

# Marsupial response to matrix conversion: results of a large-scale long-term 'natural experiment' in Australia

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## Abstract

We quantified changes in forest-dependent mammal populations when the habitat in which they live remains intact but the surrounding matrix is converted from open grazed land to closed pine plantation forest. This situation is increasingly common as plantations are often established on formerly cultivated or grazed land.

We conducted a large-scale (30 Km<sup>2</sup>), long-term (14 years) fully controlled and replicated (111 sites) 'natural experiment' in south-eastern Australia. The study focused on the effects of changes occurring in the matrix on mammals which inhabit patches of native *Eucalyptus* woodland.

We found that none of the five target species in our study (two macropods, two possums and a glider) responded negatively to pine plantation establishment. For three species (the sugar glider *Petaurus breviceps*, the red necked wallaby *Macropus rufogriseus* and the swamp wallaby *Wallabia bicolor*) the response to plantation establishment was positive (i.e. increase in colonization/patch use in sites surrounded by pine plantations) whereas the two possums (the common ringtail possum *Pseudocheirus peregrinus* and the common brushtail possum *Trichosurus vulpecula*) were positively affected by the amount of native tree cover surrounding sites, rather than pine plantation establishment.

We foresee two strong implications of our work for the conservation of mammal species in agricultural areas subject to multiple land-use changes: 1) Our results suggest that converting agricultural land to pine plantations will not affect our target mammalian species negatively; rather, it may facilitate colonization of remnant patches of native vegetation by some species. 2) Our findings underscore the critical importance of preserving remnant native vegetation within plantations, as it may decrease the risk of local extinction for some species or facilitate the colonization of new sites for others. Thus, retention of patches of remnant native vegetation should be part of the design of future plantations.

Key words: land-use change; mammals; pine plantations; habitat loss; colonization; extinction.

## 1. Introduction

The conversion of forested and agricultural land to tree plantations is a major driver of global change (Foley et al., 2005). Humans have converted natural forests to forest plantations for thousands of years (e.g. Romans used to convert oak forests to pine plantations for timber production; Ginanni, 1774). However, in the last few decades, there has been an unprecedented global increase in planted forests as the Food and Agriculture Organization recorded a worldwide increase of 5 million

51 hectares/year in the period 2000-2010. This is due to an increased demand for wood and for carbon  
52 storage (Jackson et al., 2005; Paquette and Messier, 2010).

53 A key distinctive feature of tree plantations compared to other types of crops is that they are often  
54 extremely large (i.e. covering areas thousands of hectares in size) and need to be managed over long  
55 time periods (crop rotation length is usually 7-50 years; Pawson et al., 2013). Consequently, the  
56 conversion of agricultural lands to tree plantations can have broad scale and long-lasting impacts on  
57 landscapes. How does biodiversity respond to these large-scale and long-term changes? The  
58 majority of existing studies have focused on birds, where response to plantations has ranged from  
59 positive to negative (Luck and Korodaj, 2008; Mortelliti et al., 2014, 2015; Tomasevic and Estades,  
60 2008; Villard and Haché, 2012). Similarly, the few studies focused on mammals have found complex  
61 responses to plantation establishment (Lindenmayer et al., 2008, 1999a; Youngentob et al., 2013),  
62 with some studies showing an increase in dispersal and connectivity due to plantation establishment  
63 (e.g. Banks et al., 2005; Taylor et al., 2007) and others suggesting an opposite effect (e.g. Lancaster  
64 et al., 2011). Previous studies, however, have focused mainly on comparing remnant patches  
65 surrounded by forest plantations with contiguous non-fragmented areas (i.e. have contrasted forest  
66 plantations vs native forested habitat, Stephens and Wagner, 2007; Youngentob et al., 2013). Other  
67 studies have compared different matrix types (e.g. pine plantations vs. others) but have typically  
68 focused on single species or have employed an observational approach (e.g. Anderson et al., 2007;  
69 Umetsu and Pardini, 2006). Therefore, clear patterns of mammalian responses to the conversion of  
70 the agricultural matrix to forest plantations have not yet emerged in the existing literature.

