

1 Empirically validating a dense woody regrowth ‘problem’ and
2 thinning ‘solution’ for understory vegetation

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11

12 **Abstract**

13 In landscapes with a short history of intensive land use, woody plant regrowth on
14 cleared land is often favorably received as a shift back to a more natural state.

15 However, it is common for these regrowth stands to be much denser than undisturbed
16 forest. High stem density can adversely affect stand structure, understory

17 composition, and habitat for dependent fauna. Thinning to reduce stem density is one
18 common silvicultural method used to manage dense stands for ecological or

19 restoration objectives. The effect of thinning on the stand structure is well understood
20 but those on the understory vegetation are not. We address this knowledge gap in

21 anticipation of an increasing call for public investment in ‘ecological’ thinning across
22 public and private land. Our case study is from the eucalypt woodlands and forests of

23 central Victoria, Australia, an ecosystem in which dense woody regrowth is common.

24 From a broad survey of 98 sites, spanning a range of stem densities, we explored the
25 effect of density on understory vegetation. High densities of small trees (< 20 cm

26 DBH) caused the greatest suppression of native and exotic cover and species richness.

27 We compared our observations with benchmarks and found that sites with stem

28 densities exceeding their benchmark had median values approximately one-seventh of
29 the benchmark native understory cover, which was also less than a quarter of the
30 cover of those sites with benchmark or lower stem density. We conducted an
31 additional targeted survey of 11 thinned sites paired with non-thinned sites to evaluate
32 the effects of thinning. We built models combining broad and targeted survey data
33 relating understory response to stem density, thinning, land tenure and environmental
34 covariates. These models predicted that thinning is likely to elicit positive responses
35 from the understory plant community in the short term. This is the desired response
36 from native species, but we caution that thinning can equally favor exotic plant
37 species.

38 **Keywords**

39 Dense stand, regrowth, thicket, suppression, encroachment, thickening

40 **1. Introduction**

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

47 The cultural and ecological context and origin of dense woody regrowth typically
48 determine how it is perceived. In Europe, where dense woody regrowth following
49 land abandonment is common (Flinn and Vellend 2005; Gellrich *et al.* 2007), it is
50 generally regarded negatively, having replaced anthropogenic grassland meadows
51 maintained for centuries by clearing and grazing (Anthelme *et al.* 2001). Similarly,

52 woody encroachment into natural savannas (Smit 2004, Wiegand *et al.* 2006), and
53 grasslands (Van Auken 2000) following changes to grazing or fire regimes can reduce
54 the capacity of grazing land. In the Neotropics, the structural and functional attributes
55 of dense regrowth can be ecologically similar to pre-cleared forest and represent a
56 desirable state (Aide *et al.* 2000; Aide *et al.* 2012). Elsewhere, there can be
57 considerable nuance where dense stands are defined in comparison to benchmark or
58 reference states that are thought to have existed prior to the post-industrial period of
59 anthropogenic impact. Dense stands are generally considered ecologically undesirable
60 compared to stands with benchmark density. In Australia and North America, these
61 benchmarks typically represent vegetation states predating European arrival (Eyre *et al.*
62 *et al.* 2011; Gibbons *et al.* 2010; Gibbons and Freudenberger 2006; Jackson *et al.* 2000;
63 Parkes *et al.* 2003; Wallin *et al.* 2004). In Australia for example, spontaneous woody
64 regrowth is positively received while the plants are young but there is concern about
65 the biodiversity and habitat value of these simplified stands as they age (e.g., Geddes
66 *et al.* 2011; Kyle & Duncan 2012). Dense woody regrowth is considered problematic
67 because it is presumed to retard or exclude desirable biodiversity and habitat values.
68 However, few have attempted to (a) validate the existence of a dense woody regrowth
69 problem (but see Geddes *et al.* 2011), or (b) demonstrate the efficacy of thinning as a
70 proposed solution.

71 Effects of high stand density on tree growth are reasonably well understood and
72 abound in the silvicultural literature. However, the impact that dense stands have on
73 understory vegetation remains largely unresolved (Dwyer *et al.* 2010b). The negative
74 impacts of high stand density may include suppression of understory floristic richness
75 and cover (Aguilar *et al.* 1996; Briggs *et al.* 2005; Harrington and Edwards 1999;
76 Hobbs and Mooney 1986; Lett and Knapp 2003; McHenry *et al.* 2006; Price and

77 Morgan 2008; Wienk *et al.* 2004), reduction in stand growth rate (Kenkel 1988;
78 McHenry *et al.* 2006; Sala *et al.* 2005; Vesik *et al.* 2008), delayed provision of
79 desirable habitat features such as large boughs and hollows (Vesik *et al.* 2008),
80 reduced stand fecundity (Vesik *et al.* 2010), and increased risks of fire, pathogens and
81 insect attack (Sala *et al.* 2005; Wallin *et al.* 2004) and soil degradation (McHenry *et*
82 *al.* 2006). There is also concern that regrowth stands may stabilise as degraded novel
83 ecosystems (Cramer *et al.* 2008; Fensham 2008; Geddes *et al.* 2011).

84 Eventually, dense stands will self-thin (Kenkel 1988; Olson *et al.* 2014; Westoby
85 1984). However, intervention with mechanical or chemical thinning has been
86 demonstrated to benefit tree growth, hasten the development of structural diversity,
87 reduce pest attack risk and tree mortality, and increase carbon storage (Dwyer *et al.*
88 2010b; Harrington and Edwards 1999; Horner *et al.* 2010; McHenry *et al.* 2006;
89 Pollock & Beechie 2014; Wallin *et al.* 2004). It is often assumed that reducing stem
90 densities will maintain or increase understory condition, and in combination with
91 increasing the growth rate of remaining trees, maintain or increase ecosystem
92 diversity, function and structural complexity (Czembor and Vesik 2009; Fensham
93 2008; Good *et al.* 2011; Good *et al.* 2012; Horner *et al.* 2010; Stanturf *et al.* 2014).

