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Planning iterative investment for landscape restoration: Choice of biodiversity indicator makes a difference

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ABSTRACT

Natural regrowth vegetation offers a cost-effective means of restoring some degraded landscapes. Worldwide, policy responses to climate change are increasing the attractiveness of investment in regrowth protection or facilitation which with strategic planning could also deliver substantial dividends for biodiversity conservation. This study compares the performance of two commonly used indicators of biodiversity conservation priority, irreplaceability and complementarity, as tools to support planning for iterative investment to protect natural regrowth of Brigalow, an endangered ecological community in subtropical eastern Australia. Brigalow covered more than seven million hectares prior to clearing, it now persists 'intact' on less than a tenth of that area but there are significant areas of regrowth.

Data on Brigalow regrowth derived from mapping and remote sensing identify 10,555 patches covering 280,000 hectares in total. Two different classifications are used to represent Brigalow biodiversity: a land-type classification of 16 'regional ecosystems' mapped at 1:100,000 scale, and a landscape-scale classification of 40 biogeographic subregions that discriminate relatively uniform landscapes at about 1:500,000 scale. Conservation targets are expressed as the extent of regrowth needed to increase the extent of intact or 'remnant' areas of each biodiversity feature to either 5% or 10% of its former extent. In each case, irreplaceability and complementarity are positively correlated, and either metric type could be used to identify relatively large sets of high-priority patches. However, regional-scale restoration is likely to involve iterative investment and therefore to require discrimination of relatively small sets of patches of the highest priority for biodiversity conservation. Irreplaceability is not an ideal measure of biodiversity value when planning such iterative processes, simply because irreplaceability is uninformative for ranking 'high-value' patches; they all have the highest possible score. This study demonstrates the importance of considering quite fundamental points when choosing metrics for conservation planning, such as the frequency distribution of values they produce. Where planning aims to identify quite small sets of very high value features metrics that are most variable among the highest value patches, like the one used for complementarity in this study, will be more useful than metrics that are strongly bounded at higher values.

1. Introduction

Facilitating ecosystem restoration by fostering 'passive' natural regeneration and regrowth has considerable potential for cost-effective landscape-scale restoration (Moran et al., 1996; Aide et al., 2000). There are substantial areas of natural regrowth in some extensively cleared regions, and their value for biodiversity conservation and other purposes is increasingly recognised (Bowen et al., 2007; Chandler et al., 2007; Cramer et al., 2008; Fensham and Guymer, 2009; McAlpine et al., 2009). This paper applies concepts developed for designing conservation reserve networks in order to assess biodiversity conservation 'value' among patches of natural regrowth of a widespread 'endangered' ecosystem in eastern Australia, known as Brigalow.

Brigalow ecosystems have been extensively cleared (Seabrook et al., 2006), but the dominant tree species, *Acacia harpophylla* (Brigalow), is renowned for its regenerative power (Johnson, 1964), resulting in thousands of hectares of regrowth which if protected from re-clearing, or perhaps facilitated by thinning or weed management, offers a low-input means of restoration to mitigate some negative consequences of over-clearing (McAlpine et al., 2002; Dwyer et al., in press). However, since Brigalow regrowth occurs in fragmented patches across thousands of square kilometres the question of which patches, or sets of patches, will deliver higher biodiversity conservation returns on restoration investment is not trivial.

The field of systematic conservation planning (SCP) has developed quantitative techniques that help reserve-network planners

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efficiently identify representative samples of regional-scale biodiversity (Margules and Pressey, 2000; Sarkar et al., 2006). Much of SCP concerns techniques that distinguish 'optimal-sets' of areas that satisfy explicit conservation targets for minimal cost. However, Faith et al., (2003) criticise the strong focus of SCP on optimal-sets. They argue for techniques to plan staged or incremental implementation of conservation programs, not least because few if any optimal-sets are rapidly realised (Margules and Pressey, 2000; Pressey and Taffs, 2001). An attractively simple approach to incremental implementation was considered by Meir et al. (2004), who found that simple rules such as "protect the available site with the highest irreplaceability or richness" can outperform optimal-sets that cannot be implemented immediately.

Immediate implementation is unlikely for extensive restoration at regional or even landscape scales, but the prospects for incremental broad-scale restoration are improving. Economic incentives to restore natural vegetation are increasing due, for instance, to emerging carbon economies, environmental stewardship programs, and increasing interest in 'offsets' negotiated to defray permitted environmental harm. Of course final investment decisions must consider cost-efficiency (Naidoo et al., 2006), and there are increasingly sophisticated techniques to integrate biodiversity values with other values and costs in order to identify investment targets or portfolios (e.g. Higgins et al., 2008). As well as costs and benefits, the potential for ongoing losses are also important for incremental restoration planning (Newburn et al., 2005). For example, the risk that a regrowth patch might be cleared before an investor can be identified to underwrite its protection should be considered when scheduling restoration investment (Pressey et al., 2004). However, while questions of cost and threat are clearly important, this study maintains a narrower focus on the way in which one might estimate the relative value of restoring particular regrowth patches for biodiversity conservation. Two 'value' measures are considered. One is irreplaceability; the other is 'complementarity'.

Irreplaceability in SCP refers to the likelihood that an area will need to be protected for nominated conservation targets to be met (Pressey et al., 1993). Targets are specified as quantities of biodiversity features, which in practice are often expressed in terms of extent of ecosystems or terrain classes because these are often the most continuous and comprehensive spatial data on biodiversity across regional scales (Margules and Pressey, 2000). Patches of restricted, or 'endangered' ecosystems typically attract the highest irreplaceability score (i.e. 1 out of 1), since there are few alternative sites with which to meet conservation targets for such ecosystems (e.g. Carwardine et al., 2007). While this high irreplaceability appropriately reflects the importance of sites containing endangered ecosystems, it is unhelpful in distinguishing priorities among patches of endangered ecosystems. This raises one of the questions about irreplaceability asked in this study, which is whether simply setting smaller conservation targets increases the usefulness of irreplaceability to identify the 'highest' priorities among patches that are completely irreplaceable under more desirable targets. A second question addressed concerns the degree to which patterns of irreplaceability change with different ways of classifying biodiversity.

The second concept of 'value' assessed is called 'complementarity'. Complementarity in SCP refers to the extent by which the addition of an area increases biodiversity representation and persistence (Faith et al., 2003). For regional restoration planning, complementarity might mean the potential of a restoration area to increase biodiversity representation and persistence across regional landscapes. It is expressed in this study as the amount that removing a patch would reduce capacity in the system to achieve conservation targets. This sense of complementarity differs somewhat from its more established use in relation to conservation reserves. The key point for this study is that complementarity is a patch-by-patch measure of conservation value based on the contribution each patch makes to system-wide targets, whereas irreplaceability also incorporates the 'tradability' or 'redundancy' of patches.

A difficulty with SCP is the question of how to evaluate the outcomes? The most commonly applied metrics relate to 'efficiency' or the economic cost incurred in reaching conservation targets. While cost-efficiency is clearly important, the focus of this study on measures of value rather than investment priorities per se, make cost-efficiency a premature measure. Instead, this study compares the frequency distributions of the value metrics, and what any differences might mean for planning. Furthermore, other facets of biodiversity value such as patch size, connectivity, and congruence with the modelled distribution of threatened species are also evaluated in order to consider the conservation value of the various sets of high-value patches identified. These factors could have been incorporated into value metrics but are used here to enable discussion of the more generally interesting questions of how changing targets and approaches to biodiversity classification affect patterns of irreplaceability, and the comparative performance of irreplaceability and complementarity as tools for measuring biodiversity value for strategic planning of broad-scale restoration or any other iterative or incremental conservation program.

2. Methods

2.1. Study area and ecosystem

The subject of this study is the 'Brigalow ecological community' (Brigalow) as listed under the Australian *Environment Protection and Biodiversity Conservation Act 1999*. It occurs mainly in a bioregion called the 'Brigalow Belt' in subtropical eastern Australia, which spans two Australian States, Queensland and New South Wales (Fig. 1). Intact Brigalow ecosystems typically have little value to pastoralists, but their soils can support productive agriculture following clearing. Governments have actively promoted closer settlement and clearing of Brigalow lands, particularly since the 1950s (Seabrook et al., 2006). Consequently these ecosystems are now recognised as endangered, and State and National laws protect remaining intact areas. However, regrowth Brigalow has been relatively poorly protected, at least until very recently. A moratorium on clearing regrowth of endangered ecosystems was established by the Queensland Government in April 2009, and negotiations about future levels of protection of regrowth vegetation were ongoing at the time of publication. Substantial areas of Brigalow regrowth are likely to remain outside future State regrowth clearing regulation as they are subject to binding agreements between landholders and the State Government.