71 Afforestation of cultivated or grazed land is increasingly common worldwide (Cyranoski, 2007; Sedjo,  
72 1999) and thus empirical evidence to support decision-making is urgently needed. To contribute to  
73 filling this knowledge gap we focused our study on the following research question: ***What happens***  
74 ***to mammal populations when the habitat in which they live remains intact but the surrounding***  
75 ***matrix is converted from open grazed land to closed plantation forest?***

76 Vagility is a key driver of animal responses to land-use changes (Kennedy et al. 2010; Watson et al.,  
77 2014), indeed many species of non-volant mammals are limited in their movements and are  
78 therefore very sensitive to matrix modifications (Anderson et al., 2007; Gascon et al., 1999; Sozio et  
79 al., 2013). The conversion of open agricultural land to a closed plantation environment may thus  
80 facilitate the movement of forest-dependent species. Tree plantations may therefore represent an  
81 opportunity for keeping landscapes productive for commodities like wood and paper whilst also  
82 increasing connectivity between patches of remnant vegetation (Brockerhoff et al., 2008; Tomasevic  
83 and Estades, 2008).

84 To evaluate the effects of matrix conversion on mammals, we conducted a unique large-scale (30  
85 Km<sup>2</sup>) long-term (14 years) fully controlled and replicated (111 sites) landscape scale 'natural  
86 experiment' in south-eastern Australia. The goal of the experiment was to compare mammal  
87 populations living within 55 *Eucalyptus* patches surrounded by maturing pine (*Pinus radiata*)  
88 plantations (*treatment sites*), with mammal populations living within 56 *Eucalyptus* patches where  
89 the surrounding matrix remained unchanged (*control sites*, where the matrix remained pasture).  
90 We targeted five forest dependent marsupials varying in body size and with contrasting mobility,  
91 ranging from arboreal marsupials (the common ringtail possum *Pseudocheirus peregrinus* and the  
92 common brushtail possum *Trichosurus vulpecula*) and gliders (the sugar glider *Petaurus breviceps*),  
93 to wide-ranging macropods (the red-necked wallaby *Macropus rufogriseus* and the swamp wallaby  
94 *Wallabia bicolor*). We predicted that the target mammalian species would display an overall positive  
95 response (i.e. increase in patch use or patch colonization) to the conversion of agricultural land to  
96 forest plantations, as the new plantation matrix surrounding the native woodland was expected to  
97 provide more sheltered cover (compared to grazed land) for ground-dwelling species and facilitate  
98 movement for arboreal species.

99

## 100 **2. Methods**

### 101 **2.1 Study area**

102 Our study was conducted in the Nanangroe area (New South Wales, Australia; Fig. 1). The  
103 Nanangroe area lies approximately 500 km northeast of Melbourne (co-ordinates 34°54' - 35°4' and  
104 148°32' - 148°18' E, altitudinal range: 250-750 m a.s.l.), covers approximately 30 km<sup>2</sup> and the region  
105 is characterised by hot summers and cool winters (temperate climate). The native vegetation is  
106 characterised by open woodlands dominated by white box (*Eucalyptus albens*), red box (*E.*  
107 *polyanthemos*), yellow box (*E. melliodora*), red stringybark (*E. macrorhyncha*) and Blakely's red gum  
108 (*E. blakleyi*). More than 80% of the original temperate *Eucalyptus* woodland has been cleared for  
109 grazing.

## 110 **2.2 Experimental design**

111 The Nanangroe area hosts a large-scale landscape transformation experiment known as 'the  
112 Nanangroe experiment' (Lindenmayer et al., 2001). In 1998 and in 2000 Forest New South Wales  
113 established a series of large scale Radiata pine (*Pinus radiata*) plantations in formerly grazed areas  
114 for the purpose of a) timber and pulp production and b) carbon storage. During the establishment of  
115 the plantations native *Eucalyptus* patches remained uncleared and thus were surrounded by a  
116 changing matrix (i.e. native pastures being converted to maturing pine plantations).

117 The experimental design of the study is composed of 55 treatment *Eucalyptus* patches surrounded  
118 by maturing pine plantations and 56 control *Eucalyptus* patches where the surrounding matrix sites  
119 has remained composed of pastures. The selection of sites followed a replicated, random stratified  
120 procedure. Treatment sites were selected based on the following factors: a) patch size b) age of the  
121 pine plantations and c) number of boundaries between the patch and the plantations. Patch size was  
122 selected according to the following size classes: 0.5-0.9 ha (15 replicates), 1.0-2.4 ha (20 replicates),  
123 2.5-4.9 ha (15 replicates), 5.0-10 ha (4 replicates), >10-15 ha (2 replicates). *Eucalyptus* patches were  
124 surrounded by pines belonging to two age-cohorts (cohort 1= pines planted in 1998; cohort 2= pines  
125 planted in 2000). Eleven *Eucalyptus* patches had 1-2 open boundaries with grazed land, whereas the  
126 remaining patches had 1 boundary with grazed land or were completely surrounded by pines. Each  
127 treatment site was matched with a control site of similar size. A summary of the experimental design  
128 is provided in Table S1.

