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Rapidly quantifying reference conditions in modified landscapes

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ABSTRACT

Reference conditions remain widely used as a benchmark for ecosystem management, but there remains conjecture about the definition of the reference state. Many techniques used to predict reference conditions are difficult to apply operationally because they are resource-intensive, subjective, or applicable for a limited suite of environmental variables or over a narrow range of environmental variation. We defined the reference state as variation in native vegetation exhibiting relatively little evidence of modification by humans since European settlement. Using data from 462 sites supporting native vegetation in a fragmented landscape in south-eastern Australia, we demonstrated a relatively quick and cost-effective way of objectively predicting reference conditions for various surrogates of biodiversity. We predicted reference values for several variables that are used as biodiversity surrogates (i.e., tree densities by diameter class, trees with hollows, tree regeneration, trees with mistletoe, fallen timber, vegetation cover by vertical stratum, litter cover, cryptogam cover and native plant species richness) using generalized additive models (GAMs) fitted with predictors representing measures of human modification since European settlement (exotic plant cover, number of stumps, evidence of firewood collection, evidence of rabbits, evidence of recent grazing by stock, surrounding land use) and measures of environmental variation (floristic composition, mean annual precipitation, mean annual temperature, solar insolation, aspect, slope). Reference values for each response variable were predicted from these models by holding the significant explanatory variables representing modification since European settlement at their minimum observed values, that is, our definition of the reference state. We demonstrated the importance of independently evaluating predictions of this type using generic ecological models and estimates of reference conditions derived from other sources.

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1. Introduction

Reference conditions (variously known as historic variability, naturalness, biodiversity intactness, old-growth, pre-European) remain widely used as benchmarks for ecosystem management. Reference conditions underpin techniques used to assess the condition of, impacts of development on, and restoration targets for, marine, freshwater and terrestrial ecosystems (e.g., Gibbons et al., 2009; Karr, 1991; McElhinny et al., 2005; Pandolfi et al., 2003; Parkes et al., 2003; Parsons et al., 2004; Rheinhardt et al., 2007).

Despite conjecture about the definition and identification of reference conditions (e.g., Aronson et al., 1995; Haila, 1997; Hunter, 1997), the reference concept is prominent in ecosystem management for several reasons: (1) ecosystems approaching conditions that prevailed prior to major periods of modification (e.g., European settlement) will generally better reflect the conditions to which persistent communities of native biota are adapted (Landres et al., 1999); (2) ecosystems are more resilient within their historical range of variation than ecosystems managed outside this range (Fule et al., 1997; Holling and Meffe, 1996); (3) it is a pragmatic approach for assessing and managing ecosystems where data for communities and species or processes are lacking, or such data cannot be collected within the constraints of rapid assessment (Gibbons et al., 2009); (4) ecosystems are assessed in relative rather than absolute terms, thereby avoiding the perverse situation where ecosystems that are naturally more structurally diverse or species rich are always assessed as in higher condition than ecosystems that are naturally less structurally diverse or species rich; and (5) there is empirical evidence to support the concept (Laughlin et al., 2004; Whiteley and Bendell-Young, 2007).

Reference conditions are used as the benchmark for several biodiversity surrogates. These include: species richness, composition and abundance (Nielson et al., 2007; Tison et al., 2007); the extent (Cawsey et al., 2002), spatial arrangement (Hessburg et al., 1999), structural characteristics (Bragg, 2002; Lunt et al., 2006; Moore et al., 1999) and functional attributes (Brinson and Rheinhardt, 1996) of vegetation communities; soil properties (Prober et al., 2002a); and disturbance regimes (Fule et al., 1997). Several techniques are employed to derive benchmarks for these surrogates including historical accounts, such as explorers' journals (Flannery, 1994) and surveyors' records (Martin, 2005); reconstructions of ecosystems using paleontology (Simpson et al., 2005), dendroecology (Fule et al., 1997; McEwan and McCarthy, 2008) and tree stumps (Lunt et al., 2006); observations from existing examples of relatively unmodified ecosystems (Cawsey et al., 2002; Tinker et al., 2003); and expert judgment (Muxica et al., 2007). However, it remains difficult to quantify reference conditions in modified landscapes because these techniques can be resource-intensive, are difficult to apply in all ecosystems or across large areas, can be applied to only some ecosystem characteristics (e.g., trees), or contain a large element of subjectivity that leaves them open to debate.

The aim of this study was to develop an objective method that can be applied operationally to estimate reference conditions for several biodiversity surrogates across a large study area encompassing a broad range of environmental variation. We defined the reference state as the range of variability in ecosystems exhibiting least evidence of modification by humans since European settlement (e.g., sites with relatively little clearing, agricultural development, fertilization, logging, firewood collection, mining, weed invasion or occupation by domestic or feral herbivores).

