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Empirically validating a dense woody regrowth 'problem' and thinning 'solution' for understory vegetation

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ABSTRACT

In landscapes with a short history of intensive land use, woody plant regrowth on cleared land is often favorably received as a shift back to a more natural state. However, it is common for these regrowth stands to be much denser than undisturbed forest. High stem density can adversely affect stand structure, understory composition, and habitat for dependent fauna. Thinning to reduce stem density is one common silvicultural method used to manage dense stands for ecological or restoration objectives. The effect of thinning on the stand structure is well understood but those on the understory vegetation are not. We address this knowledge gap in anticipation of an increasing call for public investment in 'ecological' thinning across public and private land. Our case study is from the eucalypt woodlands and forests of central Victoria, Australia, an ecosystem in which dense woody regrowth is common. From a broad survey of 98 sites, spanning a range of stem densities, we explored the effect of density on understory vegetation. High densities of small trees (<20 cm DBH) caused the greatest suppression of native and exotic cover and species richness. We compared our observations with benchmarks and found that sites with stem densities exceeding their benchmark had median values approximately one-seventh of the benchmark native understory cover, which was also less than a quarter of the cover of those sites with benchmark or lower stem density. We conducted an additional targeted survey of 11 thinned sites paired with non-thinned sites to evaluate the effects of thinning. We built models combining broad and targeted survey data relating understory response to stem density, thinning, land tenure and environmental covariates. These models predicted that thinning is likely to elicit positive responses from the understory plant community in the short term. This is the desired response from native species, but we caution that thinning can equally favor exotic plant species.

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1. Introduction

Prolific recruitment of one or few woody plant species commonly occurs where agricultural production or intensive resource extraction has ceased on land formerly occupied by woodlands and forests (Doherty, 1998; Geddes et al., 2011; Gifford and Howden, 2001; Lunt, 1998; Lunt et al., 2006; Rumpff et al., 2011; Wallin et al., 2004). Hereafter we refer to this phenomenon as "dense woody regrowth". It is particularly common in landscapes that retain substantial remnant woodland and forest cover as a seed source.

The cultural and ecological context and origin of dense woody regrowth typically determine how it is perceived. In Europe, where dense woody regrowth following land abandonment is common (Flinn and Vellend, 2005; Gellrich et al., 2007), it is generally regarded negatively, having replaced anthropogenic grassland meadows maintained for centuries by clearing and grazing (Anthelme et al., 2001). Similarly, woody encroachment into natural savannas (Smit, 2004; Wiegand et al., 2006), and grasslands (Van Auken, 2000) following changes to grazing or fire regimes can reduce the capacity of grazing land. In the Neotropics, the structural and functional attributes of dense regrowth can be ecologically similar to pre-cleared forest and represent a desirable state (Aide et al., 2000; Aide et al., 2012). Elsewhere, there can be considerable nuance where dense stands are defined in comparison to benchmark or reference states that are thought to have existed prior to the post-industrial period of anthropogenic impact. Dense stands are generally considered ecologically undesirable compared to stands with benchmark density. In Australia and North America, these benchmarks typically represent vegetation

states predating European arrival (Eyre et al., 2011; Gibbons et al., 2010; Gibbons and Freudenberger, 2006; Jackson et al., 2000; Parkes et al., 2003; Wallin et al., 2004). In Australia for example, spontaneous woody regrowth is positively received while the plants are young but there is concern about the biodiversity and habitat value of these simplified stands as they age (e.g., Geddes et al., 2011; Kyle and Duncan, 2012). Dense woody regrowth is considered problematic because it is presumed to retard or exclude desirable biodiversity and habitat values. However, few have attempted to (a) validate the existence of a dense woody regrowth problem (but see Geddes et al., 2011), or (b) demonstrate the efficacy of thinning as a proposed solution.

Effects of high stand density on tree growth are reasonably well understood and abound in the silvicultural literature (e.g., Goodwin, 1990; Kariuki, 2008). However, the impact that dense stands have on understory vegetation remains largely unresolved (Dwyer et al., 2010b). The negative impacts of high stand density may include suppression of understory floristic richness and cover (Aguiar et al., 1996; Briggs et al., 2005; Harrington and Edwards, 1999; Hobbs and Mooney, 1986; Lett and Knapp, 2003; McHenry et al., 2006; Price and Morgan, 2008; Wienk et al., 2004), reduction in stand growth rate (Dwyer et al., 2010a; Kenkel, 1988; McHenry et al., 2006; Sala et al., 2005; Vesk et al., 2008), delayed provision of desirable habitat features such as large boughs and hollows (Vesk et al., 2008), reduced stand fecundity (Vesk et al., 2010), and increased risks of fire, pathogens and insect attack (Sala et al., 2005; Wallin et al., 2004) and soil degradation (McHenry et al., 2006). There is also concern that regrowth stands may stabilise as degraded novel ecosystems (Cramer et al., 2008; Fensham, 2008; Geddes et al., 2011).

Eventually, dense stands will self-thin (Kenkel, 1988; Olson et al., 2014; Westoby, 1984). However, intervention with mechanical or chemical thinning has been demonstrated to benefit tree growth, hasten the development of structural diversity, reduce pest attack risk and tree mortality, and increase carbon storage (Comfort et al., 2010; Dwyer et al., 2010b; Harrington and Edwards, 1999; Horner et al., 2010; McHenry et al., 2006; Pollock and Beechie, 2014; Wallin et al., 2004). It is often assumed that reducing stem densities will maintain or increase understory condition, and in combination with increasing the growth rate of remaining trees, maintain or increase ecosystem diversity, function and structural complexity (Czembor and Vesk, 2009; Fensham, 2008; Good et al., 2011; Good et al., 2012; Horner et al., 2010; Stanturf et al., 2014). Yet it is unclear to what extent thinning achieves these aims and if it varies according to context. The ecological and silvicultural literatures contain examples of positive, negative and neutral responses of understory cover, composition and species richness to thinning treatments (Dwyer et al., 2010b; Eldridge et al., 2011; Good et al., 2011, 2012; Harrington and Edwards, 1999; McHenry et al., 2006; Olson et al., 2014; Thomas et al., 1999; Tolsma, 2012; Walker et al., 1972, 1986). Some studies have reported greater effects of thinning on understory vegetation than the effect of stem density alone (Good et al., 2011, 2012; Scanlan and Burrows, 1990).