## 129 **2.3 Mammal surveys**

130 Sites were surveyed for the presence of target mammal species by means of spotlighting transects  
131 (length of the transect =200m; 1 transect per site). Each *Eucalyptus* patch was surveyed by an  
132 observer holding a 50W spotlight and walking at an average speed of 3 km/h. Sites were surveyed  
133 during spring of the following years: 1999, 2001, 2004, 2006, 2009, 2011, 2012 and 2013. Surveys  
134 were conducted starting one hour after dusk and terminated 3 hours later to reduce observers  
135 fatigue and consequent bias in detectability. Additional surveys conducted within pastures and  
136 within plantations showed that mammals were virtually absent from these areas, confirming that  
137 these areas are 'matrix' used for occasional movements rather than habitats for the target species  
138 (Lindenmayer et al., 2008). For this reason, these data were not included in our analyses.

## 139 **2.4 Data analysis**

140 False absences are a major source of bias in wildlife distribution studies (MacKenzie, 2005),  
141 particularly in studies focusing on mammals (Mortelliti and Boitani, 2007). To control for potential  
142 bias caused by false absences, multiple season occupancy models (MacKenzie et al., 2003) were  
143 fitted on detection history data gathered through the spotlighting surveys conducted in the period  
144 1999-2013. Each of our 111 *Eucalyptus* patches was defined as a *site* (MacKenzie et al., 2003). The  
145 transect was divided into two segments (0-100 m and 100-200m) and each segment was considered  
146 as a *visit* to a site (see discussion below on spatial replication in spite of temporal replication).  
147 Populations were assumed to be closed between visits occurring in the same year, but open to  
148 colonization/extinction between years. We emphasise that while the term 'colonization' and  
149 'extinction' of local populations may be appropriate for our smaller target species these should be  
150 interpreted as 'change in patch use' for the larger macropods (MacKenzie, 2005) as these species  
151 may include several patches within their home range (Tyndale-Biscoe, 2005; Van Dyck and Strahan,  
152 2008).

153 The substitution of spatial replicates for temporally repeated surveys has been adopted elsewhere  
154 (e.g. François et al., 2008; Sadoti et al., 2013; Sirami et al., 2008). Following Hines et al. (2010), a  
155 ‘multiple season for correlated detection’ model was preliminarily fitted through software Presence  
156 (version 7.1) to check for evidence of potential spatial dependence between visits. As little support  
157 for spatial dependence was found (i.e. correlated-detection models ranked lower than the null  
158 model), analyses were conducted using ordinary multiple season models through the ‘unmarked’  
159 package (Fiske and Chandler, 2011) in R.

#### 160 2.4.1 Predictor variables.

161 Four variables were selected to be included as predictors in the occupancy models: a) treatment  
162 (e.g. pine vs grazing context), b) time elapsed since the beginning of the study c) vegetation type  
163 (based on dominant tree species, categories are listed in Table S2) and d) *Eucalyptus* tree cover  
164 surrounding the site. *Eucalyptus* tree cover was measured in a circle (250m radius) centred on each  
165 site. Tree cover included habitat patches and isolated trees and was measured by using digitised  
166 aerial photography in ArcGIS 10.1. We chose to use the tree cover in the circle rather than patch size  
167 because of the critical role played by scattered trees in determining the occurrence of Australian  
168 native fauna (Fischer et al., 2010; Manning et al., 2006). Following Fahrig (2013), tree cover in the  
169 circular area (including the *Eucalyptus* patch and scattered trees) was considered to be a proxy for  
170 habitat amount and isolation. The 250 m radius was selected following preliminary analyses (i.e. best  
171 model fit compared to other distances).