2. Materials and methods

2.1. Study area

The study area spanned over five degrees of latitude of central New South Wales (NSW) in south-eastern Australia (-29.5 to $-36.0°$ latitude, 144.7–150.0° longitude). The area has a long history of Aboriginal occupation (circa 50,000 BP) and was settled by Europeans from the early 1800s. The area is dominated by land managed principally for grazing and cultivation with the different bioregions containing 16–40% of their predicted pre-European cover of native vegetation (Pressey et al., 2000). Because this research was intended to support methods for rapidly assessing land clearing and agri-environmental incentive schemes, we focused on the most wide-spread ecosystems across the study area. To capture variation within these ecosystems we stratified our sampling by: (1) dominant over-storey species observed in the field (eight levels), (2) mean annual precipitation (four levels), and (3) major catchment (six levels). The eight vegetation strata identified by dominant over-storey species were: yellow box (*Eucalyptus melliodora*), grey box (*E. microcarpa*), white box (*E. albens*), red (or mugga) ironbark (*E. sideroxylon*), red stringybark (*E. macrorhyncha*), white cypress pine (*Callitris glaucophylla*), poplar box (*E. populnea*) and coolibah (*E. coolabah*). The four mean annual precipitation classes derived from ESOCLIM (Houlder et al., 2000) and a 250 m digital elevation model were: 400–500 mm, 501–600 mm, 601–700 mm and >700 mm. The six major catchments were: Murray catchment, Murrumbidgee catchment, Lachlan catchment, Central West catchment (comprising Macquarie and Castlereagh catchments), Namoi catchment and Border Rivers/Gwydir catchment.

2.2. Identifying potential reference sites

We initially attempted to find least modified remnants of native vegetation by sampling the largest remnants in each stratum. However, vegetation mapping at a scale across the study area to facilitate this was not available and modification history (e.g., grazing) can be more indicative of remnant condition than remnant size in these landscapes (Prober and Thiele, 1995). Instead we identified a set of least modified remnants of native vegetation across the study area by drawing on 18 sources of information including: ecological researchers; naturalists; consultants; local staff in state, local and non-government land management organizations; existing databases; and our own field observations. Field measurements were then undertaken on a sample of all remnants identified from these sources to achieve a relatively balanced sampling design across all strata. We sampled sites with different histories of fire, flooding and storm damage and did not knowingly bias our sampling towards sites affected or not affected by these events.

2.3. Measured variables

A total of 462 plots were measured across the study area. Three 50 m × 20 m (0.1 ha) plots were typically established in each native vegetation remnant. One plot was established in each of the upper, mid and lower part of the topographic sequence represented in the remnant (where a topographic gradient occurred). Plots were randomly located at least 50 m from the edge of the remnant or from a formed road, unless the dimensions of the remnant did not permit this. The long axis of the plot was randomly oriented, although an angle was rejected if more than one level for any of topographic position, vegetation community, aspect or tenure was represented within any single plot. All plots were measured from August 2002 to November 2003, which coincided with a period of below average annual precipitation.

Surrogates (response variables) for: (a) biodiversity and ecological function (Table 1); (b) post-European modification (Table 2); and (c) environmental variation (Table 3) were recorded at each plot. These variables were either measured in the 50 m × 20 m plot, in a 20 m × 20 m (0.04 ha) plot nested within the larger plot, along a 50 m transect running down the centre of the larger plot, in the landscape around each plot, or remotely (see Tables 1–3). The chosen response variables are used commonly in rapid biodiversity assessments (e.g., Newsome and Catling, 1979; Parkes et al., 2003; Gibbons et al., 2009) and/or have been associated statistically with several taxa (McElhinny et al., 2006).

A classification of the vegetation communities in the study area was constructed from partial floristics recorded at 405 of the 462 20 m × 20 m plots (see Table 3). This classification followed the approach outlined in Cawsey et al. (2002) using the Bray–Curtis measure of association and a hierarchical cluster analysis fused using Unweighted Pair-Group Arithmetic Averaging. This classification was used to assign each plot to a discrete vegetation community. The remaining 57 plots in which comparable floristic information was not recorded were each assigned in the field to a vegetation community defined by Gellie (2005).