In Australia, dense woody regrowth commonly manifests as dense stands of one or few tree or shrub species (Doherty, 1998; Dwyer et al., 2010a; Geddes et al., 2011; Good et al., 2012; Lunt, 1998; Lunt et al., 2006; Rumpff et al., 2011). Thinning is increasingly being considered as a management tool for ecological restoration objectives, as large regions of Australia are shifting from agriculture to amenity land uses (Fensham, 2008; Geddes et al., 2011). However, deciding whether to apply thinning is a policy challenge (Cramer et al., 2008; Czembor and Vesk, 2009; Fensham, 2008; Gibbons et al., 2008; Lindenmayer et al., 2012). Native vegetation clearing is controlled in Australia, but some government agencies have sought flexibility for land-holders to

manage their dense stands, recognizing that dense woody regrowth can impede native vegetation management (Fensham, 2008). However, thinning is viewed as a risky management action because many of the claimed ecological benefits are yet to be demonstrated equivocally (Czembor and Vesk, 2009).

The Box-Ironbark eucalypt woodlands and forests of central Victoria were extensively cleared in the early 19th century (Sinclair et al., 2012) and are an ideal system to research the management of dense woody regrowth. In the last 50 years dense woody regrowth has increased over an expanding area (Geddes et al., 2011; Kyle and Duncan, 2012). Thinning has been infrequently implemented in Victoria for ecological purposes but has recently come into favor with land-managers and is likely to be employed at greater rates in the future (Archibald et al., 2010; Cunningham et al., 2009; DSE, 2009; Horner et al., 2010; Pigott et al., 2010).

Here we address the knowledge gaps impeding informed management of the commonly perceived problem of dense woody regrowth and 'ecological' thinning, its commonly cited solution. We focused our research on understory effects because they are the least well understood, yet are ecologically important, and can experience rapid and detectable rates of change. We conducted a broad survey to corroborate the link between dense stands and low understory richness and cover relative to benchmarks (Gibbons et al., 2010). We also exploited the few Victorian examples of thinning for ecological outcomes by conducting a paired-site survey to estimate understory response to thinning in Box-Ironbark eucalypt woodlands and forests, where we evaluated stem density influences and short term responses to thinning on a range of understory attributes. We then tested the applicability and generality of regression models of understory vegetation that incorporate stem density, thinning, land tenure, and environmental covariates.

2. Materials and methods

2.1. Study area

The study area was central Victoria, Australia, approximately 150–180 km from Melbourne (see Supplementary Material). The region has a temperate climate with average annual temperatures of 8–9 °C (min) and 21 °C (max) and an average annual rainfall of 515–650 mm (BOM, 2012). We sampled 120 sites from Box-Ironbark woodlands and forests. Of these, 98 sites were from a broad survey of sites (hereafter "background"), and a targeted survey of 11 pairs of thinning treatment and control sites (hereafter "experimental"). Sites with high stem densities formed the majority of the background sample, but sites with lower stem densities were also surveyed for comparison. Land tenures were categorized into two types: Crown and Freehold, based on current and historical land ownership and use (see Table 1, and see Sinclair et al., 2012). Land use history has influenced site condition, with all sites in our study experiencing some form of tree clearing and anthropogenic disturbance, but detailed histories are very difficult to acquire for individual sites (Foster et al., 2003; Lunt and Spooner, 2005). The exception in this study being a group of 16 (8 control and 8 treatment) sites on Crown land that were part of the Box-Ironbark Thinning Trial (Pigott et al., 2010). Prior to the thinning trial, these sites had been used primarily for timber and firewood provision (ECC, 2001).

Thinning was conducted between 2004 and 2012 using a cut-and-paint herbicide technique to prevent resprouting. Since exact thinning dates could not be determined, and uncertainty about them was considerable relative to the full range, we analyzed thinning as a binary proposition. Variable rates of stem removal were employed at the Box-Ironbark Thinning Trial sites (8 out of 11 treatment sites) to assess the efficacy of different final densities (Pigott et al., 2010).

Table 1
Variables indicating the two major types of land tenure in the survey area and the primary uses that define them.

Tenure category	Description	Current and historic uses
Crown	Public use and extraction/production	Reserves
		Timber production
		Mine/goldfields
		Roadsides
Freehold	Dryland agriculture	Dryland agriculture
		Livestock grazing
		Improved pasture/cropping

2.2. Sampling design

We sampled the 98 background sites between October 2011 and March 2012, while the 22 paired experimental sites were surveyed between November 2012 and February 2013. The survey method involved two sampling units for each site: point quadrats along 100 m of transect and a 100 m × 5 m long quadrat bounded around the transect. Transects and quadrats were split into smaller units of 50 m or 25 m depending on the size and shape of each site. Sampling units were stratified within the survey area to ensure that equivalent vegetation types were surveyed by each set of transects (i.e., to avoid isolated patches of disturbance or vegetation elements not typical of the survey area).

Since we could not collect data prior to thinning we were unable to directly evaluate vegetation change, and were limited to a cross-sectional survey of control and treatment pairs. The 11 thinning treatment sites were paired with 11 control sites that were less than 200 m away and part of the same contiguous vegetation patch. These 22 sites included the 16 (8 control and 8 treatment) Box-Ironbark Thinning Trial sites mentioned above. Control and treatment surveys were identical to the background surveys except for the number of point quadrats measured along the transects. Background sites were surveyed at points every 50 cm along each transect, with 204 points in total per site. The treatment/control sites were surveyed at 20 cm intervals along each transect, with 504 points in total per site. The increased sampling effort at thinning sites was undertaken to ensure sufficient power to detect effects where cover was low. For all sites, at each survey point the life form and origin (native or exotic) of every contacted life form was recorded, as well as the substrate (i.e., bare ground, coarse woody debris, rock or organic litter).