172 We adopted a three step approach to fitting models:

- 173 a) *Detection probability* ( $p$ ) was modeled as either constant or as function of year (both as  
174 categorical and continuous covariate). The continuous covariate implied a trend in  
175 detectability whereas the categorical covariate implied a year-specific probability of  
176 detection which could be caused by several factors such as variability in weather and  
177 fluctuations in resource availability. The variable(s) included in the top ranking models (as  
178 measured through the Akaike Information Criteria) were retained in the following steps (b-  
179 c).
- 180 b) Factors influencing  $\psi_1$  (probability of a site being occupied in the first study year) were then  
181 modelled. Predictor variables included: vegetation type and tree cover in the 250 m circle  
182 (Table S2). Variable(s) included in the top ranking model were retained the in the following  
183 step.
- 184 c) Finally, we modelled factors affecting the *probability of colonisation* ( $\gamma$ ) and the *probability*  
185 *of extinction* ( $\epsilon$ ). Predictor variables included: treatment (a site surrounded by pines vs  
186 control), year since the beginning of the study (continuous variable) and tree cover in the  
187 250 m circle. Two-way interactions for these variables (e.g. treatment\* year) also were  
188 included as well as models with different effects for colonization and extinctions: e.g.  
189  $\gamma(\text{treatment}*\text{time})$ ,  $\epsilon(\text{tree cover})$ . Although our sample size is relatively large for landscape  
190 ecological studies, we opted to keep the ratio of the number of parameters to number of  
191 sites relatively small, so did not include three way interactions. Furthermore, as our sample  
192 design was specifically focused on the evaluation of the treatment effect we chose not to  
193 include treatment\*tree cover interactions, as the number of replicates for larger patches  
194 was limited (which is a typical feature of many large scale fragmentation studies; Gibson et  
195 al., 2013; Laurance et al., 2011).

196 Inference was based on model averaged estimates (including models within 2  $\Delta$ AIC; Burnham and  
197 Anderson, 2002). Goodness of fit of each model was measured using Nagelkerke’s pseudo  $R^2$  (range  
198 of values:0-1).

199 The variable “year” should be interpreted as ‘time since the beginning of the study’, which in the  
200 case of treatment sites, also acted as a proxy for the time since plantation establishment. We were  
201 not able to identify a method to include a time covariate for treatments only as a value of ‘zero’ in  
202 the control sites would not be meaningful. Similarly, it was not possible to distinguish between the  
203 two cohorts of plantation establishment and simultaneously modelling control sites. We opted to

204 use the variable 'time since start of the study' to avoid conducting separate analyses for treatments  
205 and controls. We therefore acknowledge that this variable was only a proxy for time since the  
206 establishment of the plantation. Occupancy models were fitted using the *unmarked* package for R  
207 (Fiske and Chandler, 2011).

208 Our experiment was designed to reduce the amount of spatial dependence between sites. Key  
209 features of the design included: 1) The inclusion of four independent plantations as 'treatments' (Fig.  
210 1). 2) Woodland control sites were distributed among six different farms. 3) Average nearest  
211 neighbour distance was 507 m (range 114-1158 m) for treatment sites and 507 m (range 188-3195  
212 m) for control sites. Nevertheless, we checked for spatial autocorrelation in the residuals of the most  
213 parameterised model by using a spline correlogram (Zuur et al., 2009). We calculated correlograms  
214 for each of the eight time periods and could not find evidence of spatial autocorrelation for any of  
215 the target species.

### 216 **3. Results**

217 Throughout the duration of the study, arboreal marsupials were detected more often than the  
218 macropods (total number of detections for arboreal marsupials: common brushtail possum=316,  
219 common ringtail possum=199, sugar glider=36; total number of detections for macropods: swamp  
220 wallaby=35 detections, red-necked wallaby=29 detections). All five species were detected in both  
221 treatment and control sites.

222 The detectability of the swamp wallaby and the sugar-glider increased through the years, the  
223 detectability of the common ringtail possum varied on a year-by-year basis, whereas the  
224 detectability of the common brushtail possum and the red-necked wallaby was constant throughout  
225 years (Table 1).

