

The vacant planting: limited influence of habitat restoration on patch colonization patterns by arboreal marsupials in south-eastern Australia

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Keywords:	Vegetation restoration, lag effects, woody cover, marsupials, possums, temperate woodlands

The vacant planting: limited influence of habitat restoration on patch colonization patterns by arboreal marsupials in south-eastern Australia

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Running head: Mammal extinction and colonization

Abstract

Many key questions remain unresolved about how biodiversity responds to temporal increases in native vegetation cover resulting from extensive restoration efforts. We quantified occupancy and colonization probability of old growth, regrowth and planted woodland patches by arboreal marsupials within Australian agricultural landscapes subject to woodland restoration over an 11 year period. Our analyses focussed on the Common Brushtail Possum (*Trichosurus vulpecula*) and Common Ringtail Possum (*Pseudocheirus peregrinus*). We found strong evidence of a gradient in occupancy levels ranging from highest in old growth woodland, approaching zero in plantings, with regrowth woodland intermediate between these two broad types of vegetation structure. Plantings were not occupied by either species at the outset of our investigation and were rarely colonized throughout the subsequent 10 years. We hypothesize that a lack of shelter sites in large old hollow-bearing trees is one of the key factors limiting the occurrence of plantings by cavity-dependent arboreal marsupials, suggesting a lag between planting establishment and the time required for plantings to become suitable habitat. We found the probability of colonization was positively related to the amount of vegetation cover in the surrounding landscape. Unexpectedly, colonization probability was not influenced by a temporal increase in woody vegetation cover surrounding a patch. A paucity of relationships between patch colonization and the temporal change in vegetation cover may be explained by the fact that most of the increased vegetation cover in our study landscapes over the past decade has resulted from establishment of plantings which are generally not suitable nesting habitat for arboreal marsupials.

Our findings have key management implications such as emphasizing the value of old growth woodland for arboreal marsupials and of targeting restoration efforts around old growth and

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regrowth woodland patches, and the flawed notion of biodiversity offsets that allow replantings to compensate for clearing old growth woodland.

Keywords: Vegetation restoration, lag effects, woody cover, marsupials, possums, temperate woodlands

INTRODUCTION

Increases in human population coupled with higher levels of resource consumption (Tilman & Clark, 2014) are projected to double the demand for food from agricultural areas in the next 40 years (Foley, 2011; Godfray, Beddington, Crute *et al.*, 2010; Tilman, Balzer, Hill *et al.*, 2011). Yet, intensification of food production may threaten the ecological integrity of agricultural areas (Allan, Manning, Alt *et al.*, 2015; Lindenmayer, Cunningham & Young, 2012a), and accelerate biodiversity loss (Garnett, Appleby, Balmford *et al.*, 2013; Loos, Abson, Chappell *et al.*, 2014). Integration of agricultural production and other values such as biodiversity conservation therefore remains a key challenge worldwide (Carrasco, Larrosa, Milner-Gulland *et al.*, 2014; Phalan, Balmford, Green *et al.*, 2011).

Several, often inter-related, approaches have been employed in an attempt to integrate conservation and production in agricultural areas. One is to better protect and manage existing areas of remnant vegetation such as through improved land stewardship (e.g. via agri-environment schemes) (Michael, Wood, Crane *et al.*, 2014; Perkins, Maggs, Watson *et al.*, 2011). Indeed, considerable research effort has focused on documenting the biodiversity value of remnant native vegetation patches and overall levels of vegetation cover in agricultural landscapes (Haslem & Bennett, 2008; Mac Nally, Horrocks & Bennett, 2002). Another approach to enhancing biodiversity conservation in agricultural landscapes is to attempt to reverse the amount of habitat loss through restoration to increase native vegetation cover (Clewell & Aronson, 2007; Menz, Dixon & Hobbs, 2013; Suding, Higgs, Palmer *et al.*, 2015). A body of evidence is accumulating on the value for biodiversity of vegetation restoration in agricultural areas (reviewed by (Munro & Lindenmayer, 2011; Rey Benayas, Newton, Diaz *et al.*, 2009)). However, whilst much has been written about biodiversity response to losses of vegetation cover (e.g. Galetti, Guevara, Cortes *et al.*, 2013; Pimm, Jenkins, Abell *et al.*, 2014; Radford, Bennett & Cheers, 2005), a recent global meta-analysis

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3 (Crouzeilles, Curran, Ferreira *et al.*, 2016) has revealed the reverse – the response of biota to
4 spatial **increases** in vegetation cover over time – has received far less attention. This includes
5 temporal responses of biota to large scale revegetation efforts leading to spatio-temporal
6 changes in vegetation cover (Rey Benayas *et al.*, 2009). For example, in parts of south-
7 eastern Australia, restoration programs (coupled with natural regeneration) have led to a
8 significant increase in vegetation cover over the past decade (Geddes, Lunt, Smallbone *et al.*,
9 2011) but how biodiversity responds to these spatial changes in vegetation cover remains
10 poorly understood (e.g. Tschardtke, Tylianakis, Rand *et al.*, 2012). Indeed, there are few
11 available data to determine when planted woodland becomes suitable for various groups of
12 biota and individual species within these groups (Lindenmayer, Lane, Barton *et al.*, 2016b).