Within the 100 × 5 m quadrats we recorded the species identity and size of all woody individuals (shrubs and trees), and the total species richness of all vascular plants. Size data collected included height of all shrubs and trees <1.3 m; and diameter at breast height (DBH) of trees ⩾1.3 m. The stems of multi-stemmed trees ⩾1.3 m were recorded as separate individuals.

2.3. Vegetation and benchmarks

Sites belonged to 16 Ecological Vegetation Classes (EVCs, Woodgate et al., 1994) from three bioregions. The EVCs were woodlands and forests, with dominant canopy species including *Eucalyptus microcarpa, E. melliodora, E. polyanthemos, E. tricarpa, E. macrorhyncha, E. leucoxylon, E. goniocalyx,* and *E. blakelyi.*

We compared the understory vegetation cover at each site to the relevant EVC benchmarks. Life forms other than trees and large and medium shrubs (>1 m tall) were combined to give a total understory projective foliage cover, which exceeded 100% when vegetation overlapped.

Few data are available on the stem characteristics of pre-European Victorian woodland and forest communities. EVC benchmarks include density estimates of large trees only. Czembor and Vesk (2009) found that expert-elicited estimates of historical (pre-European) healthy Box-Ironbark Forest stem densities varied markedly and are therefore unsuitable for comparing them to modern sites. As a compromise, we compared our survey data to stem density benchmarks developed by Gibbons et al. (2010) for a range of similar vegetation types across New South Wales. Each vegetation type was defined by the dominant tree species using stem density data from a range of high quality sites to determine a set of benchmark densities for different tree size classes (Table 2).

Because the Gibbons et al. (2010) vegetation types did not exactly match our survey site EVCs, we took the conservative approach of combining (using the minimum and maximum value among vegetation types) the ranges of each of the relevant vegetation types and compared all our survey sites with this broad-level benchmark (see Table 2 'combined range'). Reclassifying the benchmarks and vegetation types is appropriate here as it overstates uncertainty in stem density estimates.

2.4. Environmental covariates

We began with a large set of environmental predictor variables sourced from State Government databases that we expected could influence the development or persistence of dense woody regrowth. These included evaporation, rainfall, max/min temperatures, wetness, radiometrics, evapotranspiration, insolation and visible sky. We used boosted regression tree (BRT) analyses of understory cover as an exploratory data analysis tool to select the most influential variables (results not shown here). The three most influential predictors (January mean rainfall, July mean rainfall, and January maximum temperature) were used in further analysis of stem density and thinning (Table 3).

2.5. Data analysis

2.5.1. Stem density effects on understory vegetation

The first part of the study involved an analysis of stem density effects from a range of sites on understory vegetation attributes (cover, species richness and native shrub counts). These analyses were based on the background and experimental control site data ($n = 109$). Tree size classes were initially defined as per the categories of the specified benchmarks (i.e., 5–20, 21–30, 31–40 cm DBH, etc., see Gibbons et al., 2010). Size classes larger than 50 cm DBH were excluded from the analyses and those stems ignored as too few sites had trees of this size. For subsequent models of stem data we divided the previous smallest class into two: 0–10 cm and 11–20 cm, such that classes increased in 10 cm increments, since pooling the data into a large category of 5–20 cm would impair interrogation of the effects of these smaller stems.

On these background and control sites ($n = 109$) we first ran exploratory models of the influence of stem density on understory cover with varied forms of stem density predictor variables. These

Table 2
Modelled stem densities per 0.05 ha in a range of size classes within vegetation types present in the study area (modified from Gibbons et al., 2010).

Vegetation type	DBH class (cm)			
	5–20	21–30	31–40	41–50
Grey box (*E. microcarpa*)	4.7–8.0	3.0	1.2–1.8	0.4–1.0
Red ironbark (*E. tricarpa*)	14.1–17.4	5.7	2.1–2.8	0.7–1.2
Red stringybark (*E. macrorhyncha*)	7.55–17.2	6.5	2.3–3.3	0.8–1.4
Yellow box (*E. melliodora*)	6.2–11.4	2.6	1.0–1.8	0.3–0.6
Combined range	4.7–17.4	2.6–6.5	1.0–3.3	0.3–1.4

Table 3
Environmental covariates selected for final models of understory cover response.

Variable	Description	Data	Scale	Range
Rainfall Jan	Average rainfall in January	Continuous	Rainfall (mm)	29–48
Rainfall Jul	Average rainfall in July	Continuous	Rainfall (mm)	40–121
MaxTemp Jan	Average maximum temperature in January	Continuous	Degrees celsius	24–31

included using densities of each of the stem size classes either separately or combined, or using basal area. This was an attempt to trade-off model fit with model complexity.

Subsequent models explored the effects of stem density predictor variables and additional variables on three different aspects of understory vegetation: projective foliage cover, species richness, and native shrub counts.

2.5.2. Evaluation of thinning

Preliminary analyses were based solely on the data from 11 thinned and paired control sites ($n = 22$). These models were then expanded to incorporate background data to allow the models to better partition effects into thinning and stem-density effects. We excluded a subset of the background survey sites that had distinct land use histories (heavy livestock grazing and pasture improvements) with stem density and exotic understory cover characteristics well outside the range of those in experimental sites. The final models were built on a set of 94 sites comprising the 22 experimental sites and 72 background sites.

2.5.3. Linear models

We used generalized linear models (GLMs) to relate understory attributes to covariates. All understory response variables were modelled as count data assuming Poisson error distributions and therefore we used a log link function. Because the number of points assessed at the control and treatment sites was different, the data were scaled by multiplying the control data by 504/204, (i.e., number of points at treatment sites/control sites). Predictor variables were centred and scaled by two standard deviations. Model performance was evaluated using Akaike's Information Criterion (AIC), proportion of explained deviance (D^2), and adjusted leave-one-out cross-validation (CV delta). All analyses were performed using the statistical software package R version 3.0.2 (R Development Core and Team, 2012).