This study is restricted to Queensland because Brigalow is much more widespread there, and consistent vegetation mapping is lacking in NSW. The Queensland portion of Brigalow is defined using the Queensland Environmental Protection Agency's (EPA) Regional Ecosystem (RE) classification (Sattler and Williams, 1999; EPA, 2005). It includes 16 REs (Table 1), each of which is also listed as endangered under Queensland legislation. This study uses EPA 1:100,000 map data for Brigalow prior to clearing and 'remnant' in 2003 (Neldner et al., 2005). The data were acquired in December 2006 and are version 5.0 of the RE mapping plus amendments made after its release in December 2005.

2.2. Regrowth mapping

Spatial data on regrowth Brigalow were developed by combining the RE mapping with data on woody vegetation cover from

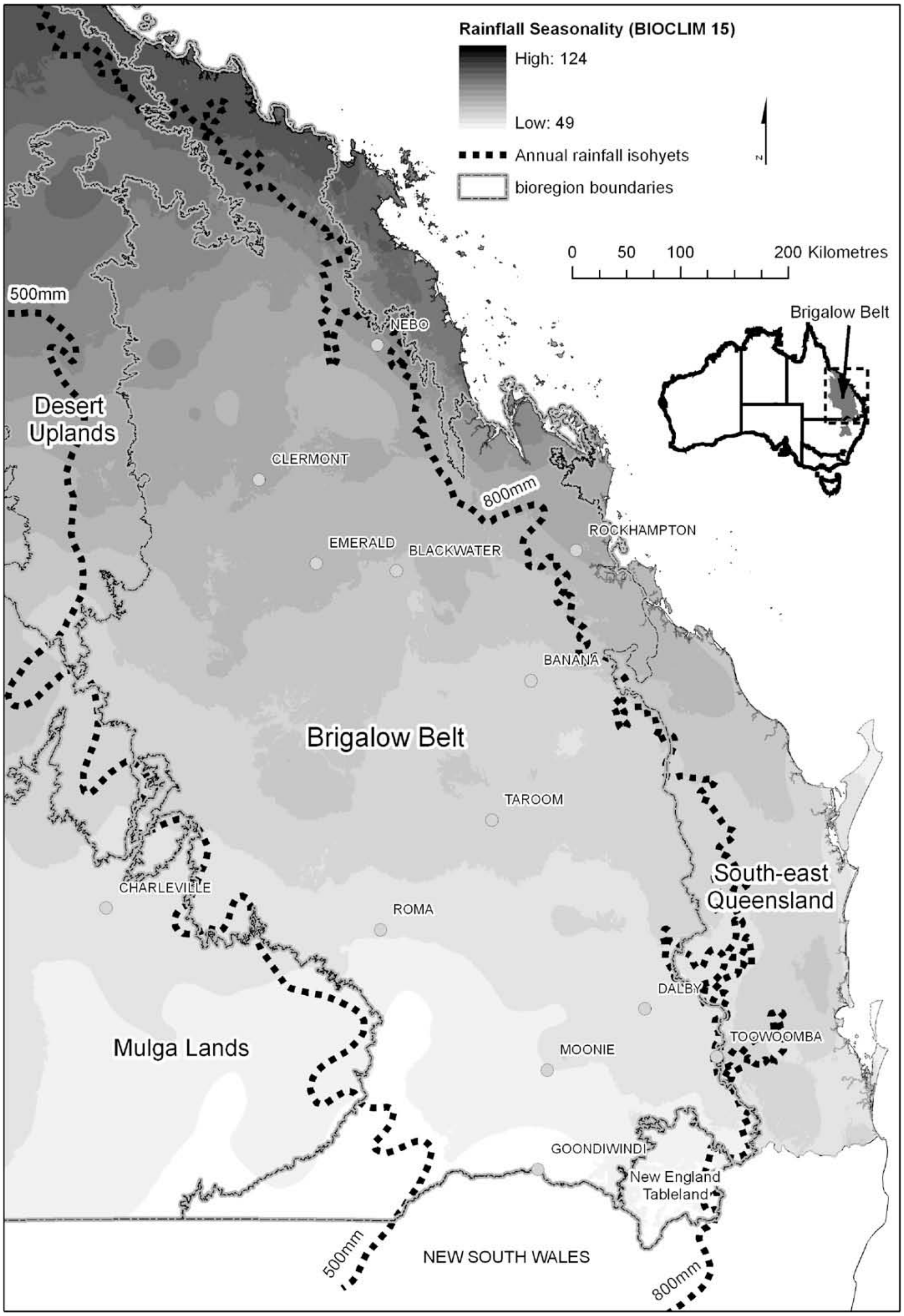

Fig. 1. Map of the study area including bioregion boundaries, mean annual rainfall isohyets (500 mm and 800 mm) and rainfall seasonality (standard deviation of weekly rainfall estimates expressed as a percentage of the mean annual rainfall).

the Queensland Statewide Landcover and Trees Study (SLATS; Department of Natural Resources, 2007). Non-remnant 'cleared' areas in the EPA's 2003 remnant RE maps, which the pre-clearing data showed were either homogeneous areas of a target RE or a heterogeneous area in which a target RE was the greatest component, were identified as regrowth if the SLATS estimate of woody cover (foliage projective cover; FPC) in 2004 was greater than 18%. The 18% threshold was chosen after comparison of results using higher and lower thresholds with scanned aerial photographs (1:40,000 scale or smaller). The aim was to identify relatively dense regrowth because it arguably has the greatest current habitat value and potential to mature into Brigalow forests. The data provide a conservative estimate of regrowth extent, more prone to errors of omission than over-estimation, and con-

Table 1
Short descriptions and extent of regional ecosystems included in Brigalow in Queensland.

RE	Short description	Pre-clearing extent (ha)	Extent as remnant in 2003 (ha)	Extent of remnant in reserves (ha)
11.3.1	*Acacia harpophylla* and/or *Casuarina cristata* on alluvial plains	781,775	77,080	10,115
11.4.3	*Acacia harpophylla* and/or *Casuarina cristata* shrubby open forest on Cainozoic clay plains	1,564,204	76,656	9083
11.4.7	Open forest of *Eucalyptus populnea* with *Acacia harpophylla* and/or *Casuarina cristata* on Cainozoic clay plains	209,921	21,280	266
11.4.8	Open forest of *Eucalyptus cambageana* with *Acacia harpophylla* or *A. argyrodendron* on Cainozoic clay plains	724,652	73,472	7045
11.4.9	*Acacia harpophylla* shrubby open forest with *Terminalia oblongata* on Cainozoic clay plains	1,012,463	91,543	7819
11.4.10	*Eucalyptus populnea* or *E. pilligaensis*, *Acacia harpophylla*, *Casuarina cristata* open forest on margins of Cainozoic clay plains	63,123	6313	2266
11.5.16	*Acacia harpophylla* and/or *Casuarina cristata* open forest in depressions on Cainozoic sand plains/remnant surfaces	12,379	3059	79
11.9.1	*Acacia harpophylla-Eucalyptus cambageana* open forest on Cainozoic fine-grained sedimentary rocks	572,964	56,536	6915
11.9.5	*Acacia harpophylla* and/or *Casuarina cristata* open forest on Cainozoic fine-grained sedimentary rocks	1,927,640	147,195	26,859
11.9.6	*Acacia melvillei* ± *A. harpophylla* open forest on Cainozoic fine-grained sedimentary rocks	15,316	368	0
11.11.14	*Acacia harpophylla* open forest on deformed and metamorphosed sediments and interbedded volcanics	39,712	4742	1174
11.12.21	*Acacia harpophylla* open forest on igneous rocks; colluvial lower slopes	72,869	6751	1078
12.8.23	*Acacia harpophylla* open forest on Cainozoic igneous rocks	7949	516	0
12.9-10.6	*Acacia harpophylla* open forest on sedimentary rocks	33,778	903	0
12.12.26	*Acacia harpophylla* open forest on Mesozoic to Proterozoic igneous rocks	9094	1208	350
6.4.2	*Casuarina cristata* ± *Acacia harpophylla* on clay plains	264,567	18,085	184
Total of above REs	Brigalow-EC in Queensland	7,312,406	585,707	73,233
Other Brigalow REs	Brigalow woodlands and box/Brigalow woodlands other than brigalow-EC components (mostly outside the study area to the west and north)	1,700,404	316,946	13,273

For explanations of the RE codes and more detailed descriptions see http://www.epa.qld.gov.au/nature_conservation/biodiversity/regional_ecosystems.

siderable areas of more diffuse regrowth are known in some parts of the region.

