) but no difference between the former two land types \((Q = 1.2, P>0.01)\). In 2001, there was considerably higher mesquite canopy cover over the riparian zone than the stony flats \((Q = 20.5, P<0.01)\) and red-loamy soils \((Q = 14.5, P<0.01)\) and considerably more cover on red-loamy soils than on stony flats \((Q = 5.9, P<0.01)\).

4.2. Ground verification of canopy cover densities within quadrats

The relationship between mesquite canopy cover per quadrat (%) observed in the field and that estimated from image processing within the 60 ground truthing quadrats was very strong \((R^2 = 0.98;\) Fig. 6). The largest mesquite shrub found within the zero cover class in the field that was not detected from image processing had

![Fig. 6. Field measurements of canopy cover plotted against estimates of canopy cover found from image processing within 60 randomly selected (400 m²) quadrats \((Y = 1.01x + 1.25, R^2 = 0.98, P<0.001)\).](image-url)
a canopy diameter of 2 m and a surface area of 2.95 m². Furthermore, the smallest shrub that was detected from image processing and corroborated in the field had a surface area of 3.3 m², with the longest diameter spanning 3 m with a diameter perpendicular to it of 2 m. Therefore, the minimum detectable canopy size, using 1.4 m resolution imagery, appears to be within the range of approximately 2.95 and 3.3 m².

5. Discussion

Longitudinal studies using aerial photographs to monitor mesquite cover in its native range have indicated rates of increase between 0.4% year⁻¹ and 1.2% year⁻¹. For example, rates between 0.4% year⁻¹ and 1.2% year⁻¹ have been observed in South Texas (Archer et al., 1988); 0.7–1.1% year⁻¹ in New Mexico (Goslee et al., 2003; Warren et al., 1996); and 0.6% year⁻¹ in Arizona (Glendening, 1952). Differences in reported rates of mesquite cover increases are the results of differences in initial canopy cover, soils, precipitation (Ansley et al., 2001), availability of dispersal agents and the time it took for initial mesquite plants to reach detectable sizes. However, from these reports it can be assumed that long-term increases in mesquite cover in its native range rarely exceeds 1% year⁻¹ (Ansley et al., 2001). In this study, rates of increase became more rapid between the two periods examined (0.09–0.71% year⁻¹). Rates of increase observed in the second period (0.36–1.16% year⁻¹, depending on land type) were, thus, comparable with those observed for native range mesquite populations (Ansley et al., 2001).

Mesquite showed a strong preference for riparian and red-loamy soils over stony flats, as reflected by a higher rate of initial colonisation by patches, higher rate of increase in canopy cover and the formation of larger patches. This could be due to both higher propagule pressure and higher recruitment, although it is not possible to differentiate these mechanisms using our data. Stony flats have low grass cover (van Klinken et al., 2006), and herbivores are therefore likely to spend less time grazing, and consequently fewer seeds will be deposited there (Andrew, 1988; Brown and Carter, 1998). Also, stony flats present a harsh environment for establishment and growth of young plants, as indicated by the low densities of perennial grasses and shrubs found there (van Klinken et al., 2006) and is a likely explanation for the relatively slow increases in patch sizes. Nonetheless, patch number and size did increase dramatically over stony flats in the period from 1970 to 2001, supporting conclusions based on demographic data that suggest that mesquite densities will continue to increase over all land types (van Klinken et al., 2006).

Mesquite had already spread throughout our 450 ha site by 1970, including into areas that would rarely, if ever, have been inundated (e.g. stony flats), within approximately 35 years of being introduced to the area. In the following 30 years patch formation continued, and existing patches increased in size. This invasion pattern is therefore consistent with dispersal occurring primarily through the gut of animals, rather than by extreme flood events. An important ecological difference between invasive mesquite populations in its native range and the study population in Western Australia is the dispersal agents. A wide range of animal species consume mesquite pods and subsequently disperse viable seed in both the native and introduced ranges (van Klinken and Campbell, 2001; Pasiecznik et al., 2001). The introduction of cattle is considered to be responsible for the rapid spread of mesquite within its native range from riparian zones into uplands in historical times (Brown and Archer, 1987). An important factor is that a high proportion of seeds survive the passage through the digestive system of cattle, ca. 60% (Brown and Archer, 1987). In contrast, the study property in Australia had sheep through the twentieth century (Van Vreeswyk et al., 2004; T. Patterson personal communication, 2004), and the most abundant dispersers were therefore sheep and macropods. Sheep grind their food, and as a result seed survival through to the dung is very low (ca. 13%; Cox et al., 1993). Seed survival through macropods is not known, but they grind their food in a similar manner to sheep (Griffiths and Barker, 1966). Much higher rates of patch formation may therefore be expected in this region with the recent introduction of cattle.