94 Yet it is unclear to what extent thinning achieves these aims and if it varies according
95 to context. The ecological and silvicultural literatures contain examples of positive,
96 negative and neutral responses of understory cover, composition and species richness
97 to thinning treatments (Dwyer *et al.* 2010b; Eldridge *et al.* 2011; Good *et al.* 2011;
98 Good *et al.* 2012; Harrington and Edwards 1999; McHenry *et al.* 2006; Olson *et al.*
99 2014; Thomas *et al.* 1999; Tolsma 2012; Walker *et al.* 1972; Walker *et al.* 1986).

100 Some studies have reported greater effects of thinning on understory vegetation than

101 the effect of stem density alone (Good *et al.* 2011; Good *et al.* 2012; Scanlan and
102 Burrows 1990).

103 In Australia, dense woody regrowth commonly manifests as dense stands of one or
104 few tree or shrub species (Doherty 1998; Geddes *et al.* 2011; Good *et al.* 2012; Lunt
105 1998; Lunt *et al.* 2006). Thinning is increasingly being considered as a management
106 tool for ecological restoration objectives, as large regions of Australia are shifting
107 from agriculture to amenity land uses (Fensham 2008; Geddes *et al.* 2011). However,
108 deciding whether to apply thinning is a policy challenge (Cramer *et al.* 2008;
109 Czembor and Vesk 2009; Fensham 2008; Gibbons *et al.* 2008; Lindenmayer *et al.*
110 2012). Native vegetation clearing is controlled in Australia, but some government
111 agencies have sought flexibility for land-holders to manage their dense stands,
112 recognizing that dense woody regrowth can impede native vegetation management
113 (Fensham 2008). However, thinning is viewed as a risky management action because
114 many of the claimed ecological benefits are yet to be demonstrated equivocally
115 (Czembor and Vesk 2009).

116 The Box-Ironbark eucalypt woodlands and forests of central Victoria were
117 extensively cleared in the early 19th century (Sinclair *et al.* 2012) and are an ideal
118 system to research the management of dense woody regrowth. In the last 50 years
119 dense woody regrowth has increased over an expanding area (Geddes *et al.* 2011;
120 Kyle and Duncan 2012). Thinning has been infrequently implemented in Victoria for
121 ecological purposes but has recently come into favor with land-managers and is likely
122 to be employed at greater rates in the future (Archibald *et al.* 2010; Cunningham *et al.*
123 2009; DSE 2009; Horner *et al.* 2010; Pigott *et al.* 2010).

124 Here we address the knowledge gaps impeding informed management of the
125 commonly perceived problem of dense woody regrowth and ‘ecological’ thinning, its

126 commonly cited solution. We focused our research on understory effects because they
127 are the least well understood, yet are ecologically important, and can experience rapid
128 and detectable rates of change. We conducted a broad survey to corroborate the link
129 between dense stands and low understory richness and cover relative to benchmarks
130 (Gibbons *et al.* 2010). We also exploited the few Victorian examples of thinning for
131 ecological outcomes by conducting a paired-site survey to estimate understory
132 response to thinning in Box-Ironbark eucalypt woodlands and forests, where we
133 evaluated stem density influences and short term responses to thinning on a range of
134 understory attributes. We then tested the applicability and generality of regression
135 models of understory vegetation that incorporate stem density, thinning, land tenure,
136 and environmental covariates.

137 **2. Materials and methods**

138 *2.1 Study area*

139 The study area was central Victoria, Australia, approximately 150–180 km from
140 Melbourne (see Supplementary Material). The region has a temperate climate with
141 average annual temperatures of 8–9°C (min) and 21°C (max) and an average annual
142 rainfall of 515–650 mm (BOM 2012). We sampled 120 sites from Box-Ironbark
143 woodlands and forests. Of these, 98 sites were from a broad survey of sites (hereafter
144 “background”), and a targeted survey of 11 pairs of thinning treatment and control
145 sites (hereafter “experimental”). Sites with high stem densities formed the majority of
146 the background sample, but sites with lower stem densities were also surveyed for
147 comparison. Land tenures were categorized into two types: Crown and Freehold,
148 based on current and historical land ownership and use (see Table 1, and see Sinclair
149 *et al.* 2012). Land use history has influenced site condition, with all sites in our study
150 experiencing some form of tree clearing and anthropogenic disturbance, but detailed

151 histories are very difficult to acquire for individual sites (Foster *et al.* 2003, Lunt and
 152 Spooner 2005). The exception in this study being a group of 16 (8 control and 8
 153 treatment) sites on Crown land that were part of the Box-Ironbark Thinning Trial
 154 (Pigott *et al.* 2010). Prior to the thinning trial, these sites had been used primarily for
 155 timber and firewood provision (ECC 2001).

156

157 Table 1. Variables indicating the two major types of land tenure in the survey area and the
 158 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

159

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

166 2.2 Sampling design

167 We sampled the 98 background sites between October 2011 and March 2012, while
 168 the 22 paired experimental sites were surveyed between November 2012 and
 169 February 2013. The survey method involved two sampling units for each site: point
 170 quadrats along 100 m of transect and a 100 m x 5 m long quadrat bounded around the

171 transect. Transects and quadrats were split into smaller units of 50 m or 25 m
172 depending on the size and shape of each site. Sampling units were stratified within the
173 survey area to ensure that equivalent vegetation types were surveyed by each set of
174 transects (i.e., to avoid isolated patches of disturbance or vegetation elements not
175 typical of the survey area).

176 Since we could not collect data prior to thinning we were unable to directly evaluate
177 vegetation change, and were limited to a cross-sectional survey of control and
178 treatment pairs. The 11 thinning treatment sites were paired with 11 control sites that
179 were less than 200 m away and part of the same contiguous vegetation patch. These
180 22 sites included the 16 (8 control and 8 treatment) Box-Ironbark Thinning Trial sites
181 mentioned above. Control and treatment surveys were identical to the background
182 surveys except for the number of point quadrats measured along the transects.