Spatial data intersections were carried out using ArcInfo 9.0 (ESRI, 2004). The data were simplified into 'regrowth patches' using the 'focal majority' function in ArcGrid to identify the majority value (i.e. regrowth or not) across neighbourhoods of 8 × 8 cells in the SLATS 25 × 25 m FPC grid data, and by eliminating all subsequent patches smaller than 5 ha. The regrowth coverage was also intersected with SLATS 'change-detection' data to identify the last time each area was cleared. The change-detection data identified clearing during the intervals 1991–1995, 1995–1997, 1997–1999, and each year from 2000 to 2005. The final patches used as planning units in this study could include regrowth of various pre-clearing REs, or of various ages (including areas cleared in 2004 and 2005). The total area of regrowth in each patch was tallied after multiplying by a modifier for regrowth age, which down-weighted younger regrowth (Table 2). There is ample evidence that older regrowth generally has greater habitat value for forest biota than younger regrowth (Bowen et al., 2007).

The derived data were spot checked and corrected against satellite imagery and aerial photography but no field assessment was conducted for accuracy. The most substantial and consistent error concerned towns built on former Brigalow land, where gardens provided a woody 'regrowth' signature.

Table 2
Extent and age of woody non-remnant "regrowth" Brigalow in Queensland and the modifiers used to down-weight young regrowth for irreplaceability analysis.

Regrowth age	Area modifier	Area
Uncleared since 1991	1	203,860
Last cleared between 1991 and 1997	0.5	14,466
Last cleared between 1998 and 2001	0.25	32,356
Last cleared in 2002 or 2003	0.1	13,288
Last cleared in 2004 or 2005	0	20,306

2.3. Patch Irreplaceability

Irreplaceability in this study was estimated using C-Plan (Pressey et al., 2005). Irreplaceability is calculated for a given patch 'x' (Irr_x) as the proportions of sets of patches that satisfy specific targets that must contain the patch in question.

$$\mathrm{Irr}_x = (R_{x\_\mathrm{included}} - R_{x\_\mathrm{removed}})/(R_{x\_\mathrm{included}} + R_{x\_\mathrm{excluded}})$$

where R_{x_included}, R_{x_removed} and R_{x_excluded} are the number of sets of patches that meet specified targets with patch 'x' included, removed or excluded, respectively (Ferrier et al., 2000).

Irreplaceability values range between 0 and 1, with values of 1 indicating completely 'irreplaceable' patches. In this study, results are presented for sets of 'high-irreplaceability' patches, with irreplaceability defined as greater than or equal to 0.5 for specified targets; these patches have high importance for meeting targets.

Two sets of biodiversity features were used in this study. One consists of the 16 REs to which Brigalow is mapped across the study area, providing a 'land-type' classification. The second is the extent of Brigalow (all REs) within 40 biogeographic subregions that supported at least 1000 ha of Brigalow before clearing. The relevant subregions are shown in Fig. 2.

Regional ecosystems are a three-tiered land-type classification incorporating bioregions, landzones that differentiate substrate classes, and vegetation classes (Sattler and Williams, 1999; EPA, 2005). The subregions provide a landscape-scale geographic classification for biodiversity at about 1:500,000 scale. They represent broadly coherent landscapes, the boundaries of which often follow the boundaries of substantial geomorphic features. As such, they help to incorporate geographic variation that may be poorly captured by REs alone since some REs span more than 10° of latitude.

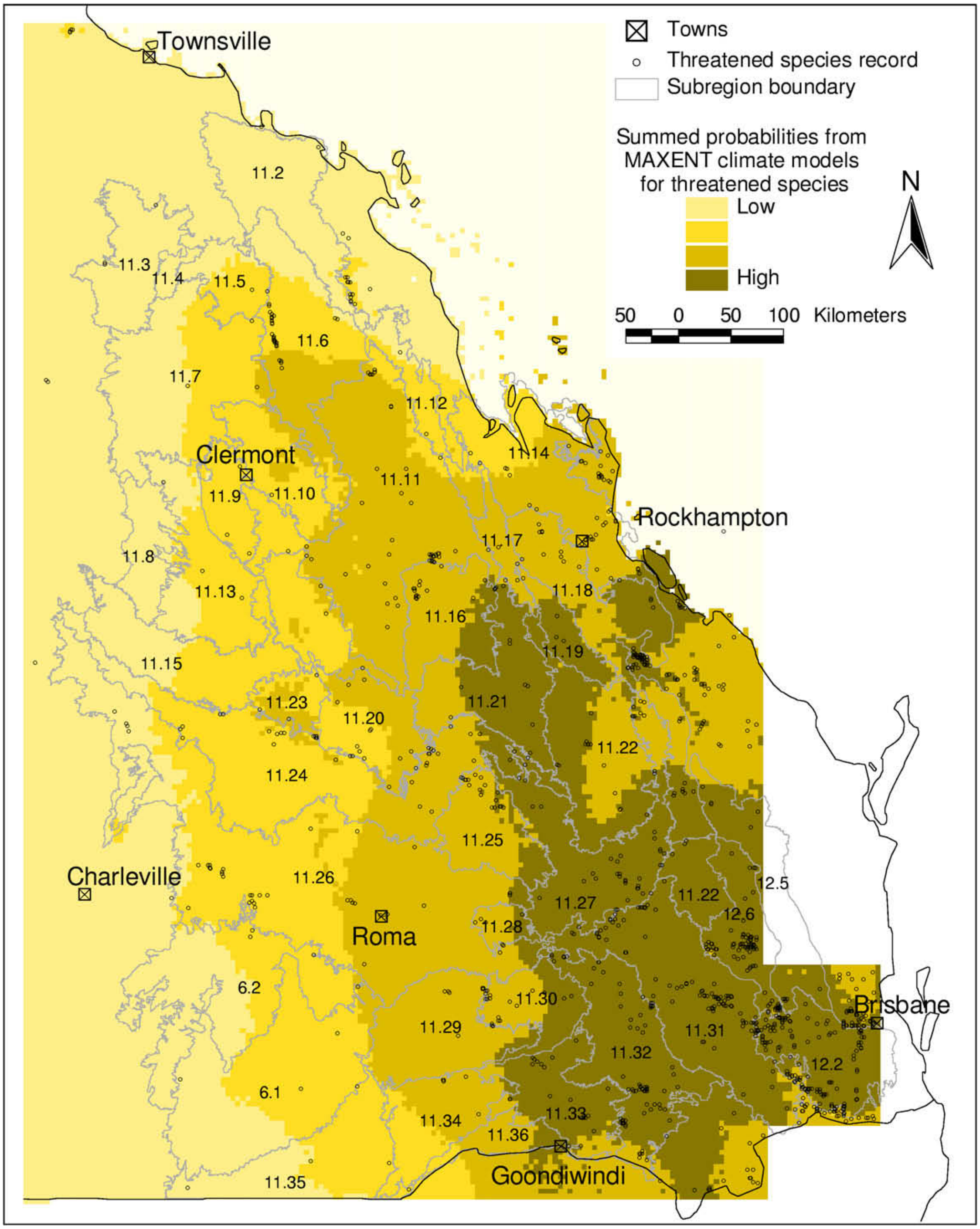

Fig. 2. Map showing the boundaries and identifying codes of the biogeographic subregions used in this study (labels link to data in Appendix A), the location of some larger towns and cities in the study area, point records for threatened flora and fauna. Shading illustrates change in probability of threatened species occurrence based on Maxent models built from climate data using the point records displayed.

It is likely that two patches of different Brigalow REs in the same or a neighbouring subregion will be more ecologically similar, than either will be to patches of the same REs in more distant subregions. This is known to be true for vascular plant composition in dry rainforests, with which Brigalow merges in its most productive aspects (Fensham, 1995, 2000). Combining all REs within subregions for the landscape-scale classification, rather than simply specifying targets for each RE in each subregion (i.e. using 16 + 40 targets rather than 16×40), minimises the increase in numbers of unachievable targets associated with adding the landscape-scale classification.

Irreplaceability was assessed for four target scenarios:

1. 10% RE targets – targets were the extent of regrowth required to increase the current remnant extent to 10% of the pre-clearing extent for each Brigalow RE (16 features);
2. 10% subregion targets – targets were the extent of regrowth required to increase the current remnant extent to 10% of the pre-clearing extent for Brigalow in each subregion (40 features);
3. 5% RE and subregion targets – targets were the extent of regrowth required to increase the current remnant extent to 5% of the pre-clearing extent for each RE and for Brigalow in each subregion (56 features); and

4. 10% RE and subregion targets – targets were the extent of regrowth required to increase the current remnant extent to 10% of the pre-clearing extent for each RE and for Brigalow in each subregion (56 features).