The invasion process mirrors the early phase of mesquite invasion in its native range, at least in the riparian zone and red-loamy soils where coalescence of patches was common. However, in its native range, Archer (1995) observed that as mesquite plants matured they often served as nursery sites for native shrubs, facilitating the ingress and establishment of subordinate woody species from other habitats. These subordinate species may ultimately replace mesquite, resulting in successional change from grassland to mesquite shrubland to native non-mesquite shrubland (Archer, 1995). We did not track individual mesquite patches in our study. However, no decline in mesquite density was recorded in any 20 × 20 m quadrat, suggesting that
mesquite is relatively long-lived (or the study period is too short to detect mortality) or that dying plants are being replaced by mesquite. Also, field-based studies have found no evidence that mesquite is passively facilitating the ingress of native shrubs in our population (van Klinken et al., 2006). In the current context, successional change beyond mesquite shrubland seems unlikely.

Mesquite could not be discriminated from native background shrubs and trees using aerial photography due to the poor spectral resolution of the aerial photographs. Access to an image prior to invasion by mesquite allowed us to overcome this constraint, although it does assume that mesquite did not replace native vegetation, mesquite did not reside in the understory of native vegetation, and that there was no subsequent change in native vegetation cover. However, native vegetation that was removed had a similar shape and size for all subsequent years, suggesting it was not mesquite. Mesquite has been introduced to several areas throughout the world, and in many cases after the commencement of aerial photography (e.g. Harding and Bate, 1991). Therefore, the methods used for mesquite extraction in this study may have wide application. Notwithstanding, recent advances in object-oriented image processing software have assisted discrimination between species in panchromatic imagery, typically by including such variables as shape, size, scale and colour coupled with user defined membership functions such as mean brightness values and relationships between layers segmented at different scales (e.g. Laliberte et al., 2004; McGlynn and Okin, 2006). As the three main woody vegetation types in this study exhibit a unique shape and the canopy size of native vegetation is consistent, this software may be appropriate for future studies, particularly one aimed at broad-scale mapping of mesquite from panchromatic and other very high resolution imagery.

The required spatial resolution for mapping weed patches has been estimated as less than one-quarter of the smallest patches that need to be mapped (Hunt et al., 2005). In this research it was determined that the spatial resolution of the aerial photography was sufficient to reliably detect individual small adults with a canopy of approximately 3 m². This suggests that a spatial resolution of approximately one-half the size of the shrub requiring detection may be adequate for mapping mesquite. Current panchromatic satellite imagery provides higher spatial resolution than most historical aerial photography (e.g. IKONOS-2, 1 m; CartoSat-2, 0.8 m; QuickBird, 0.61 m), and therefore may be able to detect shrubs with canopies smaller than 3 m². However, the most promising options for effectively detecting and differentiating isolated mesquite plants from other species clearly require similar resolution to that obtainable from current high resolution panchromatic imagery, but with greater spectral information. This is currently achievable with very high resolution multispectral and hyperspectral imagery and discrimination between woody species has been demonstrated using DMSI (e.g. Robinson et al., 2006), IKONOS-2 (e.g. Carleer and Wolff, 2004) and the airborne visible/infrared imaging spectrometer (AVIRIS) (e.g. Wylie et al., 2000). Furthermore, the potential spatial resolution achievable using Unmanned Aerial Vehicles (UAVs; e.g. <5 cm) makes them an extremely attractive option for weed mapping and spatial analysis in future applications (e.g. Rango et al., 2006).

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