183 Background sites were surveyed at points every 50 cm along each transect, with 204
184 points in total per site. The treatment/control sites were surveyed at 20 cm intervals
185 along each transect, with 504 points in total per site. The increased sampling effort at
186 thinning sites was undertaken to ensure sufficient power to detect effects where cover
187 was low. For all sites, at each survey point the life form and origin (native or exotic)
188 of every contacted life form was recorded, as well as the substrate (i.e., bare ground,
189 coarse woody debris, rock or organic litter).

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

195 *2.3 Vegetation and benchmarks*

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

200 We compared the understory vegetation cover at each site to the relevant EVC
 201 benchmarks. Life forms other than trees and large and medium shrubs (> 1 m tall)
 202 were combined to give a total understory projective foliage cover, which exceeded
 203 100 % when vegetation overlapped.

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

214
 215 Table 2. Modelled stem densities per 0.05 ha in a range of size classes within vegetation
 216 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 (<i>E. microcarpa</i>)	4.7–8.0	3.0	1.2–1.8	0.4–1.0
Red ironbark (<i>E. tricarpa</i>)	14.1–17.4	5.7	2.1–2.8	0.7–1.2
Red stringybark (<i>E. macrorhyncha</i>)	7.55–17.2	6.5	2.3–3.3	0.8–1.4
Yellow box (<i>E. melliodora</i>)	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

217

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

224 *2.4 Environmental covariates*

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

234

235 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

236

237 *2.5 Data analysis*

238 2.5.1 Stem density effects on understory vegetation

239 The first part of the study involved an analysis of stem density effects from a range of
240 sites on understory vegetation attributes (cover, species richness and shrub counts).

241 These analyses were based on the background and control site data (n=109). Tree size
242 classes were initially defined as per the categories of the specified benchmarks (i.e. 5–
243 20, 21–30, 31–40 cm DBH, etc., see Gibbons *et al.* 2010). Size classes larger than 50
244 cm DBH were excluded from the analyses and those stems ignored as too few sites
245 had trees of this size. For subsequent models of stem data we divided the previous
246 smallest class into two: 0–10 cm and 11–20 cm, such that classes increased in 10 cm
247 increments, since pooling the data into a large category of 5–20 cm would impair
248 interrogation of the effects of these smaller stems.

249 On these background and control sites (n=109) we first ran exploratory models of the
250 influence of stem density on understory cover with varied forms of stem density
251 predictor variables. These included using densities of each of the stem size classes
252 either separately or combined, or using basal area. This was an attempt to trade-off
253 model fit with model complexity.

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

257 2.5.2 Evaluation of thinning

258 Preliminary analyses were based solely on the data from 11 thinned and paired control
259 sites (n=22). These models were then expanded to incorporate background data to
260 allow the models to better partition effects into thinning and stem-density effects. We
261 excluded a subset of the background survey sites that had distinct land use histories

262 (heavy livestock grazing and pasture improvements) with stem density and exotic
263 understory cover characteristics well outside the range of those in experimental sites.
264 The final models were built on a set of 94 sites comprising the 22 experimental sites
265 and 72 background sites.

266 2.5.3 Linear models

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

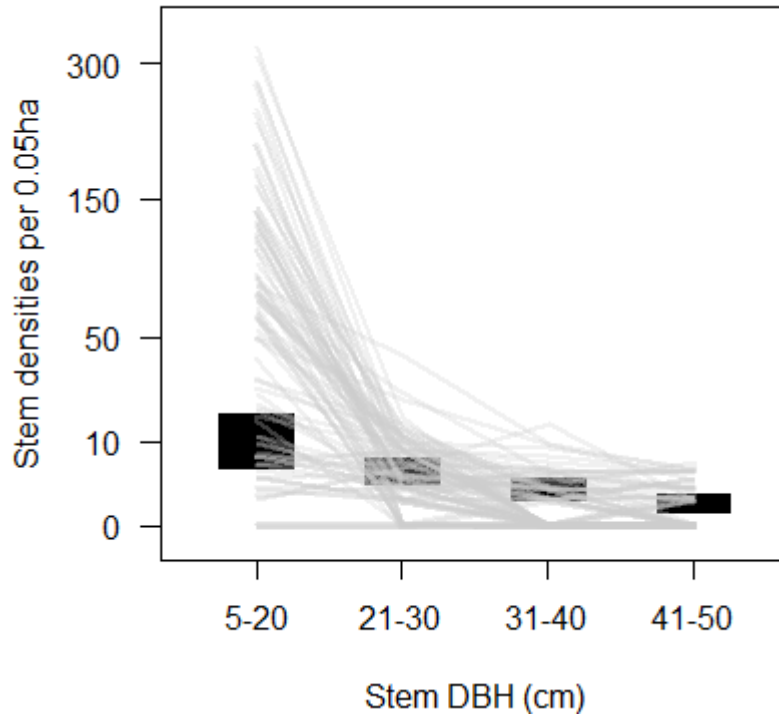
277 Results for GLMs are presented as standardized effect sizes with 95 % confidence
278 intervals. As a guide, the effect can be considered significantly different (i.e., $P < 0.05$)
279 when the interval does not overlap one (1), which signifies no 'significant' effect on a
280 multiplicative scale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

281 **3. Results**

282 3.1 Tree density

283 Stem densities varied among background sites, from 0 to the maximum for each size
284 class (i.e., 324, 42, 14 and 6 stems per hectare) which spanned a range above and

285 below the expected benchmark densities of Gibbons et al. (2010) (Figure 1). All sites
286 contained more than one tree.