These targets are necessarily modest, because more biologically suitable targets, such as 30% or more of pre-clearing extent (Soule and Sanjayan, 1998; McAlpine et al., 2002; Huggett, 2005), far exceed available regrowth.

2.4. Patch complementarity

The percentage contribution of the ith patch to biodiversity representation and persistence was estimated by summing scores for its constituent biodiversity features according to the formula below:

$$\mathrm{IC}_i = 0.5 \times \left(\left[\sum_{j=1}^{r} p_j \times \left(\frac{T_j}{A_j - x_{ij}} - \frac{T_j}{A_j} \right) \right] + \left[\sum_{k=1}^{s} p_k \times \left(\frac{T_k}{A_k - x_{ik}} - \frac{T_k}{A_k} \right) \right] \right)$$

where r is the number of targeted regional ecosystems represented in the ith patch; s is the number of subregions spanned by the ith patch; T_j and T_k are the extents of regrowth required to increase the current remnant extent to 10% of pre-clearing extent for the jth RE and kth subregion, respectively; A_j and A_k are the areas of regrowth available to meet the target for the jth RE and kth subregion, respectively; x_{ij} and x_{ik} are the extents of the jth RE and the kth subregion, respectively, in patch i, and; p_j and p_k are the percentages of the total extent of the ith patch represented by x_{ij} and x_{ik}.

The IC metric averages contributions due to the land-type classification and the landscape-scale subregion classification, this avoids double counting contributions to these two overlapping value sets, which would exacerbate differences in patch size. It differs from calculation of complementarity as the percentage contribution of patch to targets (e.g. Margules and Pressey, 2000), which exaggerates the importance of patches of widely available ecosystems with small targets, and downplays ecosystems with limited extent relative to targets. Faith and Walker (2002) describe complementarity as the marginal gain in biodiversity when a patch is added to a system of reserves. The metric applied here uses the inverse of this concept. It estimates reduction in capacity to achieve specified biodiversity targets if a given regrowth patch is removed, by the change in the ratio of target to available area (i.e. T_j/A_j).

Complementarity changes as implementation progresses and decisions are taken to protect, restore or clear particular patches. In this study, sets of high-irreplaceability patches (Irr $\geqslant$ 0.5) under the four target scenarios outlined above are compared with sets of the same number of patches chosen based on initial complementarity scores calculated based on a 10% target for each of the 16 REs and 40 Brigalow subregions (e.g. a set of n patches with Irr $\geqslant$ 0.5 for a given target scenario was compared with the set of n patches with the highest initial complementarity scores). Note that the sets based on complementarity were not identified using an iterative selection procedure, whereby patches with highest complementarity are selected one at a time with complementarity re-calculated at each step (Kirkpatrick, 1983; Pressey and Nicholls, 1989), but were defined using 'initial complementarity' scores. This approach is reasonable for this study because the assessment is concerned with the onset of the planning process and implementation will not necessarily proceed according to the order of complementarity. Real application of the value metrics trialled here should ideally also include cost, opportunity and risks such as ongoing clearing to determine investment strategies. Value metrics such as complementarity or irreplaceability would be re-calculated for successive iterations of the investment cycle.

2.5. Assessment against point records for priority species

To assess whether priorities indicated by high irreplaceability or high complementarity align with other established conservation priorities, sets of high-value patches were compared with climatic 'niche' models of the distributions of 21 endangered or vulnerable species for which Brigalow provides important habitat (Appendix B). The probability of each threatened species occurring in each cell of a 2.5° grid, spanning the study area, was modelled with climate data from the WorldClim dataset (Hijmans et al., 2005) using Maxent version 3.2.19 (Phillips et al., 2004) trained on point records with high to moderate spatial location precision (radius $\leqslant$ 1600 m) drawn from the Queensland EPA's 'Wildnet' database. The modelling was constrained to cover the same region as that covered by the species location records. The 21 individual species niche models were combined by summing the probabilities returned for each species in each cell, producing a broad model of the distribution of threatened species associated with Brigalow across the study area which should be less biased than the threatened species records towards conservation reserves and roadsides (Margules and Pressey, 2000). The summed value was averaged per area so it is not inherently correlated with patch size.

Association between the five measures of biodiversity conservation priority value (Irr under the four target scenarios plus IC) and the summed probability estimated from the species niche models was tested using Kendall's rank correlation (R Development Core Team, 2008). Student's t-tests (R Development Core Team, 2008) were used to compare summed probabilities from species niche models between the sets of patches scoring high Irr ($\geqslant$0.5) under each of the four target scenarios, with sets of the same n selected for maximum IC. An effect size (Cohen, 1988) was also calculated for these comparisons as the difference in the means of the two sets divided by the standard deviation among patches that occurred in either of the sets.

2.6. Size and connectivity

The question of whether high-value patches align with restoration priorities based on landscape context and sustainability is considered alongside data on patch size and connectivity to remnant vegetation. Data on patch size were for the real spatial extent of each regrowth patch, not modified by age. Connectivity was as-

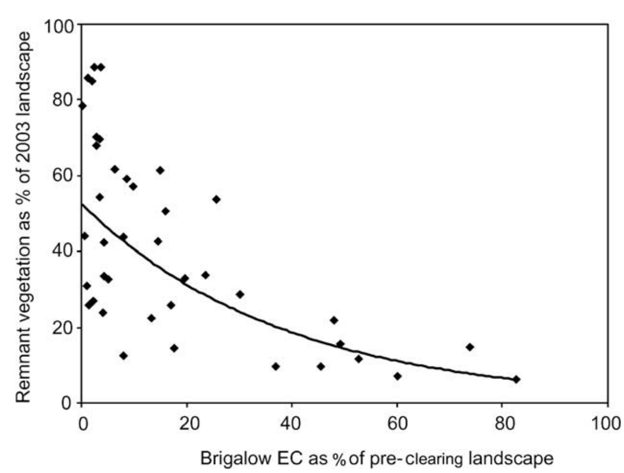

Fig. 3. Dominance of Brigalow in the pre-clearing landscape in relation to the extent of remnant vegetation in the modern landscape for the 40 biogeographic subregions in Queensland that supported more than 1000 ha of Brigalow prior to clearing.

sessed by buffering regrowth patches by 50 m (chosen based on mapping scale), calculating the extent of remnant vegetation within these 50 m buffers, dividing this area by 50, and then expressing this value as a percentage of the regrowth patch's perimeter. Correlation of Irr and IC with patch size and connectivity was assessed with rank correlation (R Development Core Team, 2008).

3. Results

The targets and available age-modified extent of regrowth for each of the 56 biodiversity features used in these analyses are provided in Appendix A. Subregions in which Brigalow was most dominant before clearing consistently rank among the most extensively cleared parts of the study area (Fig. 3). Maps of the pre-clearing and remnant extent of areas dominated by Brigalow and the regrowth data are provided as Fig. 4. Prior to clearing, Brigalow ecosystems considered in this study covered more than 7.3 million hectares in Queensland (Table 1). In 2003 about 8% of Brigalow's pre-clearing extent still supported relatively intact, 'remnant' vegetation. Data derived for this study suggest the extent of Brigalow regrowth is quite substantial compared to this remnant extent. Even the conservative approach taken in this study, which identified relatively dense patches of regrowth, delineated 285,000 hectares in 10,555 patches larger than 5 hectares in Queensland (Fig. 4c). Most of this area had not been cleared since 1991 (Table 2). Nearly 20,000 hectares was cleared in 2004 or 2005. About 200,000 ha of Brigalow regrowth that was uncleared since at least 1991 persisted into late 2005. This is equivalent to about one-third of the total extent of more intact Brigalow habitats.

Patch area was positively correlated ($p < 0.05$) with Irr for all scenarios except the 5% targets, and was also positively correlated with IC ($p < 0.01$). However, small patch size did not preclude high conservation value and patch size was generally a very weak predictor of irreplaceability; the strength of correlation between Irr and patch area was greatest for scenario 1 (10% targets for Res, tau = 0.13), and was slightly greater but still weak for IC (tau = 0.26, Fig. 5). There was also a very weak but significant ($p < 0.05$) negative relationship between patch connectivity and Irr under all target scenarios, and an extremely weak positive relationship with IC.

In areas with low subregion targets, such as the north and central west of the study area, only relatively large patches tended to score highly for Irr or IC (Fig. 6). In heavily cleared subregions all patches tended to receive high-Irr scores because many targets exceeded the available regrowth extent (Appendix A).