Results for GLMs are presented as standardized effect sizes with 95% confidence intervals. As a guide, the effect can be considered significantly different (i.e., $P < 0.05$) when the interval does not overlap one (1), which signifies no 'significant' effect on a multiplicative scale (see Cumming, 2007; Di Stefano, 2004).
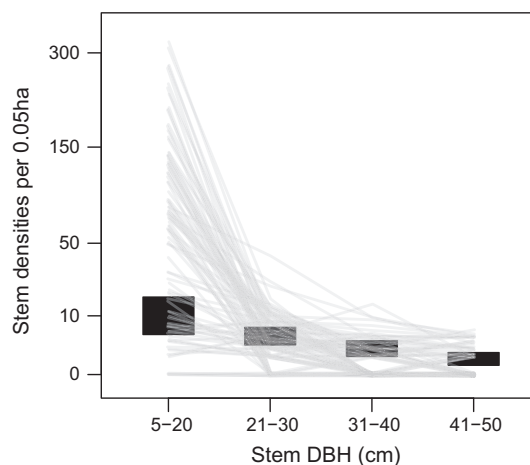
3. Results

3.1. Tree density

Stem densities varied among background sites, from 0 to the maximum for each size class (i.e., 324, 42, 14 and 6 stems per 0.05 ha) which spanned a range above and below the expected benchmark densities of Gibbons et al. (2010) (Fig. 1). All sites contained more than one tree.

3.2. Understory cover, species richness, and shrub counts

Native foliage projective cover ranged from 0% to 231% (median = 29%), and exotic cover ranged from 0% to 236% with (median = 8%). Vegetation cover was variably dominated by exotic graminoids (e.g., *Lolium rigidum*, *Briza* spp. and *Hordeum* spp.), native tufted graminoids (e.g., *Austrostipa* spp. and *Rytidosperma*
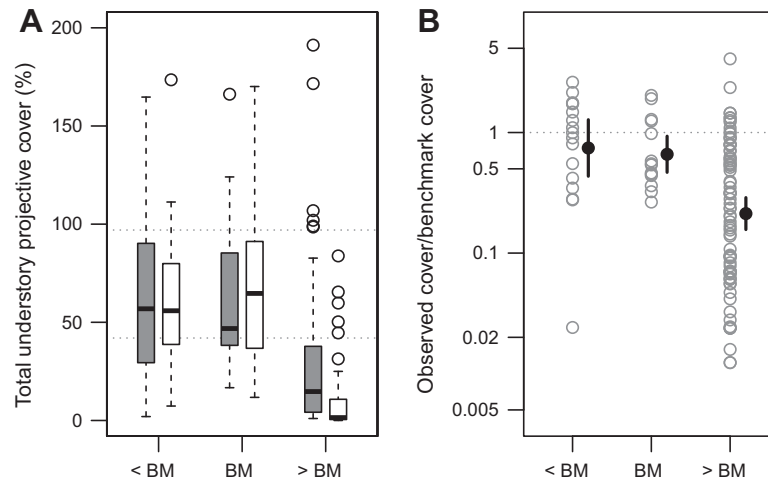

Fig. 1. Stem densities of eucalypts for four size classes at each background site ($n = 98$). Stem densities from the survey data within a site are connected by grey lines. Black rectangles indicate the benchmark range of stem densities within each size class for relevant vegetation types from Gibbons et al. (2010). Density is presented on a square root scale.

spp.), and prostrate to medium shrubs (e.g., *Acacia acinacea* and *Dodonaea viscosa*). Native species richness was higher (range = 4–38, median = 16) than exotic richness (range = 0–27, median = 6) and varied across sites. Native shrub counts were highly varied and ranged from 0 to 1388 (per 0.05 ha) across sites. Summary data for understory floristics are in Supplementary Material.

3.3. Understory cover suppression by dense stands in relation to benchmark levels

The summed individual life form EVC benchmarks to give a total understory cover varied across background and experimental control sites ($n = 109$) from 42% cover in 'box-ironbark forest' to 97% cover in 'grassy dry forest'. Sites with stem densities of the 5–20 cm DBH size class within or below their benchmark levels generally had native understory cover within their EVC benchmark range (Fig. 2A). Native understory cover in the above benchmark sites had median cover of 15% compared to medians of 47% and 57% in benchmark and below benchmark sites, respectively. The exotic understory species cover observed in above benchmark sites had median cover of 1% compared to 65% and 56% in benchmark and below benchmark sites, respectively, but for exotics the benchmark cover is zero.

The ratio of observed native understory cover to the relevant EVC benchmark for each site was calculated to determine a general model for this relationship across the range of benchmarks. 69 of 79 sites with stem densities exceeding the benchmark density had understory cover below their EVC benchmark range (Fig. 2B). Sites where native understory cover exceeded its benchmark were observed for each stem density category (Fig. 2B). Sites with stem densities below or within their benchmark had similar mean understory cover values, which were a ratio of 0.7, or two thirds, of the understory benchmark cover for each site. The mean ratio

Fig. 2. (A) Total understory foliage projective cover for densities of eucalypt stems in the 5–20 cm DBH size class ($n = 109$). Grey boxplots are cover values for native species; white boxplots are for exotic species. Horizontal dotted lines indicate the range of EVC benchmarks for understory cover within the vegetation types included in these surveys (42–97%). Boxes indicate the median, interquartile range, and whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range from the box. (B) The ratio of native understory foliage projective cover and EVC benchmark cover (on log scale) for densities of eucalypt stems in the 5–20 cm size class. Sites on the horizontal line at ratio = 1 have cover at benchmark levels. '>BM' ($n = 79$) are sites where the stem density exceeds the benchmark range stated by Gibbons et al. (2010) for equivalent vegetation types, 'BM' ($n = 14$) are sites with stem density within the benchmark range and '<BM' ($n = 17$) are sites with density below. Grey circles (○) indicate the ratio for each site; solid black circles (●) are the means with error bars showing 95% confidence intervals.

for sites with stem density exceeding the benchmark range was significantly lower, at 0.17, or one-sixth (Fig. 2B).