287

288 Figure 1. Stem densities of eucalypts for four size classes at each background site (n=98).
289 Stem densities from the survey data within a site are connected by grey line. Black rectangles
290 indicate the benchmark range of stem densities within each size class for relevant vegetation
291 types from Gibbons et al. (2010). Density is presented on a square root scale.
292

293 3.2 Understory cover, species richness, and shrub counts

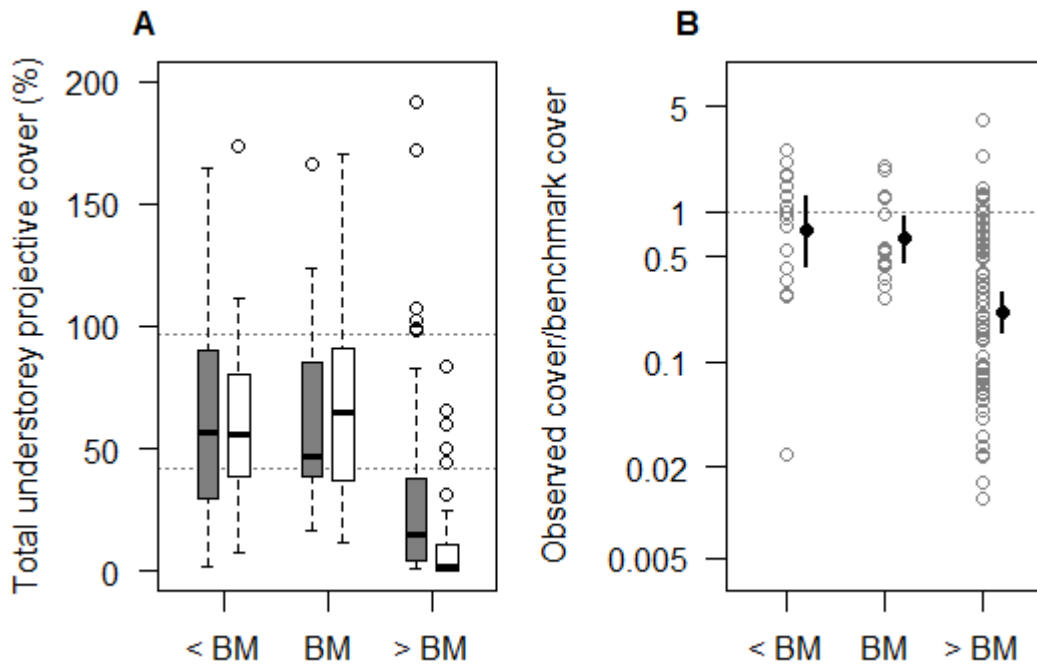
294 Native foliage projective cover ranged from 0–231 % (median = 29 %), and exotic
295 cover ranged from 0–236 % with (median = 8 %). Vegetation cover was variably
296 dominated by exotic graminoids (e.g., *Lolium rigidum*, *Briza* spp. and *Hordeum* spp.),
297 native tufted graminoids (e.g., *Austrostipa* spp. and *Rytidosperma* spp.), and prostrate
298 to medium shrubs (e.g., *Acacia acinacea* and *Dodonaea viscosa*). Native species
299 richness was higher (range = 4–38, median = 16) than exotic richness (range = 0–27,
300 median = 6) and varied across sites. Native shrub counts were highly varied and

301 ranged from 0–1388 (per 0.05 ha) across sites. Summary data for understory floristics
302 are in the Supplementary Material.

303 3.3 Understory cover suppression by dense stands in relation to benchmark levels

304 The summed individual life form EVC benchmarks to give a total understory cover
305 varied across background and thinning control sites (n=109) from 42 % cover in ‘box-
306 ironbark forest’ to 97 % cover in ‘grassy dry forest’. Sites with stem densities of the
307 5–20 cm size class within or below their benchmark levels generally had native
308 understory cover within their EVC benchmark range (Figure 2A). Native understory
309 cover in the above benchmark sites had median cover of 15 % compared to medians
310 of 47 and 57 % in benchmark and below benchmark sites, respectively. The exotic
311 understory species cover observed in above benchmark sites had median cover of 1 %
312 compared to 65 and 56 % in benchmark and below benchmark sites, respectively, but
313 for exotics the benchmark cover is zero.

314 The ratio of observed native understory cover to the relevant EVC benchmark for
315 each site was calculated to determine a general model for this relationship across the
316 range of benchmarks. 69 of 79 sites with stem densities exceeding the benchmark
317 density had understory cover below their EVC benchmark range (Figure 2B). Sites
318 where native understory cover exceeded its benchmark were observed for each stem
319 density category (Figure 2B). Sites with stem densities below or within their
320 benchmark had similar mean understory cover values, which were a ratio of 0.7, or
321 two thirds, of the understory benchmark cover for each site. The mean ratio for sites
322 with stem density exceeding the benchmark range was significantly lower, at 0.17, or
323 one-sixth (Figure 2B).



324
 325 Figure 2. A) Total understory foliage projective cover for densities of eucalypt stems in the 5–
 326 20 cm size class (n=109). Grey boxplots are cover values for native species; white boxplots
 327 are for exotic species. Horizontal dotted lines indicate the range of EVC benchmarks for
 328 understory cover within the vegetation types included in these surveys (42–97%). Boxes
 329 indicate the median, interquartile range, and whiskers extend to the most extreme data point
 330 that is no more than 1.5 times the interquartile range from the box. B) The ratio of native
 331 understory foliage projective cover and EVC benchmark cover (on log scale) for densities of
 332 eucalypt stems in the 5–20cm size class. Sites on the horizontal line at ratio=1 have cover at
 333 benchmark levels. '> BM' (n=79) are sites where the stem density exceeds the benchmark
 334 range stated by Gibbons et al. (2010) for equivalent vegetation types, 'BM' (n=14) are sites
 335 with stem density within the benchmark range and '< BM' (n=17) are sites with density below.
 336 Grey circles (○) indicate the ratio for each site; solid black circles (●) are the means with error
 337 bars showing 95% confidence intervals.