The spatial configuration of the sets of high-irreplaceability patches varied considerably between the four target/classification combinations (Fig. 6). The 5% targets (scenario 3) produced a very clumpy set of high-irreplaceability patches concentrated on a few extensively cleared subregions and REs. For the 10% targets, using only REs (scenario 1) identified a set of high-irreplaceability patches that included far fewer patches and was more biased toward large patch sizes and away from eastern areas than was the case for the set identified using subregions alone (scenario 2, Table 3).

Summing the outputs from the Maxent models suggested that Brigalow in the east of the study region is particularly important as habitat for threatened species, especially that in the south–east (Fig. 2). Patch Maxent scores were positively correlated with each of the conservation value metrics used in this study (Irr under each of the four target scenarios plus IC), although none of these correlations were very strong. Mean patch Maxent scores for sets chosen based on Irr under scenarios 2 and 4 were both marginally but significantly higher than the means for sets of the same n based on IC. However, patches with high-Irr under scenario 1 (10% RE only) had a lower mean Maxent score than patches in a set with the same n based on IC, and there was no difference for scenario 3 (5% RE and subregions). Overall, metric choice had an extremely weak effect on how well priority patches align with threatened species habitat; effect sizes for the differences were all less than 0.2. Choice of features seems a much more important issue. Of the four Irr scenarios, values based only on subregion targets (scenario 2, tau = 0.40) were much more strongly correlated with the patch Maxent scores than those based only on REs (scenario 1, tau = 0.13).

The frequency distributions of Irr were qualitatively similar for the four target scenarios, and very different to the frequency distribution of IC. Most importantly, Irr was either one or near zero (high or low) for most patches (Fig. 7). Increasing the targets from 5% to 10% exceeded available regrowth for 17 of the 40 regions and three of the sixteen REs, greatly increasing the number of patches

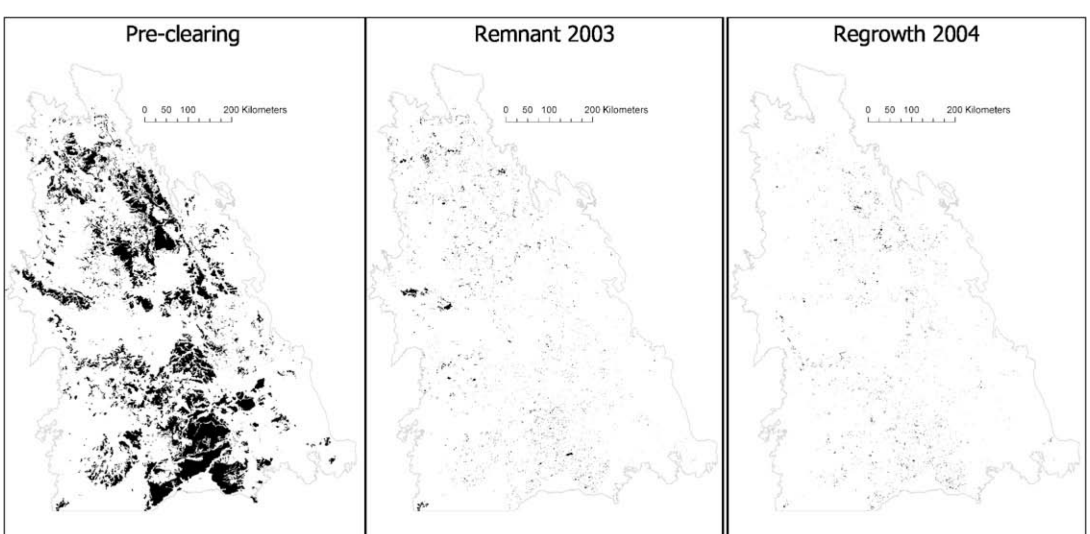

Fig. 4. Maps showing Qld. EPA regional ecosystem mapping for areas dominated by Brigalow in Queensland prior to clearing (left), in remnant condition in 2003 (centre), and regrowth data from this study (right).

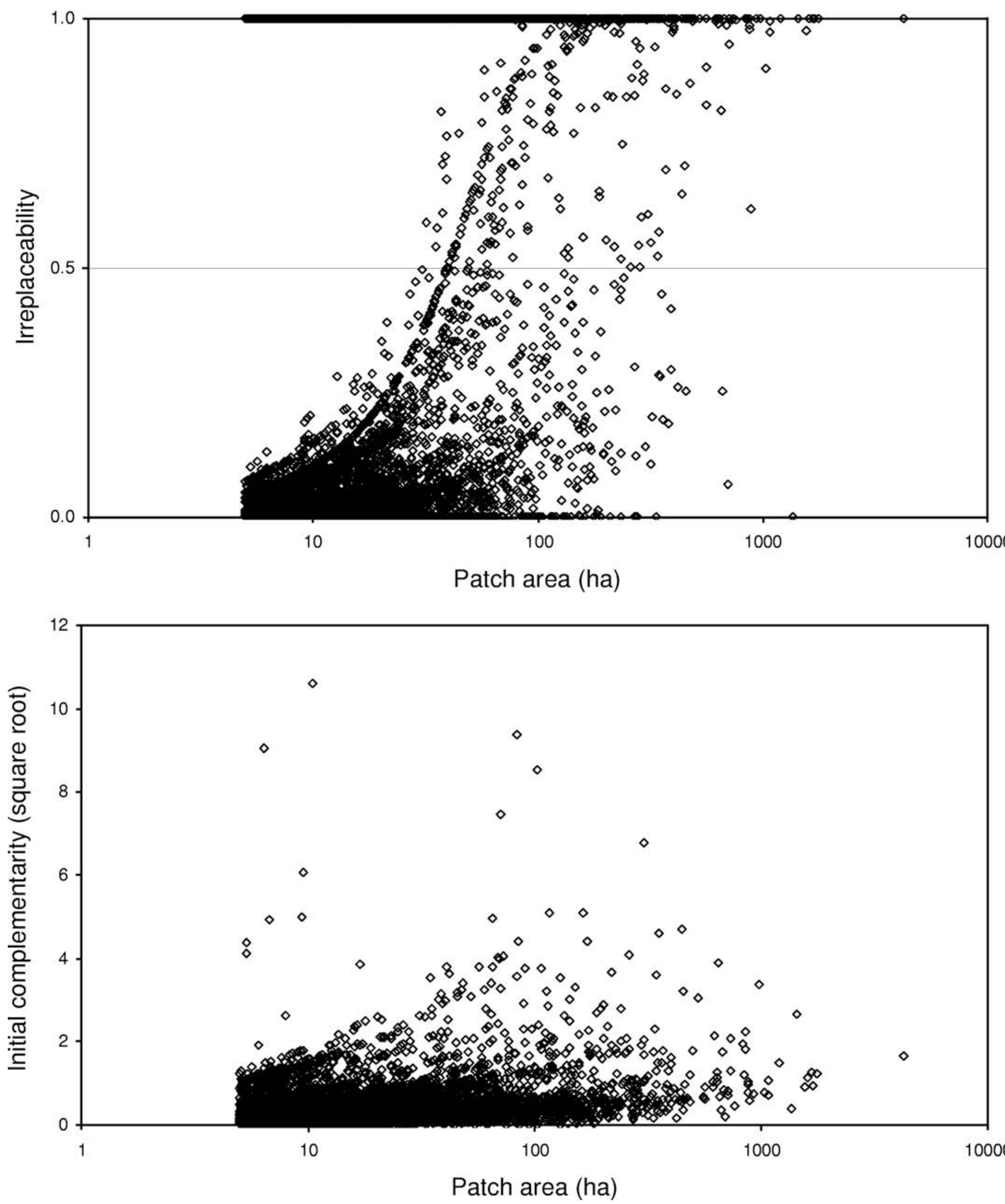

Fig. 5. Plots of Brigalow regrowth patch area against biodiversity 'value' assessed using either irreplaceability (top panel, 10% RE and sub targets) or initial complementarity (bottom panel). The light grey line is the study area boundary, it is the outer limit of the subregions shown in greater detail in Fig. 2.

attracting the highest possible Irr score. The larger targets also slightly stretched the 'tail' of Irr distribution, with many patches receiving scores between 0.2 and zero. The extent of variation in Irr among patches that scored above about 0.4 was very small under all targets.