Table 1 – Response variables for which benchmarks were predicted

Variable	Description	Plot or transect size
Tree diameter class	Count of living native over-storey trees in each of the following diameter classes: 5–20 cm, 21–40 cm, 41–60 cm and >60 cm. For trees with multiple stems at breast height only the largest stem was measured. Diameter was measured at breast height over bark (DBH)	50 m × 20 m plot
Trees with hollows	Count of living and dead trees with at least one visible hollow with an estimated minimum entrance width ⩾5 cm (excludes hollows at the base of trees, in fallen timber and in stumps)	50 m × 20 m plot
Tree regeneration	The number of stems ⩽5 cm diameter recorded for sub-canopy and canopy tree species	50 m × 20 m plot
Mistletoe occurrence	Count of trees with mistletoe	50 m × 20 m plot
Fallen timber (volume)	Calculated as $2\pi rl$ where r = radius measured at the mid-point of the log and l = log length in cm	50 m × 20 m plot
Fallen timber (length)	Mid-point diameter (cm) and length to nearest 1m for each fallen log or section of fallen log ⩾10 cm diameter	50 m × 20 m plot
Litter cover	Measured percentage cover of litter <10 cm diameter	10 × 1 m lengths along 50 m transect
Cryptogam cover	Measured percentage cover of cryptogam on soil surface	10 × 1 m lengths along 50 m transect
Native over-storey cover	Visual estimate of percentage cover for native canopy and sub-canopy tree species >4 m tall using images in Walker and Hopkins (1984)	10 points along 50 m transect
Native mid-storey cover	Visual estimate of percentage cover for native plant species (including regenerating tree species) that are 2–4 m tall	20 m × 20 m plot
Native under-storey cover	Visual estimate of percentage cover for native plant species <2 m tall	20 m × 20 m plot
Native plant species richness	Number of native plant species	20 m × 20 m plot

Table 2 – Independent (predictor) variables reflecting human modification since European settlement

Variable	Description	Plot or transect size
Stumps	Count of stumps (left where trees were cut by saw or axe) expressed as a proportion of all original trees on the plot >5 cm DBH (i.e., living and dead trees and cut stumps)	50 m × 20 m plot
Evidence of firewood collection	Evidence of firewood collection from crosscutting of fallen timber (0,1)	50 m × 20 m plot
Evidence of recent grazing by stock	Presence/absence of evidence of stock (i.e., animals, tracks or droppings) (0,1)	50 m × 20 m plot
Evidence of rabbits	Presence/absence of evidence of rabbit or hare droppings or active burrows (0,1)	50 m × 20 m plot
Exotic plant cover	Percentage cover for exotic plant species expressed as a proportion of total percentage cover of vegetation in the under-storey stratum (note that exotic plants were only observed in the under-storey stratum and the timing of surveys were such that these data predominantly represented perennial exotic cover only)	20 m × 20 m plot
Surrounding land use	Dominant land use recorded in the field as urban, cultivation, improved pasture, unimproved pasture or native vegetation	Within a nominal radius of 1 km from the plot

Table 3 – Independent (predictor) variables representing environmental variation

Variable	Definition	Plot or transect size
Mean annual precipitation	Predicted using ESOCLIM Houlder et al. (2000) and a 250 m digital elevation model and expressed as a factor with four levels: 400–500 mm, 501–600 mm, 601–700 mm, >700 mm	Not applicable
Mean annual temperature	Predicted using ESOCLIM Houlder et al. (2000) and a 250 m digital elevation model	Not applicable
Solar insolation	Solar insolation (i.e., the amount of solar radiation incident on the earth's surface) predicted using a 250 m DEM using ArcView Solar Analyst Fu and Rich (2000)	Not applicable
Vegetation community	One of eight vegetation communities (yellow box, grey box, white box, red ironbark, red stringybark, white cypress pine, poplar box or coolibah) classified from the dominant three plant species recorded in each of the over-, mid- and under-storey strata	20 m × 20 m plot
Aspect	Predicted using the standard ArcView algorithm and a 250 m digital elevation model and classified into one of five levels: flat, N (>315–45°), E (>45–135°), S (>135–225°), W (>225–315°)	Not applicable
Slope	Predicted using the standard ArcView algorithm and a 250 m digital elevation model	Not applicable
Topographic position	Recorded for each plot as flat, lower, mid or upper relative to the surrounding landscape	50 m × 20 m plot

These 57 plots were then manually re-assigned to the most similar vegetation community that we defined using the 405 plots.

2.4. *Predicting benchmark values for each variable*

Many of the sites identified by experts across the study area had some evidence of modification by humans. Thus, if we were to derive benchmarks only from sites with no evidence of modification by humans since European settlement then there would be few available sites across the study area. Further, we expected our sources to identify sites as relatively unmodified using slightly different criteria reflecting their particular expertise. Thus, instead of estimating reference conditions directly from these sites we predicted reference conditions using a series of independent variables measured at each site. A regression model of best fit was built to predict each response variable (Table 1) using potential explanatory variables representing measures of human modification since European settlement (Table 2) and environmental variation (Table 3) that were measured at each site. Models were developed to individually predict each variable in Table 1 rather than to predict groups of variables because agents of modification since European settlement have variable effects on different components of ecosystems (e.g., grazing by stock affects under-storey composition but not the volume of fallen timber). This method also enabled us to use data from all plots when predicting reference conditions.