226 The variable 'treatment' was included as predictor in the top ranked models of the 2 macropods and  
227 the sugar glider. For all the three species the establishment of pine plantations increased the  
228 probability of a site being "colonized" during the 16-year study period (Fig. 2 and Fig. 3, Table 1).  
229 Little support was found for a treatment effect on the common brushtail and common ringtail  
230 possum (i.e. variable treatment not included as predictor for  $\gamma$  and  $\epsilon$  in top-ranking models and with  
231 large standard errors for parameter estimates, Table 1). The colonization probability of the common  
232 ringtail possum was influenced mainly by the amount of native tree cover surrounding the site:  
233 higher tree cover led to higher chances of a site being colonized (Fig. 3). The extinction probability of  
234 the common brushtail possum was affected mainly by the amount of native tree cover surrounding  
235 the site: the probability of local extinction was lower in sites surrounded by higher amounts of tree  
236 cover (Fig. 3). The amount of tree cover surrounding the site was the most important predictor of  
237 the probability of a site being occupied during the first survey ( $\psi_1$ ) for all the species apart from the  
238 swamp wallaby. Vegetation type and two-way interactions had little support in the top ranked  
239 models.

240

### 241 **4. Discussion**

#### 242 *4.1 Biological interpretation of the models*

243 The positive response of the two macropods to plantation establishment is in line with existing  
244 knowledge on these species (Van Dyck and Strahan, 2008). Both species are strongly associated to  
245 forest cover (Van Dyck and Strahan, 2008) and therefore it is likely that the establishment and  
246 maturation of the plantations facilitated movement between *Eucalyptus* woodland patches.

247 The sugar glider is the most widespread glider in Australia; however, its distribution in fragmented  
248 landscapes is usually limited (Lindenmayer, 2002; Suckling, 1982; Tyndale-Biscoe, 2005). Although its  
249 gliding capabilities are relatively high (up to 50m), its ability to move across large open areas is  
250 inevitably limited and therefore afforestation may facilitate the dispersal and movement of this  
251 species. Our results suggest that pine plantations may have favoured the colonization of sites  
252 embedded within the changing matrix (i.e. the probability of a treatment site being colonized was  
253 almost twice the probability of a control site being colonised; Fig. 2).

254 Both the common brushtail possum and the common ringtail possum were relatively common in  
255 treatment and control sites, which explains the lack of a strong 'treatment' effect in both species. In  
256 accordance with previous studies (Lindenmayer et al., 1999b; Youngentob et al., 2013), we found  
257 that the amount of tree cover surrounding a site had a strong effect on the long term  
258 colonization/extinction dynamics of these species. In the case of the common ringtail possum, tree  
259 cover increased the chances of a site being colonized. Conversely, in the case of the common  
260 brushtail possum, tree cover surrounding a site decreased the likelihood of a local extinction. The  
261 chances of a local extinction were close to zero within woodland patches surrounded by areas with a  
262 moderate amount of tree cover (Fig. 3). These results underscore the critical role played by remnant  
263 native vegetation in highly fragmented and plantation-dominated landscapes (Lindenmayer et al.,  
264 1999b; Youngentob et al., 2013). Furthermore, our results highlight that the conversion of the  
265 agricultural matrix to pine plantation does not interfere with the dynamics of these two species.  
266 In line with previous theoretical and empirical studies on mammals in modified landscapes we show  
267 that the matrix matters (Driscoll et al., 2013; Prevedello and Vieira, 2009) and may be actively used  
268 by individuals thus increasing connectivity (Anderson et al., 2007; Pita et al., 2007; Sozio et al., 2013).  
269 Compared to previous studies focusing on mammals in plantation landscapes, our work provides  
270 more consistent results. We show that the response of our target forest-dependent mammal species  
271 was either positive or neutral, suggesting that matrix conversion through afforestation may not have  
272 negative effects. The relatively clear patterns that we have observed are likely to be a consequence  
273 of the experimental approach that we have followed, the strong contrast between matrices and the  
274 extensive duration of the study. The patterns we have uncovered were not identified in a previous  
275 study conducted in this area (Lindenmayer *et al.*, 2008) possibly because the present study was  
276 substantially longer (14 years vs 7 years). Most importantly, our study focused on different  
277 ecological variables (population turnover rather than occupancy).  
278 Our study was focused on two key parameters (local colonization and extinction). However, we  
279 acknowledge that future studies focusing on more detailed dynamics of the populations, such as  
280 fluctuations in abundance and assessment of connectivity through landscape genetics techniques,  
281 will provide further understanding on the mechanisms involved in determining population turnover  
282 (Mortelliti et al., 2014).