Initial complementarity produced a more continuous distribution of 'value' than irreplaceability under any of the scenarios (Fig. 8). Variation in IC was greatest at the high-value end of the distribution. Patches attracting the top 1% of IC scores spatially coincided with subregions highlighted in the irreplaceability assessment using 5% targets, but the 5% targets identified nearly all patches therein as irreplaceable (Fig. 6f and b). The 106 patches in the top 1% of IC also included a few in subregions unrepresented among the 1877 patches that received high-Irr scores under the 5% targets. The set of the same number of patches (1877) with greatest IC (Fig. 6c), was much more widespread than the set of high-irreplaceability patches under the 5% targets (Fig. 6b), more like the much larger sets ($n > 3000$) of high-irreplaceability patches under the 10% targets (Fig. 6d, e and g). The main difference between the set of 1877 patches identified using IC and the much larger sets identified as highly irreplaceable under the 10% targets for REs and/or subregions, was the higher proportion of small patches in the latter, larger sets. This was presumably due to biodiversity features for which targets exceeded available extent, so that all patches where irreplaceable. Only 55% of the 1877 highly irreplaceable patches under the 5% targets were also in the top 1877 patches based on IC, but they accounted for 81% of the extent of the high-Irr patches under the 5% targets (Table 3). Similarly, the set of 5513 patches with greatest IC included 80% of the patches and 95% of the extent of patches that scored high-Irr under the 10% targets for both RE and subregion, and also had a wider geographic spread, most

Fig. 6. Maps of Brigalow regrowth patches identified as high-value using either initial complementarity or irreplaceability ($I \geqslant 0.5$) under various targets and biodiversity features as indicated by the caption on each map. Patch sizes are exaggerated for clarity. The light grey line is the study area boundary, it is the outer limit of the subregions shown in greater detail in Fig. 2.

notably in the north (Fig. 6g and h). Median patch size was consistently larger for sets chosen for high IC than for those chosen based on Irr (Table 3).

There was a clear positive correlation between IC and Irr (Fig. 9), which should be expected since they use the same information and targets. The key difference is that complementarity

Table 3
Comparison between sets of patches assigned high irreplaceability under various target scenarios and sets of the same numbers of patches selected based on initial complementarity (after comma). Values in parenthesis indicate the percentage of overlap between the two sets.

	5% RE and sub	10% RE only	10% Sub only	10% RE and sub
Number of patches	1877 (55%)	3252 (44%)	5163 (79%)	5513 (81%)
Total extent (ha)	48,391, 130,531 (81%)	129,930, 175,907 (81%)	174,438, 222,352 (95%)	192,924, 229,408 (95%)
Median patch extent (ha)	10.4, 21.8	12.5, 16.9	11.6, 15.3	11.7, 15.1
Median summed EVR probability	8.74, 8.40	6.70, 8.02*	7.61, 7.70*	7.59, 7.66*

* Indicate significant differences between sets in summed probability (per unit area) for occurrence of threatened species listed in Appendix B ($p \ll 0.05$ in each case).

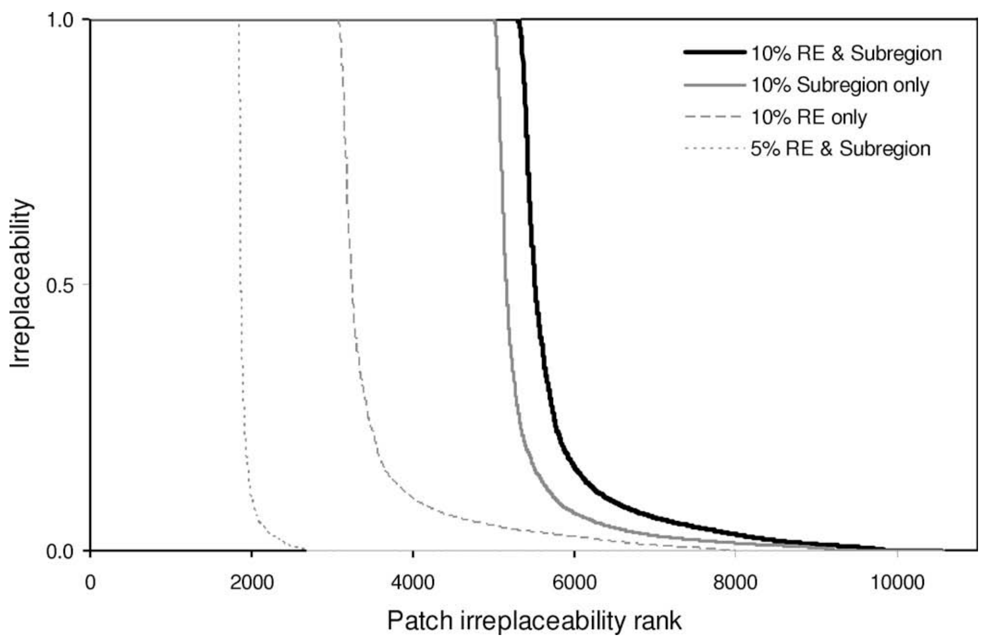

Fig. 7. Distribution of irreplaceability scores under various target and feature scenarios for 10,555 patches of Brigalow regrowth.

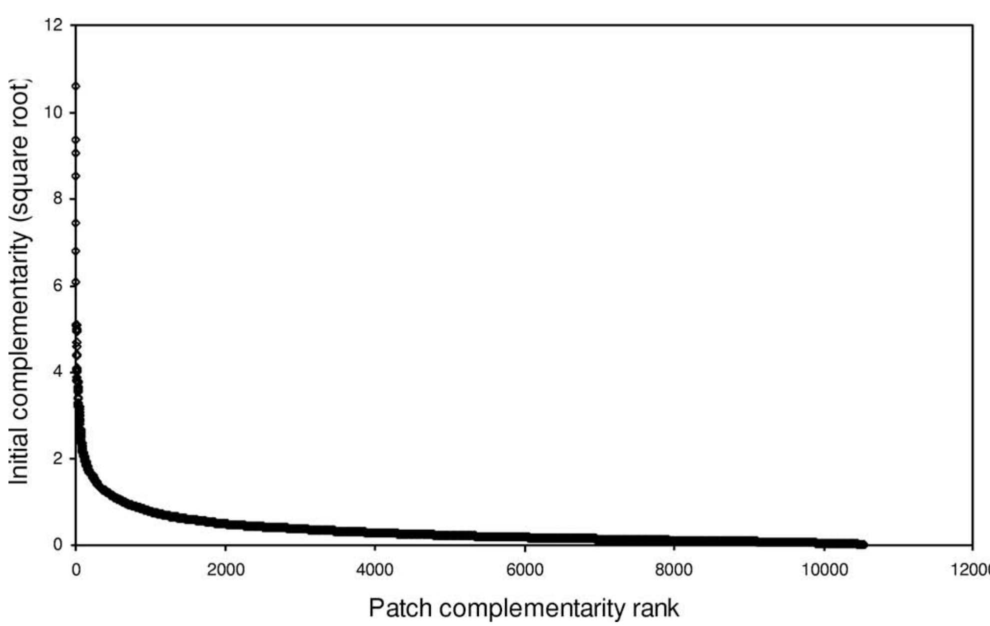

Fig. 8. Distribution of initial complementarity scores for 10,555 patches of Brigalow regrowth.

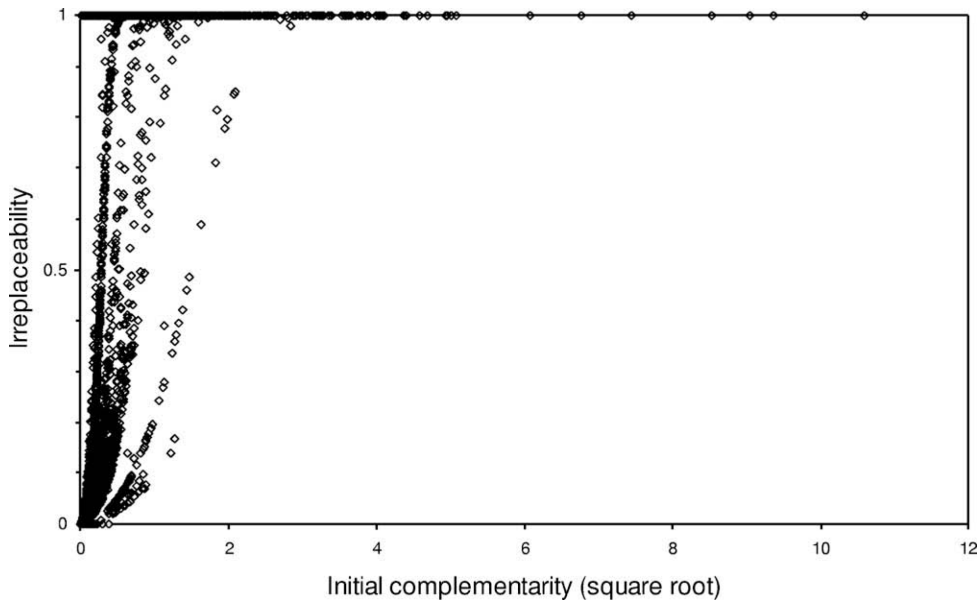

Fig. 9. Irreplaceability under the 10% RE and sub targets scenario plotted against initial complementarity scores for 10,555 patches of Brigalow regrowth.

provides information about relative values among the numerous patches attracting the maximum irreplaceability score.