We used GAMs to predict each response variable in Table 1 to allow for non-linear relationships with the predictors. All analyses were undertaken using the Generalized Regression and Spatial Prediction (GRASP) (Lehmann et al., 2003) and GRASPER packages available in the R statistical software. In GAMs the response curve is estimated with a non-parametric smoothing function instead of parametric function as in generalized linear models (GLMs) (Lehmann et al., 2003). None of the potential explanatory variables (Tables 2 and 3) were highly correlated ($r \leqslant 0.59$) except mean annual precipitation and mean annual temperature ($r = -0.79$). We chose to include the latter potential explanatory variables in model selection because, upon closer examination, the correlation between mean annual precipitation and mean annual temperature appeared to break down in the northern part of the study area. Quasi-binomial models (sensu Lehmann et al., 2003) with a logit link were developed for percentage data; quasi-Poisson models (sensu Lehmann et al., 2003) with a log link were developed for abundance data; and a Gaussian model with an identity link was developed for richness which, although count data, were normally distributed. Models of best fit were selected through a forward and backwards stepwise procedure using approximate *F*-tests. The *F*-tests were selected as this criterion produced more parsimonious models (i.e., fewer significant explanatory variables) then either Akaike's Information Criterion (AIC) or Bayesian Information Criterion (BIC). Variables were excluded if there was no significant change in deviance ($p > 0.05$) when sequentially dropped from, or added to, the model. We used the automated option in the GRASPER package to select the degrees of freedom used to smooth continuous variables. This is based on the number of clear changes in direction in the shape of the univariate relationship between the response and predictor. We reported the percentage of null deviance explained by each model instead of adjusted *r*-squared as recommended in the *R* documentation for GAMs.

Benchmarks were predicted for each response variable (Table 1) from the model of best fit by: (a) holding each significant explanatory variable representing modification by humans since European settlement at the minimum observed value (zero in all cases, except for the factor representing dominant surrounding land use which was assigned to native vegetation); and (b) holding significant explanatory variables representing environmental variation at either the mean value (for continuous variables) or most frequently recorded level (for factors) observed in each vegetation community. Benchmarks predicted from the models were expressed as a mean ± 2 × the point-wise standard error (SE).

3. Results

3.1. *Profile of sampled sites*

The distribution of plots by vegetation community and mean annual precipitation is summarized in Table 4. Plots were distributed among land tenures as follows: 31% in traveling stock reserves and routes managed by state government; 24% in private land; 14% in forests and flora reserves managed by state government; 13% in national parks and nature reserves

Table 4 – A summary of the distribution of plots by vegetation community and mean annual precipitation (mm)

Vegetation community	Mean annual precipitation (mm)				
	401–500	501–600	601–700	>700	Total plots
Coolibah	24	7	1		32
Grey box	27	46	13		86
Poplar box	39	14			53
Red ironbark	7	24	13	4	48
Red stringybark			40	29	69
White box		13	21	19	53
White cypress pine	29	21			50
Yellow box		1	37	33	71
Total					462

Table 5 – Predicted benchmarks (mean ± 2 × SE) for the number of living trees per 0.1 ha by vegetation community and stem diameter class (DBH) (cm)

Vegetation community	Diameter class (cm)			
	5–20	21–40	41–60	>60
Coolibah	4.1 ± 3.3	4.0 ± 1.8	1.7 ± 0.6	0.6 ± 0.3
Grey box	12.6 ± 3.9	8.5 ± 1.6	2.2 ± 0.4	1.5 ± 0.4
Poplar box	17.4 ± 5.5	7.9 ± 2.1	1.4 ± 0.4	0.4 ± 0.2
Red ironbark	29.9 ± 7.9	16.1 ± 2.5	3.1 ± 0.7	1.1 ± 0.4
Red stringybark	29.4 ± 6.0	18.1 ± 2.3	4.0 ± 0.7	1.1 ± 0.3
White box	8.8 ± 4.4	6.1 ± 1.8	2.3 ± 0.6	1.6 ± 0.5
White cypress	46.1 ± 11.0	13.4 ± 2.8	1.5 ± 0.5	0.4 ± 0.2
Yellow box	16.7 ± 5.7	5.7 ± 1.5	1.3 ± 0.4	1.5 ± 0.4

managed by state government; 12% in other crown land managed by local government or state government; and 6% in roadside reserves managed by local government. Overall, 85% of plots had some evidence of post-European modification in the form of stumps, firewood collection, recent grazing by stock, exotic plants, and/or evidence of rabbits. Two per cent of plots had evidence of recent fire, 57% of plots had evidence of past fires (fire scars in trees or charred logs) and 41% of plots had no visible evidence of recent or past fires.

The classification of floristic information identified 24 vegetation communities at one level of the dendrogram and eight broader vegetation communities at a higher level of the dendrogram. Our analyses were based on the broader 8-group classification because there were insufficient plots (degrees of freedom) in several levels of the 24-group classification to undertake statistical analyses. The species with greatest cover abundance in each of the eight broad vegetation communities were: (1) grey box, spear grass (*Austrostipa* sp.), wallaby grass (*Austrodanthonia* sp.) and sticky hop-bush (*Dodonaea viscosa*); (2) red ironbark, black cypress pine (*C. endlicheri*), wallaby grass, grey box and spear grass; (3) red stringybark, redanther wallaby grass (*Joycea pallida*), daphne heath (*Brachyloma daphnoides*) and red box (*E. polyanthemos*); (4) white box, wallaby grass and spear grass; (5) white cypress pine, spear grass and grey box; (6) yellow box, spear grass and Blakely's red gum (*E. blakelyi*); (7) poplar box, Warrigal greens (*Tetragonia tetragonioides*), false sandalwood (*Eremophila mitchellii*) and wilga (*Geijera parviflora*); and (8) coolibah, Warrego summer grass (*Paspalidium jubiflorum*) and couch grass (*Cynodon dactylon*).