3.4. Density effect on understory life form cover, species richness and shrub counts

Small stem size classes (0–10 cm and 11–20 cm DBH) had the strongest negative relationship with both native and exotic understory cover and species richness (Fig. 3A and B). Native shrub counts had a small positive relationship with the density of 11–20 cm DBH stems (Fig. 3C).

Binary covariates for land tenure (Freehold versus Crown), and whether a site was adjacent to a roadside, had negative relationships with native cover, species richness, and shrub counts, suggesting that Crown land away from roads was more conducive to native understory. Tenure and roadside proximity had a similar magnitude effect on cover and richness as stem densities, but had a relatively much stronger effect on shrub counts. The Box-Ironbark Thinning Trial sites that exemplify Crown land away from roads had more shrubs than all other sites. Median shrub counts per 0.05 ha site at the Box-Ironbark Thinning Trial sites were 402 (range: 0–1388) in contrast to 22 (range: 0–836) across all others.

Fitting a model with all four stem classes as predictors performed better than alternative covariate sets (see Supplementary Material). The model with all stem density categories was used for subsequent analyses.

3.5. Verifying treatment effects

We confirmed that the treatment sites had similar densities of stems to control sites before the thinning trials, by estimating the density of cut stumps at treatment sites and adding it to the density of stems still remaining (Fig. 4).
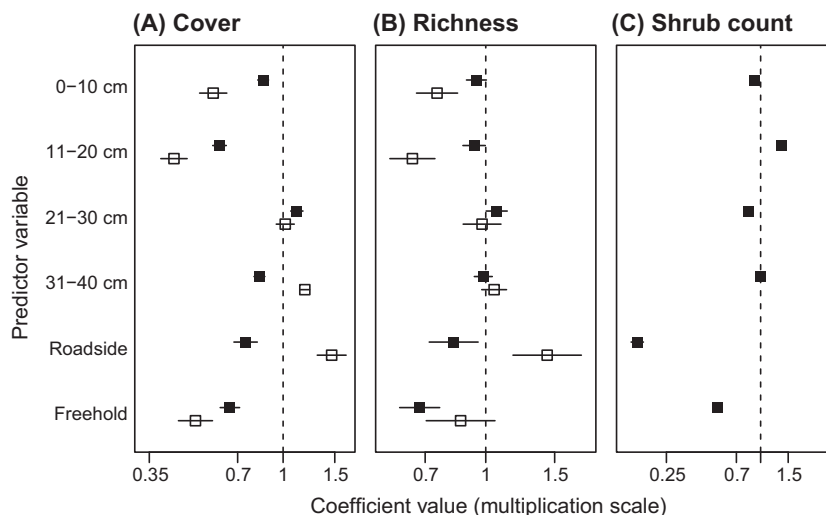
Thinning consistently decreased stem density of the smallest two size classes in all but one treatment site. For larger stem size classes, the difference between control and treatment sites was more variable (Fig. 4). As such, thinning treatments in this study refer to thinning of stems ≤20 cm DBH. Control and treatment stem densities fell within the range of densities observed in the background surveys (Fig. 4). Thinning reduced the stem densities

to within or below Gibbons et al. (2010) benchmark densities at all but one treatment site (Fig. 4, and see Fig. 1 for benchmark values).
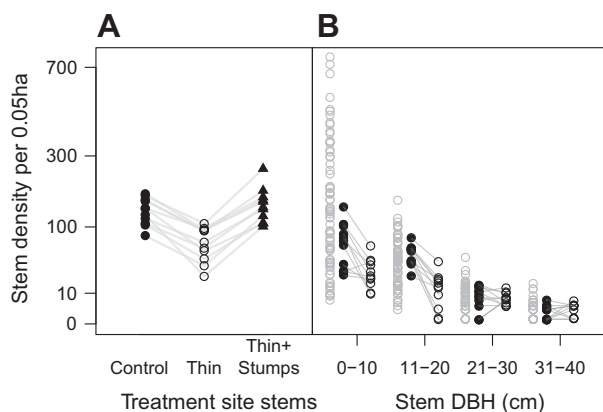
3.6. Understory response to thinning in the experimental sites

Thinning as a single binary predictor in GLMs had positive effects on native and exotic understory cover, species richness, and native shrub counts for the control/treatment paired surveys (multiplicative effect and 95% CI [lower bound, upper bound] for: native cover 2.34 [2.07, 2.59], exotic cover 8.20 [5.88, 11.44], native richness 1.39 [1.17, 1.64], exotic richness: 1.87 [1.13, 3.10], and native shrubs: 1.73 [1.65, 1.81], $n = 22$). We investigated whether the effect of thinning was due solely to the reduction in stem density, or if there were additional confounding factors. GLMs with multiple covariates indicated that the smallest stem size categories were driving the negative influence on native and exotic cover and richness, whereas native shrub counts were relatively insensitive to stem density (Fig. A.3). The roadside variable was excluded from these models since none of the thinned sites were on roadsides. Sites on Freehold land had lower native species richness, more exotic cover and species richness, and far fewer native shrubs than Crown sites.

Adding a thinning covariate to the stem density predictor improved models for native and exotic cover, but not richness (without and with thinning covariate respectively, natives – AIC: cover 631 and 589; richness 138 and 139, exotics – AIC: cover 351 and 346; richness 97 and 96). Thinning did improve the model fit for native shrub counts (without and with thinning covariate respectively, AIC: 4272 and 4103). Thinning had positive effects on each of native and exotic cover, native richness and shrub counts, though the magnitude varied between them and the effect was smallest and least certain for richness (Fig. A.3). We included an interaction term to assess the combination of thinning on Freehold versus Crown land. Thinning on Freehold land had little additional effect (beyond that on Crown land) on native cover and richness or exotic richness, an additive effect on exotic cover, and a negative effect on native shrub counts, meaning that thinning was ineffective for shrub counts on Freehold land.