4. Discussion

At regional scales, without considering the specific question of which particular patch is of greatest value for restoration, the irreplaceability results provide quite clear information about conservation priorities. However, the main directions at this broad scale, to focus on regrowth in extensively cleared landscapes (subregions) and land-types (regional ecosystems), are inherent in the methodology. Of course, the same is also true for patterns of complementarity. This highlights the prime importance of carefully considering how targets are set and how biodiversity is represented when assessing 'value' using complementarity, irreplaceability or any other metric. The metrics can only map concepts of value, encapsulated in the targets and biodiversity features, onto data-scapes.

Any choice of biodiversity features to assess irreplaceability or complementarity is a compromise (Margules et al., 2002). To be critical, the biodiversity features and conservation targets chosen for this study have some potential shortcomings, mainly due to the use of categorical land-classes as biodiversity features, without explicit information on species distributions. The use of land-classes, such as the REs in this study, has been criticised as inadequate for protection of species (Brooks et al., 2004). However, vegetation classifications such as REs are generally recognised as useful biodiversity indicators for regional scale analyses (Faith and Walker, 1996), although it must be noted that they do not represent all species or all components of biodiversity equally well (Lombard et al., 2003). The primary appeal of mapping such as the RE data is that it provides spatially unbiased information about the distribution of biodiversity across study regions, which is often used to infer habitat extent for a wider range of biota, and therefore allows conservation targets to be expressed in terms of the extent of mapped classes. Targets based on the quantity of particular biodiversity features, like RE extent, are expected to increase the chance of biodiversity features persisting within a set of priority areas compared to targets based on presence-only data (Gaston et al., 2002). Landscape-scale classification, provided in this case by the extent of Brigalow within biogeographic subregions, added a useful level of environmental discrimination to the assessment of conservation value, and substantially shifted the distribution of high-irreplaceability patches toward habitat for threatened species.

For a given suite of biodiversity features, metric choice is also clearly an important issue. The strongly bipolar distribution of irreplaceability values described in this study present an important problem for the use of irreplaceability as a measure of value for incremental restoration planning. High-value patches are effectively an optimal-set, indistinguishable using irreplaceability. Carwardine et al. (2007) also found polarised irreplaceability distributions, but Pressey and Taffs (2001) reported a more informative spread of irreplaceability scores in their analysis, although their large 400 km^2 planning units may explain this difference (Pressey and Logan, 1997).

The question of whether setting smaller targets might be a useful way to mitigate the strongly polarised distribution of irreplaceability is answered in the negative for this study, even though highly irreplaceable patches under small targets were also generally identified as priorities under larger targets (Stewart et al., 2007). The set of highly irreplaceable patches identified with the smaller targets under scenario 3 was still large and showed several arguably undesirable attributes including very clumped spatial distribution, poor alignment with threatened species distributions, the smallest median patch size of any scenario, and the most polarised distribution of irreplaceability scores. Reducing the targets down-weighted many biodiversity features, especially the REs, and focused irreplaceability on a few rare features; in this case the most cleared subregions. Therefore, simply setting smaller targets does not appear to increase the applicability of irreplaceability to the problem of scheduling incremental restoration. A more continuously variable metric that uses more desirable targets, such as that for IC in this study, seems a better way to identify small high value sets than assessing irreplaceability under smaller targets.

Incorporating additional variables or more complex approaches into the assessment of irreplaceability is also unlikely to make irreplaceability as variable and informative as complementarity. For example, C-Plan allows calculation of 'summed-irreplaceability' for planning units, which sums values for individual biodiversity features. These results were not presented here in any detail, but there were still many tied scores despite an increase in the range of scores. The technology to incorporate efficiency, compactness and connectivity into systematic conservation or restoration planning has been demonstrated and is readily available. For example, Crossman and Bryan (2006) demonstrated the utility of 'impedance surfaces' to weight restoration priorities toward areas connected to native vegetation, roadways and watercourses, in developing optimal-sets of restoration targets. Within a small planning region, an optimal-set may be more than adequate if, for example, immediate complete implementation is possible, or if implementation within the optimal-set can be more pragmatically prioritised based on some other factor such as landholder interest (Marjokorpi and Otsamo, 2006), or expert opinion (Cipollini et al., 2005). However, for larger planning regions, complementarity or a similar continuous metric of biodiversity priority will be more useful for planning broad-scale incremental restoration programs than tools that identify broader optimal sets.

Of course, cost and other factors must be combined with biodiversity metrics to identify efficient investment priorities (Newburn et al., 2005). The best way to incorporate costs will vary depending on the type of restoration or preservation mechanism deployed (Main et al., 1999), and costs may also change as restoration's economic and policy context develops. The important point from this study is that complementarity provides more information on 'value' than irreplaceability does for inclusion within multi-criteria cost-benefit-loss analyses.

As well as cost, viability should be an important consideration in investment planning, analogous to risk in financial investment. Patch size or connectivity might provide some indication of viability, and they were included in this study with that purpose in mind. At first glance the positive correlation between patch size and Irr or IC might suggest that high Irr or IC is fortuitously associated with the most viable patches. However, there are several reasons why this is an incorrect conclusion, the most important being that positive correlation of patch area with IC or Irr is a natural product of the approach taken; because value is ascribed to patches rather than to planning units of uniform size. In many ways the most notable aspect of the correlation described in this study is its weakness. In terms of landscape health and broader biodiversity considerations, the inadequate extent of remnant vegetation in the heavily cleared subregions, within which small and disconnected forest fragments tend to occur, increases the conservation priority of these patches and thereby weakens the underlying correlation between patch area or connectivity and viability. Beyond this methodological issue, lies an important ecological issue with the use of patch size or connectivity as indices of viability in planning studies. Several studies caution against assuming that patch size or connectivity is directly proportional to patch viability or biodiversity persistence. Threatened species distributions can be poorly aligned with patch size or condition (Kirkpatrick and Gilfedder, 1995), and patch condition and edge contrasts are often more important than patch size to biodiversity persistence (Gilfedder and Kirkpatrick, 1998; Debuse et al., 2007; Hannah et al., 2007). In the north and west of the study area, cattle-grazing is an almost ubiquitous influence on the landscape. Areas unaffected by stock, such as small remnants set in agricultural cropping lands in the south and east, may prove to be of particular importance for some species (e.g. Prober and Thiele, 1995). Anecdotal evidence suggests that for some fauna, such as reptiles, remnant Brigalow patch condition is more important for persistence than is patch size, and small patches can support diverse species assemblages (Johnson, 2001). Habitat arrangement including connectivity has also received limited support as a strong determinant of biodiversity persistence, independently of habitat area (Fahrig, 2003). Therefore, using patch size or connectivity as indicators of restoration value based on viability can be too simplistic; particularly if patch size or connectivity is strongly associated with a subset of a region and its biodiversity, such as the north and west for Brigalow, or agriculturally unproductive lands more generally (Pressey and Taffs, 2001).

Differences in regrowth and remnant patch size across Brigalow are also likely to produce differences in appropriate restoration management. The large and well connected patches with high irreplaceability in the north and west of Brigalow Belt may be good candidates for threat minimisation and prevention, at relatively low cost, whereas small, isolated patches in the south of Brigalow Belt might require more active threat reduction (Hobbs and Kristjanson, 2003). This reiterates the need for a flexible approach to assessing cost when planning strategic restoration, rather than a simple metric such as 'cost-of-acquisition' that might be suitable in more typical SCP applications. Case-by-case assessments of cost, based for example on landholder tenders, can readily be combined with complementarity as an informative measure of biodiversity conservation value, and a measure of risk of loss (such as proportion of regrowth for each biodiversity factor recently cleared), into multi-factorial cost-benefit-loss investment optimisation algorithms, to guide incremental restoration using natural regrowth.

5. Conclusion

This study demonstrates that both irreplaceability and complementarity can be used to map biodiversity conservation goals at regional scales, and highlights the sensitivity of patch-scale perceptions of 'value' to choices about conservation targets and 'biodiversity features'. Although irreplaceability and complementarity are correlated and based on the same data, this study suggests that complementarity will be substantially more useful than irreplaceability for iteratively planning incremental restoration as part of cost-benefit-loss trade-offs. This is simply because irreplaceability is uninformative in ranking 'high-value' patches, they all have the highest possible score, whereas the complementarity metric used in this study provides information about relative value among high-value patches.