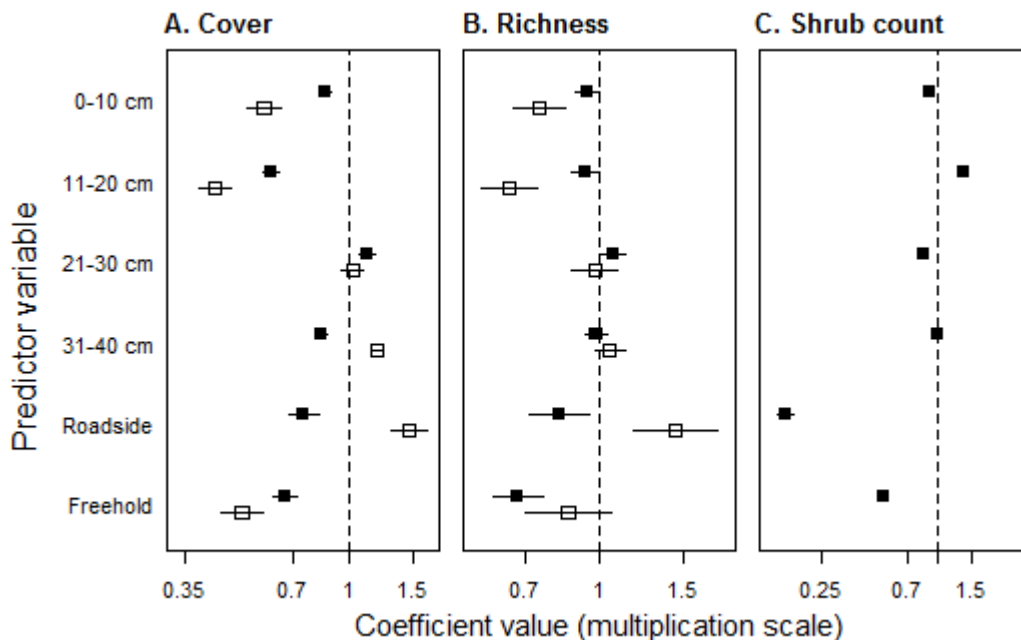
338

339 3.4 Density effect on understory life form cover, species richness and shrub counts

340 Small stem size classes (0–10 cm and 11–20 cm DBH) had the strongest negative
 341 relationship with both native and exotic understory cover and species richness (Figure
 342 3A & B). Native shrub counts had a small positive relationship with the density of
 343 11–20 cm DBH stems (Figure 3C).

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

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



356
 357
 358 Figure 3. Multiplicative effect of predictor variables in generalized linear models for A) native
 359 (■) and exotic (□) understory cover, B) native (■) and exotic (□) species richness and C)
 360 native shrub counts (n=109). Error bars show the 95% confidence intervals. Dashed vertical
 361 line indicates the position of a neutral effect.

362

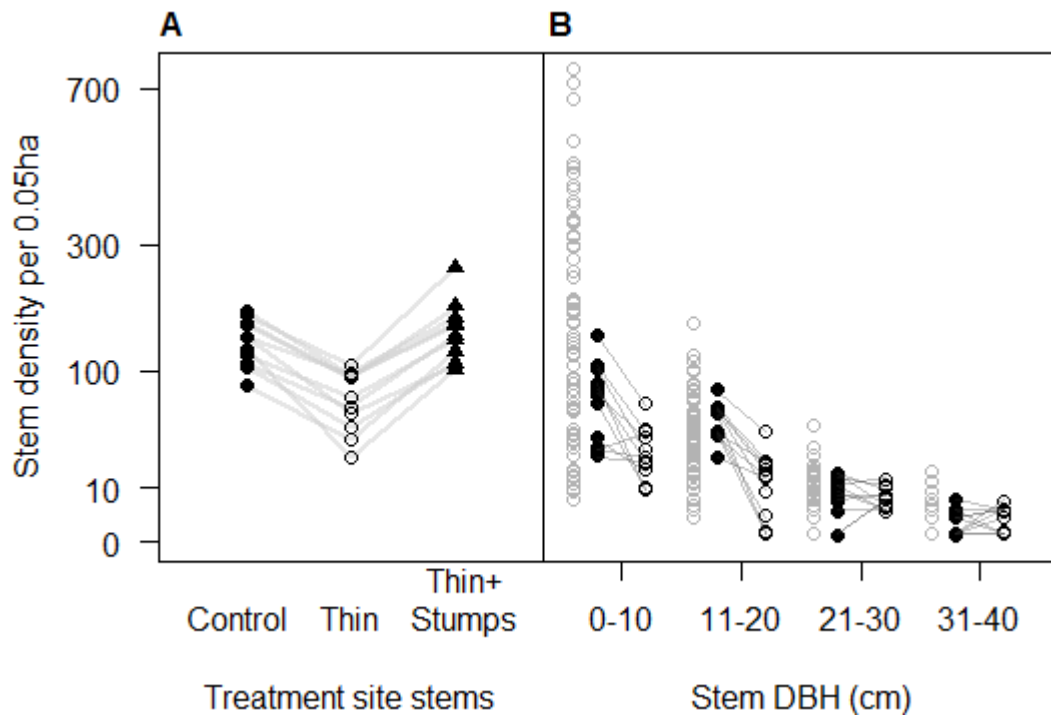
363 *3.5 Verifying treatment effects*

364 We confirmed that the treatment sites had similar densities of stems to control sites
365 before the thinning trials, by estimating the density of cut stumps at treatment sites
366 and adding it to the density of stems still remaining (Figure 4).

367 Thinning consistently decreased stem density of the smallest two size classes in all
368 but one treatment site. For larger stem size classes, the difference between control and
369 treatment sites was more variable (Figure 4). As such, thinning treatments in this
370 study refer to thinning of stems < 20 cm DBH. Control and treatment stem densities
371 fell within the range of densities observed in the background surveys (Figure 4).

372 Thinning reduced the stem densities to within or below the Gibbons *et al.* (2010)
373 benchmark densities at all but one treatment site (Figure 4, and see Figure 1 for
374 benchmark values).

375



376

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

386 3.6 Understory vegetation response to thinning in the experimental sites

387 Thinning as a single binary predictor in GLMs had positive effects on native and
 388 exotic understory cover, species richness, and native shrub counts for the
 389 control/treatment paired surveys (multiplicative effect and 95% CI [lower bound,
 390 upper bound] for: native cover 2.34 [2.07, 2.59], exotic cover 8.20 [5.88, 11.44],
 391 native richness 1.39 [1.17, 1.64], exotic richness: 1.87 [1.13, 3.10], and native shrubs:
 392 1.73 [1.65, 1.81], n=22). We investigated whether the effect of thinning was due to
 393 the reduction in stem density, or if there were additional confounding factors. GLMs
 394 with multiple covariates indicated that the smallest stem size categories were driving

395 the negative influence on native and exotic cover and richness, whereas native shrub
396 counts were relatively insensitive to stem density (Figure A.3). The roadside variable
397 was excluded from these models since none of the thinned sites were on roadsides.
398 Sites on Freehold land had lower native species richness, more exotic cover and
399 species richness, and far fewer native shrubs than Crown sites.