Fig. 3. Multiplicative effect of predictor variables in generalized linear models for (A) native (■) and exotic (□) understory cover, (B) native (■) and exotic (□) species richness and (C) native shrub counts (n = 109). Error bars show the 95% confidence intervals. Dashed vertical line indicates the position of a neutral effect.

Fig. 4. (A) Combined stem densities of all sizes for each pair (control and treatment) of thinning sites surveyed (n = 11). Each point represents a single site; black circles (●) are stem densities at control sites, white circles (○) are stem densities at thinned sites and triangles (▲) are the sums of stems and cut stumps from thinned sites. Lines join points from the same thinning pair. (B) Stem densities in four size classes from the thinned sites. Each point represents a single site; black circles are control sites (n = 11), white circles are thinned sites (n = 11). Lines join points from the same thinning pair. Grey circles (○) show the stem density for each class across background sites (n = 98). Both figures are presented on a square root density scale.

3.7. Understory response to stem and environmental variables

We combined the background and control/treatment survey data to increase our power to detect effects of stem density and other environmental covariates on understory vegetation cover. Some environmental covariates were better predictors of understory cover than stem density classes (Fig. 5). Environmental covariates had a positive relationship with exotic cover and species richness. The relationships with natives were less consistent. July rainfall and January maximum temperature were negatively related to native shrub counts.

The estimated effect size coefficients for thinning were consistent in sign but not magnitude between the control/treatment models (n = 22) and models combining the two datasets (n = 94), with the exception of the relationship between thinning and exotic richness which became slightly negative in the combined model. With all other variables at their mean, thinning nearly doubled the predicted native cover, and more than quadrupled exotic cover.

Predictions based on the above combined models were used to estimate the effect of thinning at hypothetical new sites. We predicted across a range of unthinned densities of the two smallest stem classes (≤20 cm DBH) since they are most likely to be thinned, and have the strongest relationship with understory cover. These predictions should be interpreted cautiously as they are made for scenarios where one size class is fixed and the other varies – a scenario that did not occur in our dataset. Thinning when a stand is younger (i.e., with small stems ≤10 cm DBH) was predicted to be beneficial, for native cover and species richness on both Freehold and Crown land (Fig. 6). There is likely to be a stronger response to thinning if the stems are larger (11–20 cm DBH) probably due to a greater suppressive effect on understory (see Fig. 5).
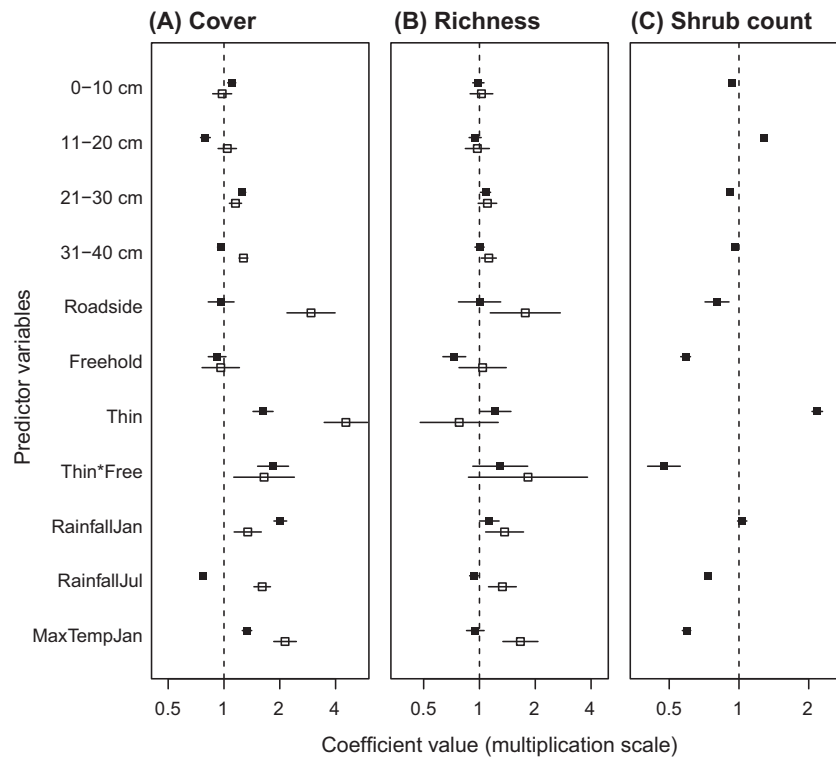
Thinning is predicted to increase each understory vegetation attribute except exotic richness in Crown sites (Fig. 6). The mean density per 0.05 ha of 11–20 cm DBH stems was 46 in control sites and 12 in treatment sites. A reduction of such magnitude on Crown land is predicted to increase native cover from 30% to 60% (top right panel of Fig. 6), which corresponds to moving from below to within the benchmark bounds. For 0–10 cm DBH stems, the mean density per 0.05 ha was 66 in control sites and 25 in treatment sites. Thinning either stem size class could substantially increase exotic cover, particularly on Freehold sites. The predicted effects on shrubs are unlike for the other understory attributes having differential effects conditional on land tenure.

4. Discussion

We found dense stands suppressed native and exotic understory cover and richness and can reduce the native projective cover to well below benchmark levels. Thinning increased native understory cover and richness from below the benchmark to within benchmark range in less than 10 years. However, the thinning effect varied between sites. In order to best inform management of dense stands, we have discussed these results in reference to the uncertainties surrounding the ecological benefit and application of thinning treatments.