For the specific case of Brigalow, the extent of natural regrowth identified in this study represents a significant potential resource for landscape-scale restoration and biodiversity conservation.

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Appendix A. Summary statistics and targets for 'Brigalow dominant' areas assessed in this study. Targets in bold font indicate those that exceed available regrowth extent

Biodiversity feature	Pre-clearing (ha)	Remnant 2003 (ha)	10% regrowth target (ha)	5% regrowth target (ha)	Available regrowth (age modified) (ha)
S_11_2 – Bogie River Hills	1518	1147	0	0	28
S_11_3 – Cape River Hills	10,760	5931	0	0	17
S_11_4 – Beucazon Hills	1920	412	0	0	3
S_11_5 – Wyarra Hills	9421	5042	0	0	108
S_11_6 – Northern Bowen Basin	175,783	29,005	0	0	5186
S_11_7 – Belyando Downs	364,958	57,633	0	0	4174
S_11_8 – Upper Belyando Floodout	42,380	3618	**620**	0	85
S_11_9 – Anakie Inlier	7463	3348	0	0	221
S_11_10 – Basalt Downs	140,982	20,987	0	0	4617
S_11_11 – Isaac – Comet Downs	1 130,235	67,582	45,442	0	50,772
S_11_12 – Nebo – Connors Ranges	25,855	2456	130	0	343
S_11_13 – South Drummond Basin	28,257	4606	0	0	721
S_11_14 – Marlborough Plains	37,847	2007	**1778**	0	1616
S_11_15 – Claude River Downs	235,173	62,238	0	0	2552
S_11_16 – Woorabinda	23,809	4775	0	0	2234
S_11_17 – Boomer Range	13,015	2513	0	0	1061
S_11_18 – Mount Morgan Ranges	58,655	2242	3624	691	4423
S_11_19 – Callide Creek Downs	103,431	1453	**8890**	**3719**	1884
S_11_20 – Arcadia	81,410	5785	2356	0	2715
S_11_21 – Dawson River Downs	349,824	6537	**28,445**	**10,954**	9971
S_11_22 – Banana – Auburn Ranges	67,419	5585	1157	0	1754
S_11_23 – Buckland Basalts	4439	3115	0	0	263
S_11_24 – Carnarvon Ranges	23,892	5924	0	0	2100
S_11_25 – Taroom Downs	380,987	10,750	**27,349**	**8299**	4604
S_11_26 – Southern Downs	795,712	55,933	23,638	0	32,544
S_11_27 – Barakula	105,660	6167	**4399**	0	2659
S_11_28 – Dulacca Downs	78,176	2847	**4971**	**1062**	1012
S_11_29 – Weribone High	279,431	18,876	**9067**	0	8868
S_11_30 – Tara Downs	418,583	15,140	**26,718**	5789	9305
S_11_31 – Eastern Darling Downs	290,652	7791	**21,274**	**6742**	2204
S_11_32 – Inglewood Sandstones	99,644	6442	**3522**	0	2352
S_11_33 – Moonie R – Commoron Creek Floodout	551,939	30,042	**25,152**	0	21,929
S_11_34 – Moonie – Barwon Interfluve	353,074	18,002	**17,305**	0	14,824
S_11_35 – Balonne – Culgoa Fan	19,857	9298	0	0	2596
S_11_36 – Macintyre – Weir Fan	12,460	265	**981**	358	777
S_12_2 – Moreton Basin	23,274	843	1484	321	1900
S_12_5 – Brisbane – Barambah Volcanics	1572	708	0	0	160
S_12_6 – South Burnett	7996	230	**570**	170	360
S_6_1 – West Balonne Plains	257,647	1313	**24,452**	**11,569**	7056
S_6_2 – Eastern Mulga Plains	7155	53	**663**	305	342
RE_11_3_1	672,842	55,225	12,059	0	27,280
RE_11_4_3	1,553,646	76,062	**79,303**	1620	48,411
RE_11_4_7	190,965	18,288	809	0	9964
RE_11_4_8	642,196	62,844	1376	0	17,885
RE_11_4_9	764,855	74,097	2389	0	25,712
RE_11_4_10	57,703	5473	297	0	2794
RE_11_5_16	11,819	2694	0	0	473
RE_11_9_1	523,554	45,441	6914	0	16,368
RE_11_9_5	1,791,966	134,853	44,344	0	47,634
RE_11_9_6	15,352	378	**1157**	**390**	69
RE_11_11_14	34,670	4546	0	0	1435
RE_11_12_21	72,081	6692	516	0	2845
RE_12_8_23	5324	412	120	0	305
RE_12_9-10_6	23,034	843	1460	309	1850
RE_12_12_26	5700	776	0	0	314
RE_6_4_2	257,612	17,387	**8374**	0	7017

Appendix B. Threatened taxa associated with Brigalow used to assess sets of priority patches generated under various scenarios. E = Endangered and V = Vulnerable under State and/or Australian laws

Scientific name	Common name	Status	Notes
Plants			
Aponogeton queenslandicus		E (NSW&QLD)	Aquatic plant that grows in 'melonhole' wetlands associated with Brigalow
Cadellia pentastylis	Ooline	V (AUST, NSW&QLD)	Large tree, often associated with SEVT but also grows in Brigalow forests
Capparis humistrata		E (QLD)	Grows on the edges of Brigalow forests near Rockhampton
Eucalyptus argophloia	Chinchilla white gum	V (AUST&QLD)	An emergent in Brigalow and belah (*Casuarina cristata*) forests near Chinchilla
Homopholis belsonii	Belson's panic	V (AUST&NSW), E (QLD)	A grass in Brigalow and associated box woodlands on the Darling Downs and Moree plain
Rutidosis lanata		E (QLD)	A daisy known between Jackson and Westmar on the Western Darling Downs
Solanum adenophorum		E (QLD)	A "bush tomato" favouring Brigalow country in the Dingo-Nebo-Clermont area
Solanum dissectum		E (QLD) – pending	One of Queensland's rarest plants. Occurred in Brigalow forests around Banana in central Queensland, now known from only one location which supported 17 plants in 2003
Solanum johnsonianum		E (QLD) – pending	In Brigalow forest between Theodore and Biloela. Now known from three locations
Xerothamnella herbacea		E (QLD)	A small herb strongly associated with Brigalow north of Chinchilla
Animals			
Calyptorhynchus lathami	Glossy black-cockatoo	V (QLD&NSW)	Feeds exclusively on Casuarinaceae seeds, including belah; a common tree in Brigalow
Delma torquata	Collared delma	V (AUST&QLD)	A cryptic species with scattered populations in a variety of vegetation types in Brigalow Belt
Denisonia maculata	Ornamental snake	V (AUST&QLD)	A specialist of low-lying, seasonally flooded areas, including Brigalow and belah forests. Endemic to Brigalow Belt, mainly in the Dawson and Fitzroy River catchments
Egernia rugosa	Yakka skink	V (AUST&QLD)	Occurs in isolated populations from southern Cape York to southern Queensland. Eats invertebrates, fruits and plant material
Furina dunmalli	Dunmall's snake	V (AUST&QLD)	Uses fallen timber for habitat in Brigalow and other woodland types. Distributed from Yepoon to Inglewood in southern Qld
Grantiella picta	painted honey-eater	V (NSW), Rare (QLD)	In Qld, Brigalow/belah is used as nesting habitat during October–December, coinciding with flowering of mistletoes in the Brigalow trees. An important habitat for this species
Hemiaspis damelii	Grey snake	V (AUST&QLD)	Inhabits floodplains and low-lying areas on heavy soils, including Brigalow–belah
Jalmenus evagoras ebulus	Northern imperial hairstreak butterfly	V (QLD)	Reportedly only uses 'virgin' Brigalow as habitat
Nyctophilus timoriensis	Eastern long-eared bat	V (AUST,QLD &NSW)	Brigalow is an important community for this species in the study area, but it almost certainly requires eucalypts for at least part of its roosting
Onychogalea fraenata	Bridled nail-tail wallaby	E (AUST&QLD), Presumed extinct (NSW)	Brigalow is important for remnant populations of this species. Also occupies open eucalypt forests and woodlands
Paradelma orientalis	Brigalow scaly-foot	V (AUST&QLD)	Occurs in other vegetation types but is relatively common in Brigalow. Feeds on plant exudates including from *Acacia* spp.(Mimosaceae)
Turnix melanogaster	Black-breasted button-quail	V (AUST&QLD), E (NSW)	Mainly occurs outside the study area but uses Brigalow scrubs in the south–east

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