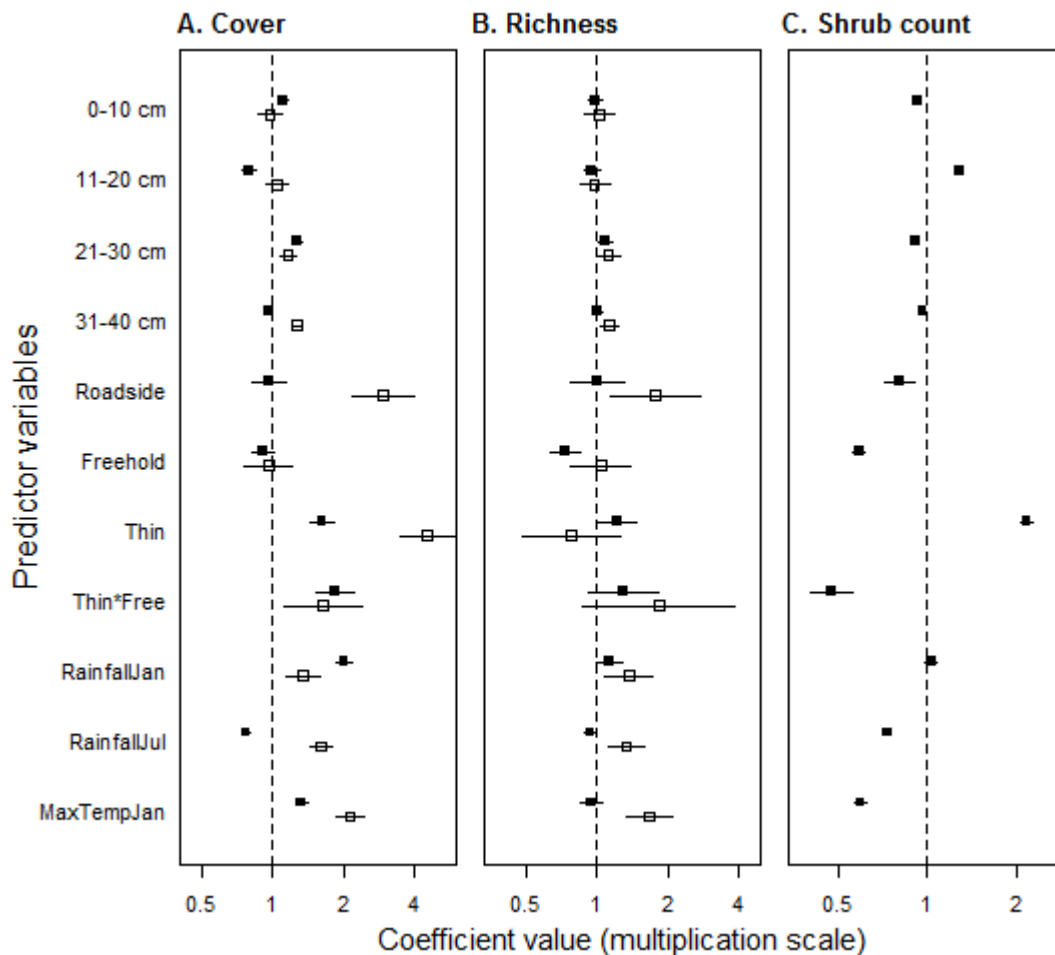
400 Adding a thinning covariate to the stem density predictor improved models for native
401 and exotic cover, but not richness (without and with thinning covariate respectively,
402 natives - AIC: cover 631 and 589; richness 138 and 139, exotics - AIC: cover 351 and
403 346; richness 97 and 96). Thinning did improve the model fit for native shrub counts
404 (without and with thinning covariate respectively, AIC: 4272 and 4103). Thinning had
405 positive effects on each of native and exotic cover, native richness and shrub counts,
406 though the magnitude varied between them and the effect was smallest and least
407 certain for richness (Figure A.3). We included an interaction term to assess the
408 combination of thinning on Freehold versus Crown land. Thinning on Freehold land
409 had little additional effect (beyond that on Crown land) on native cover and richness
410 or exotic richness, an additive effect on exotic cover, and a negative effect on native
411 shrub counts, meaning that thinning was ineffective for shrub counts on Freehold
412 land.

413 *3.7 Understory response to stem and environmental variables*

414 We combined the background and control/treatment survey data to increase our power
415 to detect effects of stem density and other environmental covariates on understory
416 vegetation cover. Some environmental covariates were better predictors of understory
417 cover than stem density classes (Figure 5). Environmental covariates had a positive
418 relationship with exotic cover and species richness. The relationships with natives

419 were less consistent. July rainfall and January maximum temperature were negatively
420 related to native shrub counts.