#### 283 *4.2 Implications for conservation*

284 How generalizable are our results? Although our study is one of the largest empirical assessments of  
285 the impact of matrix conversion on mammals ever conducted, further studies are required before  
286 we can generalize the patterns we have observed to other areas and species. Nevertheless, we  
287 emphasize two key features of our study suggesting that the patterns we have observed may  
288 observed in other systems: 1) Our study targeted the impact of pine plantation establishment. Pines  
289 are the most commonly used species in forest plantations worldwide (i.e. they occur in 20% of  
290 plantations; Brockerhoff et al., 2008). Thus the type of plantation that we have studied is highly  
291 representative of plantation establishment globally. 2) We focused on five species with contrasting  
292 mobility and encompassing a wide variation in body size (weight ranging from approximately 130g in  
293 sugar gliders to up to 20Kg in wallabies) thus we were able to include a relatively representative  
294 variety of life-history traits for a mammalian study. Furthermore, although all our species are  
295 marsupials, these have 'ecological equivalents' in Eutherian mammals (e.g. gliders are equivalent to  
296 flying squirrels etc). We acknowledge, however, that replicating our study in different continents and  
297 with different mammalian orders will surely help disclose general patterns on mammalian response  
298 to plantation establishment.

299 Finally, we emphasise that the contrast between the internal structure of the native vegetation and  
300 the forest plantation will also have a strong impact on the response observed. In our case the pine  
301 plantations have a relatively dense structure whereas *Eucalyptus* patches are relatively open.  
302 Replication of our study in different environments (i.e. rainforest with dense structure) would surely  
303 help to understand how generalizable are our results.

304 Landscape managers all over the world are increasingly faced with the issue of whether to convert  
305 agricultural areas to forest plantations (Cyranoski, 2007) - this study was designed to support such  
306 decision making. The results of our long-term large-scale 'natural experiment' have two strong  
307 implications for the conservation of mammal species in agricultural areas subject to multiple land-  
308 use changes (Watson et al., 2014):

309 **1)** For the first time we provide field-based empirical evidence that the conversion of the  
310 agricultural matrix to pine plantations does not have negative effects on the forest-dependent  
311 mammals. Our results therefore suggest that plantations may be a 'lesser evil' compared to other  
312 types of matrix and that a sequence of land-cover changes from open-areas to tree plantations may  
313 favour habitat specialists such as the mammals we have studied.

314 **2)** Our results underscore the critical importance of preserving patches of native vegetation within  
315 plantations therefore retention of patches of remnant native vegetation should be part of the design  
316 of future plantations.

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318

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326

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454

455 **Figure legends.**

456 **Fig. 1. Map of the study area.** Black triangles are control sites (*Eucalyptus* patches surrounded by  
457 grazed areas); black circles are treatment sites (*Eucalyptus* patches surrounded by pine *Pinus radiata*  
458 plantations). Barred areas are pine plantations.

459 **Fig. 2. Model predictions.** Model predictions (including 95% confidence intervals) based on model  
460 averaged estimates of top ranking models ( $\Delta AIC < 2$ ) for the red-necked wallaby *Macropus*  
461 *rufogriseus*, the swamp wallaby *Wallabia bicolor* and the sugar glider *Petaurus breviceps*. The three  
462 species responded positively to pine plantations (increase in “colonisation probability” in sites  
463 surrounded by pine plantations).  
464

465 **Fig.3. Model predictions.** Model predictions (including 95% confidence intervals) based on model  
466 averaged estimates of top ranking models ( $\Delta AIC < 2$ ) for the ringtail possum *Pseudocheirus peregrinus*  
467 and the brushtail possum *Trichosurus vulpecula*. Both species were mainly affected by the amount  
468 of tree cover surrounding the sites (measured in a 250 m radius around each site).

469 Table 1. Model ranking according to  $\Delta AIC$  (delta Akaike Information Criterion); only models  $< 2 \Delta AIC$   
 470 are shown.  $\Psi$  = probability of a site being occupied during the first survey,  $\Upsilon$  = probability of  
 471 colonization;  $\varepsilon$  = probability of extinction,  $p$  = detection probability; T= Treatment; Vegtype =  
 472 vegetation type (categories listed in table S2); Y = year (categorical covariate); Yn = year (numeric  
 473 covariate); H = tree cover within a 250 m radius circle; nPars = number of estimated parameters;  $R^2$  =  
 474 Nagelkerke's coefficient of determination; (.) = constant model (no covariate); W= cumulative model  
 475 weight (i.e. sum of the Akaike weight of the given model and higher ranked models).