3.2. *Tree diameter class*

Exotic plant cover and vegetation community were significant explanatory variables in each of the models selected to predict the benchmark number of trees by diameter class, with evidence of recent grazing by stock, the number of stumps, solar insolation, slope and mean annual precipitation significant explanatory variables in one or more of the models (see Appendix A). The predicted benchmark numbers of trees by diameter class in each vegetation community are provided in Table 5. Benchmark diameter distributions conformed to inverse *J*-distributions (i.e., fewer trees in larger diameter classes) except for the coolibah community, which had similar numbers of trees in the 5–20 cm and 21–40 cm diameter classes (Table 5).

3.3. *Trees with hollows*

We predicted that numbers of trees with hollows decreased with numbers of stumps; were lower where there was evidence of firewood collection; and varied between some vegetation communities, some levels of solar insolation and some levels of mean annual temperature (see Appendix A). The predicted mean benchmarks for numbers of trees with hollows ranged from 1.0 per 0.1 ha (10 per ha) in the yellow box vegetation community to 3.4 per 0.1 ha (34 per ha) in the white box vegetation community (Table 6).

3.4. *Tree regeneration*

Tree regeneration (stems ⩽5 cm diameter) was more likely to be present on plots with low exotic plant cover, without evidence of recent grazing by stock, and with fewer stumps; and varied with vegetation community, aspect and topographic position (see Appendix A). The predicted benchmark mean percentage of 0.1 ha plots with tree regeneration present for each vegetation community ranged from 91% to 100% (Table 6).

3.5. *Mistletoe occurrence*

The percentage of trees (>20 cm DBH) in 0.1 ha plots with mistletoe was higher on sites with low exotic plant cover, and varied with solar insolation and slope (see Appendix A). The predicted mean benchmarks for the percentage of trees with mistletoe in each vegetation community ranged from 3% in the white cypress pine community to 7% in the coolibah and poplar box communities (Table 6), although the modeling indicated that these predicted values were not significantly different between vegetation communities.

3.6. *Fallen timber*

Volumes of fallen timber (⩾10 cm diameter) were greater where there was no evidence of firewood collection and varied with vegetation community, solar insolation, mean annual temperature and slope (see Appendix A). The predicted benchmarks for mean volumes of fallen timber ranged from 0.5 m^3 (per 0.1 ha) in the grey box vegetation community, to 1.0 m^3 (per 0.1 ha) in the red stringybark vegetation community (Table 6).

Table 6 – Predicted benchmarks (mean ± 2 × SE) for selected response variables

Vegetation community	Trees with hollows (per 0.1 ha)	Tree regeneration (percentage of occurrence per 0.1 ha)	Mistletoe occurrence (percentage of trees)	Fallen timber volume (m^3 per 0.1 ha)	Fallen timber length (m per 0.1 ha)	Litter cover (%)	Cryptogam cover (%)	Plant species richness (per 0.04 ha)
Coolibah	1.7 ± 0.7	97.4 ± 0.03	7.4 ± 2.3	0.52 ± 0.25	23.7 ± 7.0	50 ± 7	0.02 ± 0.11	31 ± 2
Grey box	2.0 ± 0.7	94.4 ± 0.05	3.6 ± 1.1	0.50 ± 0.18	19.8 ± 4.7	80 ± 3	1.77 ± 0.79	16 ± 1
Poplar box	2.2 ± 0.9	98.9 ± 0.01	7.2 ± 2.3	0.88 ± 0.36	31.6 ± 8.8	65 ± 5	3.43 ± 1.77	27 ± 2
Red ironbark	2.7 ± 0.9	90.7 ± 0.08	4.0 ± 1.1	0.71 ± 0.26	30.8 ± 7.4	84 ± 3	1.16 ± 0.78	16 ± 2
Red stringybark	2.0 ± 0.7	100.0 ± 0.00	4.2 ± 1.1	1.04 ± 0.35	39.7 ± 9.4	79 ± 3	3.03 ± 1.5	23 ± 2
White box	3.4 ± 1.1	97.3 ± 0.03	3.5 ± 1	0.39 ± 0.18	20.3 ± 5.9	77 ± 4	1.33 ± 0.94	17 ± 2
White cypress	1.6 ± 0.7	97.8 ± 0.03	2.9 ± 1.1	0.90 ± 0.31	27.3 ± 7.0	72 ± 4	9.76 ± 3.54	13 ± 2
Yellow box	1.0 ± 0.5	98.8 ± 0.01	3.7 ± 1.1	0.82 ± 0.26	23.6 ± 5.7	68 ± 4	1.60 ± 0.85	17 ± 2