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

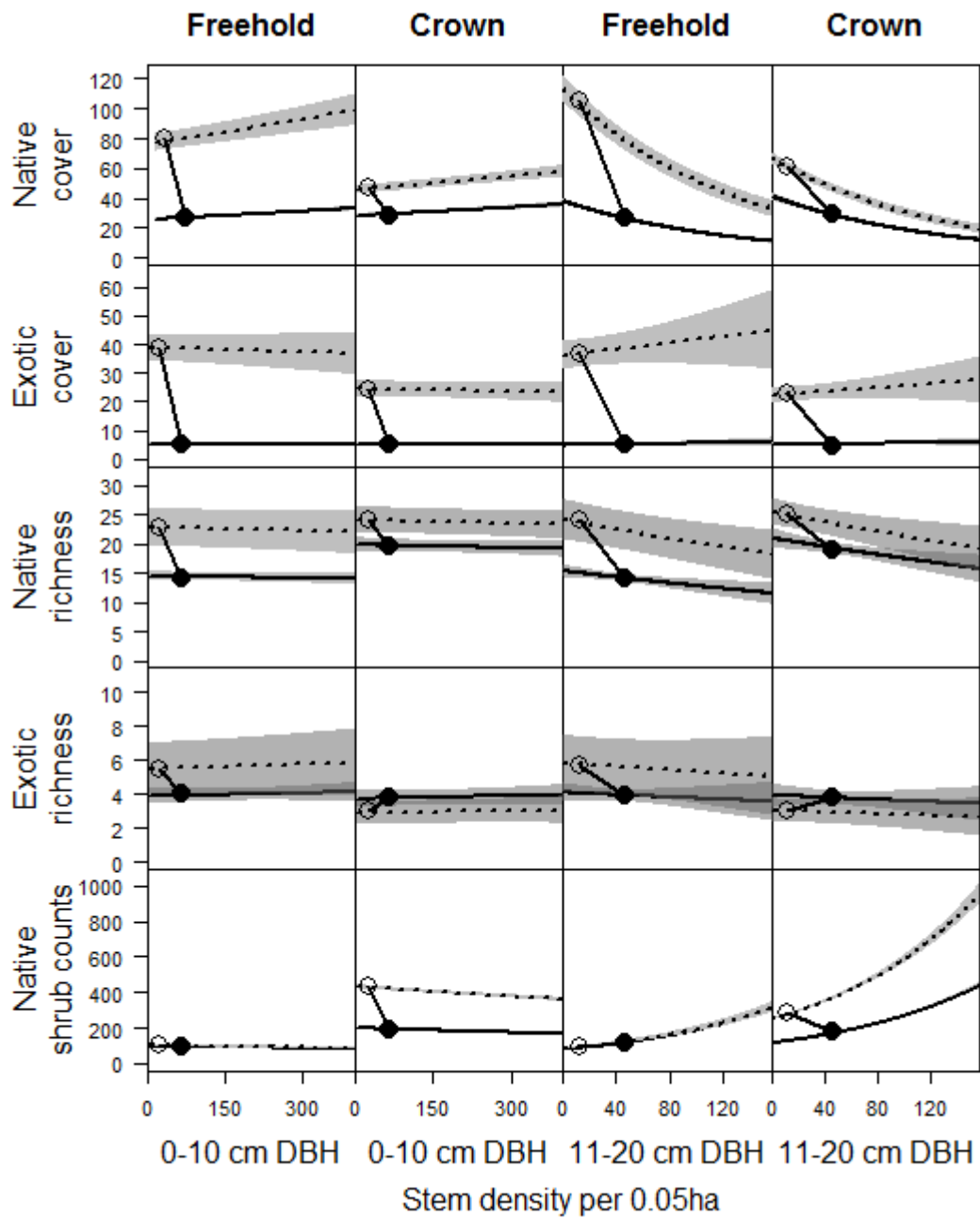


427
428 Figure 5. The multiplicative effect of stem density, tenure, thinning, and three environmental
429 covariates for native (■) and exotic (□) understory cover, species richness and shrub count
430 responses (n=94). Error bars show the 95% confidence intervals. Dashed vertical line
431 indicates no effect.

432

433 Predictions based on the above combined models were used to estimate the effect of
434 thinning at hypothetical new sites. We predicted across a range of unthinned densities
435 of the two smallest stem classes (< 20 cm DBH) since they are most likely to be
436 thinned, and have the strongest relationship with understory cover. These predictions
437 should be interpreted cautiously as they are made for scenarios where one size class is
438 fixed and the other varies - a scenario that did not occur in our dataset. Thinning when
439 a stand is younger (i.e., with small stems < 10 cm DBH) was predicted to be
440 beneficial, for native cover and species richness on both Freehold and Crown land
441 (Figure 6). There is likely to be a stronger response to thinning if the stems are larger
442 (11–20 cm DBH) probably due to a greater suppressive effect on understory (see
443 Figure 5).

444 Thinning is predicted to increase each understory vegetation attribute except exotic
445 richness in Crown sites (Figure 6). The mean density per 0.05 ha of 11–20 cm DBH
446 stems was 46 in control sites and 12 in treatment sites. A reduction of such magnitude
447 on Crown land is predicted to increase native cover from 30 % to 60 % (top right
448 panel of Figure 6), which corresponds to moving from below to within the benchmark
449 bounds. For 0–10 cm DBH stems, the mean density per 0.05 ha was 66 in control sites
450 and 25 in treatment sites. Thinning either stem size class could substantially increase
451 exotic cover, particularly on Freehold sites. The predicted effects on shrubs are unlike
452 for the other understory attributes having differential effects conditional on land
453 tenure.



454

455 Figure 6. Predictions of understory cover, species richness and native shrub counts under
 456 increasing densities of stems (n=94). Dotted lines are mean predictions for thinned sites, solid
 457 lines for un-thinned sites, where grey shading is the 95% confidence interval. As an example,
 458 the black line joins the predicted native cover at the mean density of stems in the control sites
 459 (●) with the mean density in treatment sites (○), i.e. control and treatment densities of 66 and
 460 25 for 0–10 cm DBH stems, and 46 and 12 for 10–20 cm DBH stems respectively.

461

462

463 4. Discussion

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

471 *4.1 When is a dense stand a problem for understory vegetation?*

472 In order to diagnose problematic sites, we compared stem densities and understory
473 attributes with their respective published benchmarks. Many stands in our study had
474 stem densities exceeding their benchmark densities, by as much as a factor of 10
475 (Figure 1). Cover of both native and exotic understory vegetation was lower when
476 stem densities exceeded benchmarks (Figure 2). The benchmark values may
477 approximate the carrying capacity of stems, based on resource availability, beyond
478 which there is understory and stand growth suppression. The reduction in exotic
479 understory cover at higher stem densities (Figure 2A) may be beneficial, particularly
480 in sites with high exotic cover, which contrasts against the desire to increase native
481 understory. This presents a trade-off for managers with conflicting desires to
482 minimize exotic growth or maximize native growth.