476

Species	model	nPars	$\Delta AIC$	$R^2$	W
Red-necked wallaby ( <i>Macropus rufogriseus</i> )	$\Psi(.)\Upsilon(T)\varepsilon(Yn)p(.)$	6	0.00	0.18	0.47
Swamp wallaby ( <i>Wallabia bicolor</i> )	$\Psi(H)\Upsilon(T)\varepsilon(H)p(Yn)$	8	0.00	0.44	0.42
	$\Psi(H)\Upsilon(T)\varepsilon(.)p(Yn)$	7	1.62	0.41	0.61
Sugar glider ( <i>Petaurus breviceps</i> )	$\Psi(H)\Upsilon(T)\varepsilon(.)p(Yn)$	7	0.00	0.10	0.14
	$\Psi(H)\Upsilon(.)\varepsilon(T*Yn)p(Yn)$	9	0.45	0.13	0.26
	$\Psi(H)\Upsilon(.)\varepsilon(T)p(Yn)$	7	1.91	0.08	0.33
	$\Psi(H)\Upsilon(T)\varepsilon(H)p(Yn)$	8	1.94	0.10	0.39
	$\Psi(H)\Upsilon(T)\varepsilon(Yn)p(Yn)$	8	2.00	0.10	0.45
	$\Psi(H)\Upsilon(T)\varepsilon(T)p(Yn)$	8	2.00	0.10	0.50
Common ringtail possum ( <i>Pseudocheirus peregrinus</i> )	$\Psi(H)\Upsilon(H)\varepsilon(.)p(Y)$	13	0.00	0.34	0.16
	$\Psi(H)\Upsilon(Yn)\varepsilon(.)p(Y)$	13	1.14	0.33	0.26
	$\Psi(H)\Upsilon(.)\varepsilon(.)p(Y)$	12	1.71	0.31	0.33
	$\Psi(H)\Upsilon(H)\varepsilon(H)p(Y)$	14	1.87	0.34	0.39
	$\Psi(H)\Upsilon(H)\varepsilon(T)p(Y)$	14	1.90	0.34	0.46
	$\Psi(H)\Upsilon(H)\varepsilon(Yn)p(Y)$	14	1.99	0.34	0.52
Common brushtail possum ( <i>Trichosurus vulpecula</i> )	$\Psi(H)\Upsilon(.)\varepsilon(H)p(.)$	6	0.00	0.21	0.28
	$\Psi(H)\Upsilon(H)\varepsilon(H)p(.)$	7	0.12	0.22	0.55
	$\Psi(H)\Upsilon(Yn)\varepsilon(H)p(.)$	7	1.33	0.21	0.70
	$\Psi(H)\Upsilon(T)\varepsilon(H)p(.)$	7	1.79	0.21	0.81

477

478

479 Table S1. Factorial study design of the Nanangroe study (Table modified from Lindenmayer *et al.*  
480 2008).

481

Site	Context	Cohort	No. edges	No. of replicates
Woodland	<i>Pinus radiata</i> plantation	1998	1-2	3
Woodland	<i>Pinus radiata</i> plantation	1998	3-4	16
Woodland	<i>Pinus radiata</i> plantation	2000	1-2	8
Woodland	<i>Pinus radiata</i> plantation	2000	3-4	29
Woodland	Grazing land			55

482

483

484

485 Table S2. Main characteristics of 111 sampled sites. Context: treatment = *Eucalypt* patches  
 486 surrounded by pine plantation; control = *Eucalypt* patches surrounded by grazing land. Tree cover  
 487 (hectares) measured in a 250 m radius circle surrounding the site. Vegetation type: 1 = red box and  
 488 red stringybark (codominant) with apple box (*E. bridgesiana*), long-leaf box (*E. goniocalyx*), and  
 489 broad-leaved peppermint (*E. dives*); (2) mountain swamp gum (*E. camphora*) and other kinds of  
 490 vegetation (e.g., river oak *Allocausarina cunninghamiana*); (3) yellow box, white box, red stringybark  
 491 (codominant), and Blakely's red gum.