4.1. When is a dense stand a problem for understory vegetation?

In order to diagnose problematic sites, we compared stem densities and understory attributes with their respective published benchmarks. Many stands in our study had stem densities exceed-

Fig. 5. The multiplicative effect of stem density, tenure, thinning, and three environmental covariates for native (■) and exotic (□) understory cover, species richness and shrub count responses (*n* = 94). Error bars show the 95% confidence intervals. Dashed vertical line indicates no effect.

ing their benchmark densities, by as much as a factor of 10 (Fig. 1). Cover of both native and exotic understory vegetation was lower when stem densities exceeded benchmarks (Fig. 2). The benchmark values may approximate the carrying capacity of stems, based on resource availability, beyond which there is understory and stand growth suppression. The reduction in exotic understory cover at higher stem densities (Fig. 2A) may be beneficial, particularly in sites with high exotic cover, which contrasts against the desire to increase native understory. This presents a trade-off for managers with conflicting desires to minimize exotic growth or maximize native growth.

Averaging over confounding environmental covariates, we found that suppression of cover and richness due to stem density was greatest at the highest densities of stems ≤20 cm DBH. Suppression of understory cover by dense woody vegetation has been well documented (Eldridge et al., 2011; Good et al., 2011; Le Brocque et al., 2009; Walker et al., 1986). Yet, the effects on species richness are less clear (Eldridge et al., 2011; Le Brocque et al., 2009; Milberg, 1995).

4.2. Why not just leave dense stands to self-thin?

Over time, self-thinning is expected to lower stem densities. However, whether the stand will reach a desired state and how long this may take in our study system are highly uncertain (Czembor and Vesk, 2009). Leaving stands at high density of small stems for long periods (e.g., 5–20 cm DBH, see Fig. 1) may delay the development of desirable understory attributes even if stem densities eventually decline. Competition for resources at high stem densities reduces understory cover (see Fig. 2A) excluding some understory species entirely. If some individuals of a species (or their propagules) persist they can potentially recover following stem thinning. However, seedbanks of understory species will gradually be depleted within dense stands as soil-stored seed has limited longevity (Falińska, 1999; Milberg, 1995; Thompson,

2000), although many species have mechanisms for seed longevity (Orscheg and Enright, 2011). The principal concern is that the longer it takes for a stand to thin out naturally, there will be increasingly fewer understory species present as standing biomass or soil-stored seed to allow recovery. Conversely, the main hope for a thinning intervention is that it may reduce the chances of understory species extirpation and result in a better ecological outcome, sooner.
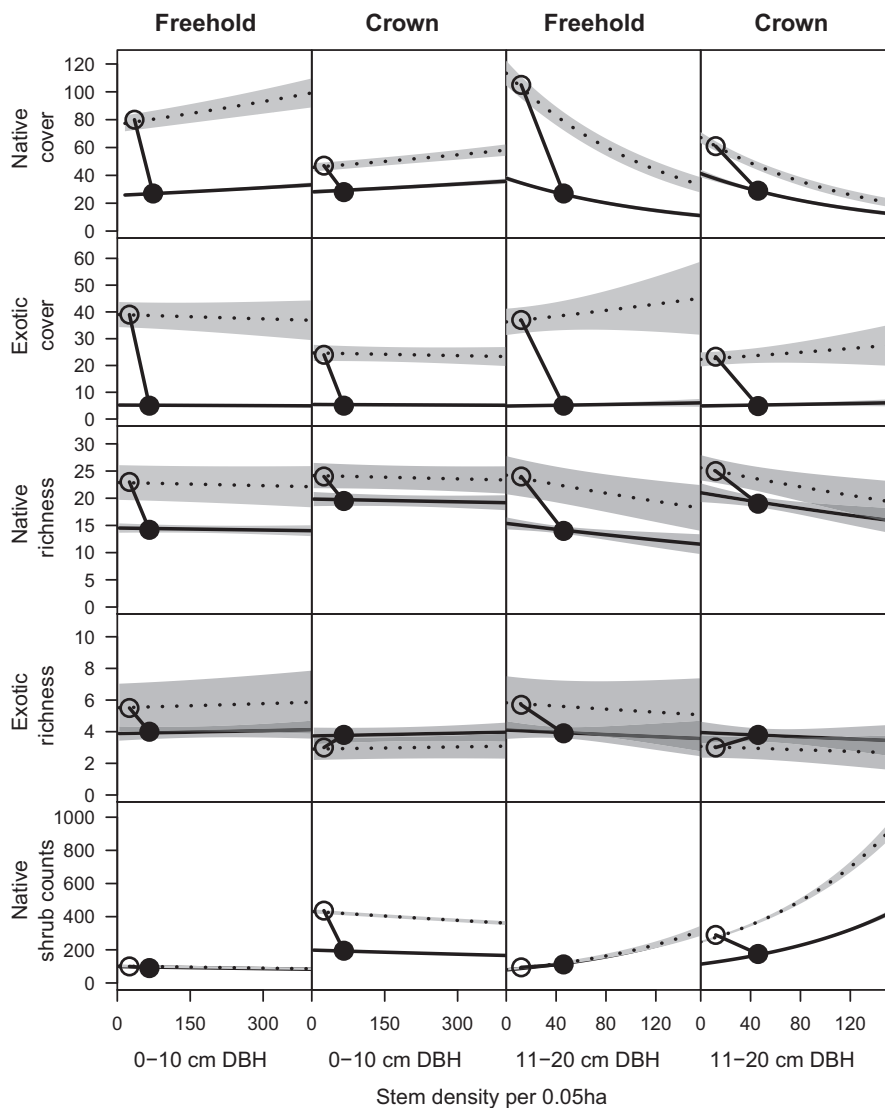
4.3. What are the expected ecological benefits of thinning, and what other drivers influence understory response?

Our models may encourage managers because they suggest thinning can increase native understory species cover, richness and shrub counts. However, these models also caution that thinning can increase exotic species cover, with its associated management problems.