483 Averaging over confounding environmental covariates, we found that suppression of
484 cover and richness due to stem density was greatest at the highest densities of stems <
485 20 cm DBH. Suppression of understory cover by dense woody vegetation has been
486 well documented (Eldridge *et al.* 2011; Good *et al.* 2011; Le Brocque *et al.* 2009;

487 Walker *et al.* 1986). Yet, the effects on species richness are less clear (Eldridge *et al.*
488 2011; Le Brocque *et al.* 2009; Milberg 1995).

489 *4.2 Why not just leave dense stands to self-thin?*

490 Over time, self-thinning is expected to lower stem densities. However, whether the
491 stand will reach a desired state and how long this may take in our study system are
492 highly uncertain (Czembor & Vesik 2009). Leaving stands at high density of small
493 stems for long periods (e.g., 5–20 cm DBH, see Figure 1) may delay the development
494 of desirable understory attributes even if stem densities eventually decline.

495 Competition for resources at high stem densities reduces understory cover (see Figure
496 2A) excluding some understory species entirely. If some individuals of a species (or
497 their propagules) persist they can potentially recover following stem thinning.

498 However, seedbanks of understory species will gradually be depleted within dense
499 stands as soil-stored seed has limited longevity (Falińska 1999; Milberg 1995;
500 Thompson 2000), although many species have mechanisms for seed longevity
501 (Orscheg & Enright 2011). The principal concern is that the longer it takes for a stand
502 to thin out naturally, there will be increasingly fewer understory species present as
503 standing biomass or soil-stored seed to allow recovery. Conversely, the main hope for
504 a thinning intervention is that it may reduce the chances of understory species
505 extirpation and result in a better ecological outcome, sooner.

506 *4.3 What are the expected ecological benefits of thinning, and what other drivers* 507 *influence understory response?*

508 Our models may encourage managers because they suggest thinning can increase
509 native understory species cover, richness and shrub counts. However, these models

510 also caution that thinning can increase exotic species cover, with its associated
511 management problems.

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

525 Following thinning, newly regenerating plants will be those with propagules available
526 from persisting plants, the soil seed bank, or nearby vegetation. We saw greater
527 understory cover, irrespective of thinning, where average January (summer) rainfall
528 was higher, likely because germination and survival depend on water availability.

529 Native understory cover and species richness increase following thinning, which is
530 likely to be facilitated by favorable rainfall and temperature conditions (Figure 5).

531 We did not assess grazing (whether by livestock, rabbits, or macropods) in this study,
532 but we expect that grazing before or after thinning treatment would influence the
533 understory response. Our treatment site that showed both the smallest native
534 understory increases, and negative exotic cover and richness responses to thinning

535 was grazed throughout much or all of the stand development prior to thinning (Lance
536 Williams pers. comm.), and were presumed to have a depauperate soil seedbank as a
537 consequence. Grazing following thinning is likely to reduce or prevent understory
538 recovery, which is undesirable except where the recovering vegetation is dominated
539 by exotic species. In those exotic dominated sites, grazing could be used to minimize
540 exotic regrowth in the absence of alternative control methods.

541 *4.4 How much and when to thin?*

542 We analyzed thinning as a binary proposition (i.e., thinned or not), but the treatment
543 could be applied in many different configurations, removing many or few stems.
544 Ideally thinning analyses would incorporate an effect of time since treatment, but this
545 was not possible for our study. Our study suggests that reducing stem density to
546 within or below benchmark levels is required to shift cover to within the
547 corresponding understory benchmarks (Figure 2). It is unclear what amount of stem
548 reduction is required to maintain benchmark understory cover over the longer term.
549 Large reduction of stems may allow new mass recruitment to occur due to
550 competitive release. Small reductions may have correspondingly short-term effects.
551 Due to the absence of pre-thinning understory cover data, we were unable to evaluate
552 the relative response rates of exotic and native species. Sites that have high exotic
553 cover prior to thinning (or development of the dense stand) are likely to have a greater
554 response of exotics after thinning due to the higher proportion of weed species in the
555 seedbank. The trade-off between increasing native and increasing exotic vegetation
556 needs to be considered. Significant exotic vegetation invasion could negate the value
557 of increasing the cover of native plants (Figures 5 and 6).

558 The best action for native understory vegetation could be to thin early to prevent
559 dense woody regrowth from becoming sufficiently established to suppress or displace

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

575 *4.5 So is my dense stand a problem, and is thinning a good solution?*

576 In sum, based on our work a manager could take published benchmark data on
577 numbers of stems, and understory to make a first assessment of a thinning proposal.
578 Stem densities above benchmark maxima are very likely to have poor understory
579 richness and cover. The manager would be relatively confident about a positive and
580 rapid native understory response to thinning on Crown lands from higher rainfall
581 areas, including roadside areas, provided there is low risk of facilitating the spread of
582 invasive exotic species. Coupled with documented faster growth of the extant stems in
583 thinned areas at high densities (McHenry *et al.* 2006; Sala *et al.* 2005), there seems
584 good evidence that thinning treatments will accelerate habitat development in both the

585 under- and overstory. On Freehold land, although the overstory improvements are
586 likely, the understory result could be positive or negative, subject to land use factors
587 that may be difficult to obtain *a priori*, as well as total grazing pressure. In these more
588 uncertain cases, management experiments may be the most constructive way to learn
589 which thinning proposals are safe bets for a good ecological outcome.

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

597 5. Conclusion

598 Providing an objective and transparent strategy for managing dense stands is difficult
599 when it is uncertain when dense woody regrowth is a problem and how vegetation
600 may respond to intervention. There are no protocols to guide the practice of thinning
601 that account for ecological responses in both canopy and understory. Here we have
602 presented an analysis of empirical research, backed up by relevant literature that
603 should aid managers considering thinning as a tool to mitigate the negative ecological
604 effects of dense woody regrowth.

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