492

Sites	Context	Tree cover	Vegetation type
AWA-1	Control	4.17	3
AWA-10	Control	8.81	3
AWA-11	Control	6.74	3
AWA-2	Control	4.18	3
AWA-3	Control	2.26	3
AWA-4	Control	7.05	3
AWA-5	Control	4.90	3
AWA-6	Control	4.60	3
AWA-7	Control	4.32	3
AWA-8	Control	3.36	3
AWA-9	Control	6.78	3
GRE-1	Control	0.79	3
GRE-2	Control	0.91	3
GRE-3	Control	7.58	3
GRE-4	Control	6.78	3
JWA-1	Control	5.87	3
JWA-10	Control	2.19	3
JWA-11	Control	4.52	3
JWA-2	Control	4.87	3
JWA-3	Control	5.01	3
JWA-4	Control	6.74	3
JWA-5	Control	10.55	3
JWA-6	Control	8.32	3
JWA-7	Control	4.31	3
JWA-8	Control	0.94	3
JWA-9	Control	6.92	3

KEA-1	Control	4.67	3
KEA-2	Control	8.07	2
KEA-3	Control	3.45	3
KEA-4	Control	3.40	3
KEA-5	Control	4.63	3
KEA-6	Control	5.04	3
LUF-1	Control	3.45	3
LUF-10	Control	6.72	3
LUF-11	Control	5.87	3
LUF-12	Control	11.64	3
LUF-13	Control	13.00	3
LUF-14	Control	5.00	3
LUF-2	Control	3.31	3
LUF-3	Control	6.85	3
LUF-5	Control	9.83	3
LUF-6	Control	3.89	2
LUF-7	Control	3.13	3
LUF-8	Control	6.11	3
LUF-9	Control	7.93	3
SKI-1	Control	6.26	3
SKI-10	Control	4.25	3
SKI-2	Control	5.47	3
SKI-3	Control	8.42	3
SKI-4	Control	4.74	3
SKI-5	Control	3.56	3
SKI-6	Control	2.96	3
SKI-7	Control	2.64	3
SKI-8	Control	2.15	1
SKI-9	Control	3.27	3
BUN-1	Treatment	7.68	3
BUN-2	Treatment	6.42	3
COT-1	Treatment	8.21	1
COT-10	Treatment	4.07	3
COT-2	Treatment	2.74	1



COT-4	Treatment	0.96	1
COT-5	Treatment	2.01	1
COT-6	Treatment	2.90	3
COT-7	Treatment	1.82	3
COT-8	Treatment	3.74	3
COT-9	Treatment	9.49	3
EAB-1	Treatment	3.32	2
EAB-2	Treatment	9.06	2
EAB-3	Treatment	8.37	2
EAB-4	Treatment	3.82	2
EAB-5	Treatment	4.28	2
EAB-6	Treatment	7.03	1
EAB-7	Treatment	9.82	2
EAB-8	Treatment	10.61	2
NAN-1	Treatment	1.09	3
NAN-10	Treatment	3.13	3
NAN-11	Treatment	3.10	3
NAN-12	Treatment	5.84	3
NAN-14	Treatment	6.18	3
NAN-15	Treatment	1.44	2
NAN-16	Treatment	2.23	3
NAN-18	Treatment	9.12	3
NAN-19	Treatment	1.93	3
NAN-20	Treatment	6.12	3
NAN-23	Treatment	3.30	1
NAN-24	Treatment	3.24	1
NAN-25	Treatment	8.35	3
NAN-26	Treatment	4.25	3
NAN-27	Treatment	7.43	3
NAN-28	Treatment	5.01	3
NAN-29	Treatment	4.37	2
NAN-30	Treatment	5.72	2
NAN-31	Treatment	1.58	1
NAN-34	Treatment	5.61	3

NAN-35	Treatment	1.26	3
NAN-36	Treatment	5.63	3
NAN-37	Treatment	5.71	3
NAN-38	Treatment	7.03	2
NAN-39	Treatment	5.10	3
NAN-4	Treatment	1.39	3
NAN-40	Treatment	9.23	3
NAN-41	Treatment	14.67	3
NAN-42	Treatment	4.22	3
NAN-43	Treatment	2.22	3
NAN-44	Treatment	4.86	3
NAN-45	Treatment	1.02	3
NAN-46	Treatment	4.49	3
NAN-5	Treatment	2.83	3
NAN-6	Treatment	2.64	3
NAN-7	Treatment	8.77	3
NAN-8	Treatment	3.50	3

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