We found that understory vegetation response to dense stands and thinning was influenced by other site factors beyond thinning and stand density (Fig. 5). Sites on Freehold land, which typically indicates a history of dryland agriculture, had lower species richness and fewer native shrub counts than Crown land. Crown land, on the other hand, was less likely to have been grazed, cleared or otherwise intensively managed. The increase in cover and richness of exotic species and decrease in native shrub counts at sites adjacent to a road reflects a land use history of disturbance without intensive grazing but one still prone to exotic species invasion. These factors highlight the importance of the land use history of a site on its current ecological character and function (Duncan and Dorrough, 2009; Foster et al., 2003). For shrub counts, the negative correlation with winter rainfall is likely due to the tendency for sites subject to higher rainfall to have greater herbaceous plant cover, which competes with shrub recruitment.

Following thinning, newly regenerating plants will be those with propagules available from persisting plants, the soil seed

Fig. 6. Predictions of understory cover, species richness and native shrub counts under increasing densities of stems (n = 94). Dotted lines are mean predictions for thinned sites, solid lines for un-thinned sites, where grey shading is the 95% confidence interval. As an example, the black line joins the predicted native cover at the mean density of stems in the control sites (●) with the mean density in treatment sites (○), i.e. control and treatment densities of 66 and 25 for 0–10 cm DBH stems, and 46 and 12 for 10–20 cm DBH stems respectively.

bank, or nearby vegetation. We saw greater understory cover, irrespective of thinning, where average January (summer) rainfall was higher, likely because germination and survival depend on water availability. Native understory cover and species richness increase following thinning, which is likely to be facilitated by favorable rainfall and temperature conditions (Fig. 5).

We did not assess grazing (whether by livestock, rabbits, or macropods) in this study, but we expect that grazing before or after thinning treatment would influence the understory response. Our treatment site that showed both the smallest native understory increases, and negative exotic cover and richness responses to thinning was grazed throughout much or all of the stand development prior to thinning (Lance Williams pers. comm.), and were presumed to have a depauperate soil seedbank as a consequence. Grazing following thinning is likely to reduce or prevent understory recovery, which is undesirable except where the recovering vegetation is dominated by exotic species. In those exotic dominated sites, grazing could be used to minimize exotic regrowth in the absence of alternative control methods.

4.4. How much and when to thin?

We analyzed thinning as a binary proposition (i.e., thinned or not), but the treatment could be applied in many different configurations, removing many or few stems. Ideally thinning analyses would incorporate an effect of time since treatment, but this was not possible for our study. Our study suggests that reducing stem density to within or below benchmark levels is required to shift cover to within the corresponding understory benchmarks (Fig. 2). It is unclear what amount of stem reduction is required to maintain benchmark understory cover over the longer term. Large reduction of stems may allow new mass recruitment to occur due to competitive release. Small reductions may have correspondingly short-term effects. Due to the absence of pre-thinning understory cover data, we were unable to evaluate the relative response rates of exotic and native species. Sites that have high exotic cover prior to thinning (or development of the dense stand) are likely to have a greater response of exotics after thinning due to the higher proportion of weed species in the seedbank. The trade-off between

increasing native and increasing exotic vegetation needs to be considered. Significant exotic vegetation invasion could negate the value of increasing the cover of native plants (Figs. 5 and 6).

The best action for native understory vegetation could be to thin early to prevent dense woody regrowth from becoming sufficiently established to suppress or displace native species. This option ought to be both cheaper, and more effective than thinning later, as native species richness and cover would not yet have declined, thereby reducing the reliance on seed immigration. Paradoxically, a young dense stand is less likely to be symptomatic and therefore less likely to be presented as a candidate for management, particularly on private land. Also, we do not know for certain that very young dense stands will develop into mature dense woody regrowth, so there is a real risk of unnecessary intervention and expense. The ability to predict which young stands will become undesirably dense will facilitate confident early intervention, reduce management costs, and minimize loss of understory vegetation. Our results suggest that densities of small stems (5–20 cm DBH) less than the maximum benchmark estimate (i.e., 350 stems per hectare), are unlikely to substantially suppress understory for the vegetation types in this study, and therefore would not justify thinning (Fig. 2). Stands with stem densities exceeding the benchmarks are more likely to have a suppressive effect on native species and are stronger candidates for a thinning intervention.

4.5. So is my dense stand a problem, and is thinning a good solution?

In sum, based on our work a manager could take published benchmark data on numbers of stems, and understory to make a first assessment of a thinning proposal. Stem densities above benchmark maxima are very likely to have poor understory richness and cover. The manager would be relatively confident about a positive and rapid native understory response to thinning on Crown lands from higher rainfall areas, including roadside areas, provided there is low risk of facilitating the spread of invasive exotic species. Coupled with documented faster growth of the extant stems in thinned areas at high densities (McHenry et al., 2006; Sala et al., 2005), there seems good evidence that thinning treatments will accelerate habitat development in both the under- and overstory. On Freehold land, although the overstory improvements are likely, the understory result could be positive or negative, subject to land use factors that may be difficult to obtain *a priori*, as well as total grazing pressure. In these more uncertain cases, management experiments may be the most constructive way to learn which thinning proposals are safe bets for a good ecological outcome.

Many questions remain about the cost-effectiveness of thinning for managing dense stands for ecological outcomes. With limited resources to manage conservation problems, being confident that thinning can improve habitat characteristics is not enough to justify a campaign of publicly funded thinning of dense woody regrowth. A better understanding of how and when dense woody regrowth develops, and how it is distributed spatially would help to consider the merit of thinning proposals alongside other options to improve biodiversity conservation at larger scales.

5. Conclusion

Providing an objective and transparent strategy for managing dense stands is difficult when it is uncertain when dense woody regrowth is a problem and how vegetation may respond to intervention. There are no protocols to guide the practice of thinning that account for ecological responses in both canopy and understory. Here we have presented an analysis of empirical research,

backed up by relevant literature that should aid managers considering thinning as a tool to mitigate the negative ecological effects of dense woody regrowth.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.12.006.

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