We found a significant linear relationship between the total volume of fallen timber ($\log_{10}$) per 0.1 ha plot and total length of fallen timber ($\log_{10}$) per 0.1 ha plot ($p < 0.01$, $R^2 = 0.77$). Given the length of fallen timber is relatively easy to measure in the field, we also predicted benchmarks for this variable. The significant explanatory variables in the GAM predicting the length of fallen timber were confined to the environmental variables vegetation community, solar insolation, mean annual temperature and slope (see Appendix A). Predicted mean benchmarks for the total length of fallen timber per 0.1 ha ranged from 20 to 40 m (Table 6).

3.7. *Native vegetation cover by vertical stratum*

We predicted benchmark percentage cover separately for native vegetation in the over-storey stratum (plant life-forms >4 m), mid-storey stratum (plant life-forms 2–4 m) and under-storey stratum (plant life-forms <2 m) (see Appendix A). Per cent cover of native vegetation in the over-storey generally decreased with evidence of rabbits (see Appendix A). Predicted benchmarks for mean over-storey cover ranged from 15% in the coolibah community to 35% in the red ironbark community (Fig. 1). Per cent cover of native vegetation in the mid-storey typically decreased with increasing exotic plant cover, evidence of recent grazing by stock and evidence of rabbits, and was higher on sites in landscapes dominated by native vegetation (see Appendix A). Predicted benchmarks for mean mid-storey cover ranged from 4% in the yellow box community to 25% in the grey box community (Fig. 1). Per cent native cover in the under-storey stratum typically decreased with increasing exotic plant cover and the number of stumps and varied with vegetation community, topographic position, solar insolation and slope. Predicted benchmark mean percentage native cover in the under-storey stratum ranged from 13% in the white cypress community to 56% in the yellow box community (Fig. 1).

3.8. *Litter cover*

Litter cover was predicted to be higher on sites with no evidence of recent grazing by stock and differed between vegetation communities (see Appendix A). Predicted benchmarks for mean litter cover ranged from 50% in the coolibah community to 84% in the red ironbark community (Table 6).

3.9. *Cryptogam cover*

Cryptogam cover was predicted to be, on average, higher on sites with less exotic plant cover, lower on sites with no evidence of rabbits and varied with vegetation community, topographic position and slope (see Appendix A). Predicted benchmark mean cryptogam cover ranged from 9.8% in the white cypress community to 0.02% in the coolibah community (Table 6).

3.10. *Native plant species richness*

Native plant species richness was predicted to decrease with exotic plant cover, was lower on sites with evidence of recent grazing by stock and varied with vegetation community and mean annual precipitation (see Appendix A). Predicted benchmark mean native plant species richness ranged from 13 to 28

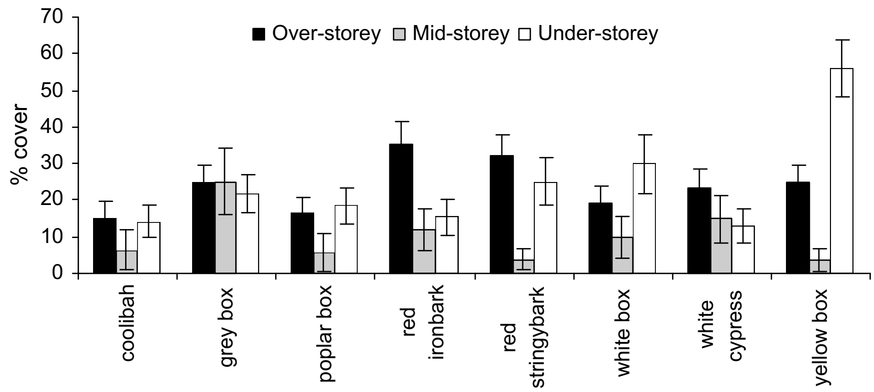

Fig. 1 – The predicted benchmark percentage vegetation cover (mean ± 2 × SE) in the over-storey stratum (>4 m), mid-storey stratum (2–4 m) and under-storey stratum (<2 m) by vegetation community.

species per 20 × 20 m plot across the different vegetation associations (Table 6).

4. Discussion

While the use of reference conditions has its critics, it has prevailed as a tool in land management because many alternatives for assessing ecosystems lack sufficient specificity to be practical, or require a level of understanding and data that do not exist or cannot feasibly be collected within the constraints of day-to-day management.

4.1. *Defining the reference state*

Much of the debate around reference conditions is in relation to the appropriate reference state for ecosystems (e.g., Aronson et al., 1995; Haila, 1997; Hunter, 1997). We defined the reference state as relatively little modification by humans since European settlement for three reasons. First, European settlement was the point after which modification of native ecosystems in many regions (including our study area) occurred at a higher rate than at any other time in human history (Millenium Ecosystem Assessment, 2005). Second, deriving reference conditions for vegetation modified by humans before this time (i.e., between the Pleistocene and the time of European settlement) may not be meaningful because other changes (e.g., climatic) have occurred since this period making comparisons difficult or inappropriate. Third, it is not generally feasible within the constraints of day-to-day management to employ techniques required to recreate conditions for many characteristics of ecosystems prior to European settlement (e.g., using paleontology or dendrochronology). These techniques can be expensive and time-consuming to undertake across large areas, they are only applicable for measuring a limited set of ecosystem features and, in the case of explorer's accounts, are keenly disputed because of an element of subjectivity or pecuniary interest at the time observations were recorded (e.g., Benson and Redpath, 1997; Flannery, 1994).

4.2. *Critical steps when predicting benchmarks for the reference state*

We consider four steps to be critical when applying our technique for predicting the reference state for ecosystem attributes. First, we identified biodiversity surrogates (response variables) to benchmark. Of particular interest in this study was benchmarks used for rapidly assessing terrestrial vegetation, so the surrogates were identified from those used in existing rapid assessment protocols (Gibbons et al., 2009; Parkes et al., 2003). Second, we defined the scale at which these surrogates were to be benchmarked and ensured that this was consistent with the scale that they were measured in the field. This is an important step because many measures of biodiversity are scale-dependent (White and Walker, 1997). Third, we identified a set of independent variables that could be used to predict the benchmark for each biodiversity surrogate. We defined benchmarks as variation on sites with relatively little evidence of modification by humans since European settlement, so the independent variables in this case were measures of human modification (Table 2). However, it would be equally feasible to use other independent variables. For example, if the definition of the reference state was ecosystems with the highest native species richness then data on species richness, provided they were available, could be used as the independent variables. Finally, we recognized the importance of variability in ecosystems (e.g., Holling and Meffe, 1996). We achieved this by sampling sites with different histories of fire, flooding and storm damage and did not knowingly bias our sampling towards sites not affected by these events. Models for predicting benchmarks were also fitted with additional independent covariates of environmental variation (Table 3). This enabled us to partition variation observed in each response variable due to environmental variation and variation due to the extent of modification by humans after European settlement. One can then define the environmental envelope in which the predicted reference conditions are applicable—a step that is difficult to take with more labour-intensive or retrospective techniques.

4.3. *Evaluating predictions of the reference state*

Two independent sources of data can be used to independently assess our predictions and identify their limitations. The first is ecological models developed to explain how ecosystems are structured in a generic sense. The second is estimates of reference conditions derived from other sources. This process can be demonstrated using our estimates of the number of trees by diameter class.

The inverse-J distribution is one ecological model often used to describe tree diameter distributions in unmanaged stands (Rouvinen and Kuuluvainen, 2005; Shugart, 1994). The model predicts that many unmanaged stands have progressively fewer trees with a larger DBH. We predicted inverse J-distributions for tree diameters in all vegetation communities except coolibah (Table 5). The dominant tree species in the coolibah community regenerates particularly after flooding. We did not record flooding regime as a potential explanatory variable in this study, so our predictions probably underestimate trees that are expected to occur in the smaller diameter classes for this community and may be improved with the inclusion of flooding regime as a potential explanatory variable. For another vegetation community (white cypress pine) there was a pronounced skew in the diameter distribution towards trees in the smaller diameter classes (Table 5). Lunt et al. (2006) conducted a detailed study of pre-European tree densities of this vegetation community based on measuring and dating stumps. Our estimates of tree densities for this vegetation community were comparable with those reported by Lunt et al. (2006), but only for trees >40 cm DBH. Lunt et al. (2006) estimated that substantially fewer trees (around 10 per ha) between 20 and 40 cm DBH occurred in these communities at the time of European settlement than our estimates for least modified sites (79–134 per ha). After European settlement cypress pine regeneration occurred in large waves with events including wildfire, logging, large rainfall events and the introduction, in the 1950s, of the myxomatosis virus for controlling rabbits (Noble, 1997). Historical events such as these are not adequately captured in our covariates representing human modification because our explanatory variables are based on contemporary evidence of human modification.

The timing of data collection should also be considered when evaluating predictions of reference conditions. For example, many native plant species across our study area are not visible in dry periods or cooler seasons. We recorded native plant species richness during a period of below average precipitation, observations were made only once at each site and observations were not all made in the peak season for native plant species richness (spring). In more favorable conditions, or after multiple visits to a site, observed richness in relatively unmodified examples of these communities would be higher than our predictions. For example, in a year with higher precipitation and with each site sampled twice (autumn and spring), Prober et al. (2002a) report mean native plant species richness of 15 and 24 per 0.01 ha for open and treed areas respectively in grassy woodlands dominated by white box, yellow box and Blakely's red gum that they considered to be in a reference state. Our predicted benchmark for mean native plant species richness in predominantly treed remnants of these communities (17 per 0.04 ha) was below the estimates by Prober et al. (2002a) and, while probably appropriate for assessments outside spring or during periods of below average rainfall, are likely to be underestimates of the reference state for sites assessed in spring. Predictions of the reference state for variables that vary with season and prevailing climate should therefore be examined critically.

4.4. *Using this information for ecosystem assessments*

Reference conditions of the type developed in this study are typically used as benchmarks against which comparable sites are assessed—the deviation from the benchmark forming the basis for the assessment (Gibbons et al., 2009; Landres et al., 1999; Nielson et al., 2007). Benchmarks of this type also represent a target for restoration actions (Brinson and Rheinhardt, 1996). However, benchmarks cannot be applied in this way in all circumstances.

In their state and transition model Westoby et al. (1989) predicted that ecosystems occur as a number of alternative stable states depending on the nature of disturbance. The state and transition model is used to model the effects of disturbance in many ecosystems (Filet, 1994; Stringham et al., 2003). In each of the state and transition models developed for ecosystems comparable with those examined in this study a single reference state is defined (McIntyre and Lavorel, 2007; Prober et al., 2002b; Yates and Hobbs, 1997). Provided benchmarks encapsulate the range of variation that occurs within this reference state, then benchmarks representing reference conditions can be used as a consistent yardstick for assessing the condition of these ecosystems. Difficulties arise when the same ecosystem can adopt multiple reference states in the absence of relatively major human modification. In ecosystems in which this variation only occurs in the period immediately after a major disturbance (e.g., fire) then assessments should be avoided in these sites for a period consistent with the profile of the benchmarked sites. In the case where an ecosystem can adopt radically different alternative reference states (e.g., an ephemeral wetland) then separate benchmarks for each different reference state must be developed to undertake assessments.

The state and transition model also provides some guidance on the use of reference conditions for restoration. Unlike classical succession (Clements, 1949) the state and transition model of Westoby et al. (1989) predicts that, once an ecosystem has moved to an alternative stable state because of a disturbance, then removal of the disturbance may not be sufficient on its own to return the ecosystem to its previous state. For example, there is currently no feasible method to return, to its reference state, the under-storey of eucalypt woodland in south-eastern Australia that is dominated by exotic plant cover, has high soil phosphorous or nitrate (e.g., due to stock camps or fertilizer application) and in which the propagules of native species are largely lost (Prober et al., 2002a). The benchmark for native plant species richness is therefore not a feasible restoration target for such a site; it may be more realistic to guide restoration using benchmarks only for those features of the ecosystem that can be feasibly and reliably restored (e.g., tree cover, mid-storey cover and under-storey cover). The state in which an ecosystem is, and the known barriers to restoration, must therefore be considered when using estimates of reference values to guide restoration efforts.

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Appendix A. Significant explanatory variables in each of the GAMs for predicting benchmarks and the percentage deviance explained by each model

Response variable	Significant explanatory variables		Percentage of deviance explained
	Variables representing modification since European settlement	Variables representing environmental variation	
5–20 cm DBH	Exotic plant cover, Stumps	Vegetation community	35.9
21–40 cm DBH	Exotic plant cover, Evidence of recent grazing by stock	Vegetation community	41.3
41–60 cm DBH	Exotic plant cover	Vegetation community, Solar insolation, Slope	26.4
>60 cm DBH	Exotic plant cover	Vegetation community, Solar insolation, Mean annual precipitation	21.5
Trees with hollows	Evidence of firewood collection, Stumps	Vegetation community, Solar insolation, Mean annual temperature	28.6
Tree regeneration	Exotic plant cover, Evidence of recent grazing by stock, Stumps	Vegetation community, Aspect, Topographic position	24.7
Trees with mistletoe	Exotic plant cover	Solar insolation, Slope	10.6
Fallen timber (volume)	Evidence of firewood collection	Vegetation community, Solar insolation, Slope, Mean annual temperature	30.6
Fallen timber (length)		Vegetation community, Solar insolation, Slope, Mean annual temperature	39.8
Native over-storey cover	Evidence of rabbits	Vegetation community, Solar insolation	29.4
Native mid-storey cover	Exotic plant cover, Evidence of recent grazing by stock, Evidence of rabbits, Surrounding land-use	Vegetation community, Mean annual precipitation, Mean annual temperature, Topographic position	46.0
Native under-storey cover	Exotic plant cover, Stumps	Vegetation community, Topographic position, Slope, Solar insolation	49.0
Litter	Evidence of recent grazing by stock	Vegetation community	30.7
Cryptogam	Exotic plant cover, Evidence of rabbits	Vegetation community, Topographic position, Slope	36.7
Native plant species richness	Exotic plant cover, Evidence of recent grazing by stock	Vegetation community, Mean annual precipitation	53.1

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