25 We sought to address several key knowledge gaps associated with the response of
26 biodiversity to the broad kinds of native vegetation cover and spatial increases in vegetation
27 cover using a large-scale (150 km (N-S) x 75 Km (E-W)), long-term (11 years) study of
28 arboreal marsupials in nationally endangered temperate woodland vegetation communities
29 (sensu Hobbs & Yates, 2000), located within agricultural landscapes in south-eastern
30 Australia. We focused on occupancy of different kinds of vegetation patches in the first year
31 of the study (2002), and temporal patterns of occupancy as reflected by the probability of
32 colonization and extinction in subsequent years. Our study region on the South West Slopes
33 of New South Wales has been the target of major restoration programs for the past 20-30
34 years. The amount of temperate woodland vegetation cover has increased by ~ 3.5% in some
35 landscapes, in part through programs of replanting as well as natural regeneration
36 (Cunningham, Lindenmayer, Crane *et al.*, 2014). Native vegetation in the region is therefore
37 now characterized by three broad structural types of patches: replanted woodland, natural
38 regrowth woodland, and old growth woodland. Given these characteristics of the vegetation
39 cover in our study region, we posed the following three questions:
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3 **Question 1. Are initial occupancy, colonization and extinction of patches influenced by**
4 **the broad structural vegetation type?** Earlier work on birds (Lindenmayer, Northrop-

5 Mackie, Montague-Drake *et al.*, 2012b) revealed inter-specific differences in occupancy
6 among structural vegetation types. At the outset of this investigation, we postulated similar
7 responses among arboreal marsupials as a result of differences in stand structure among
8 vegetation types (Ikin, Mortelliti, Stein *et al.*, 2015; Vesk, Nolan, Thomson *et al.*, 2008) that,
9 in turn, effect the suitability of such areas for nesting, foraging and other aspects of life
10 history. For example, within Australian temperate woodlands, gliding marsupials (*Petaurus*
11 spp) and the Common Brushtail Possum (*Trichosurus vulpecula*) are dependent on large old
12 hollow-bearing trees for nesting. By contrast, the Common Ringtail Possum (*Pseudocheirus*
13 *peregrinus*) is a facultative cavity user, nesting in both tree hollows and constructing stick
14 nests (termed dreys) in the understorey and crowns of overstorey canopy trees. On this basis,
15 at the outset of this investigation, we postulated that cavity-dependent arboreal marsupials
16 would be confined to old growth woodland where hollow-bearing trees are prevalent (Ikin *et*
17 *al.*, 2015), whereas the facultative Common Ringtail Possum would be found across a range
18 of woodland vegetation types.
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38 **Question 2. Are initial occupancy, colonization and extinction of patches influenced by**
39 **the amount of native vegetation cover in the surrounding landscape?** The majority of

40 species of arboreal marsupials are dependent on trees for shelter and food (Goldingay &
41 Jackson, 2004). Movement of these species also can limited by major breaks in tree cover
42 (van der Ree, Bennett & Gilmore, 2004). Therefore, at the outset of this study, we postulated
43 that occupancy, and colonization would be highest in patches surrounded by large amount of
44 surrounding native vegetation cover.
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54 **Question 3. Are colonization and extinction linked to temporal increases in the amount**
55 **of native vegetation cover in the landscape?** For similar reasons to those postulated for
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3 Question 2 above, we predicted that temporal increases in native vegetation cover would have
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5 positive temporal effects on patch colonization by arboreal marsupials and, correspondingly,
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7 lead to reduced rates of patch extinction over time.
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10 To address our three questions, we modelled the probability of patch colonization and
11
12 the probability of patch extinction as functions of the following variables: **(a)** patch type, **(b)**
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14 the amount of vegetation cover in the landscape surrounding patches, **(c)** numerical year, and
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16 **(d)** increase in tree cover since the beginning of the study.
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19 We suggest the results of this study are relevant to environments worldwide where
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21 major restoration activities are taking place (Clewell & Aronson, 2007; Crouzeilles *et al.*,
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23 2016; Menz *et al.*, 2013), with new knowledge indicating how to best design restoration
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25 programs, and frame and implement heavily funded agri-environment schemes (*sensu* Batary,
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27 Dicks, Kleijn *et al.*, 2015; Michael *et al.*, 2014).
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29 **METHODS**

30 **Study area**

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32 We focused our study on 203 long-term field sites located on 46 farms within the
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34 South-west Slopes region of New South Wales, south-eastern Australia (Fig. 1). This region
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36 was formerly dominated by temperate native woodland but has been cleared of an estimated
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38 85% of its original cover to facilitate livestock grazing and cereal cropping. As a result, the
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40 South-west Slopes region is now characterized by substantial environmental problems such
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42 as habitat fragmentation, land degradation, soil erosion, increased salinity and biodiversity
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44 loss, and many species of conservation concern inhabit an array of endangered woodland
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46 vegetation communities. In an attempt to tackle these problems, major planting programs
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48 have been established (Barrett, Freudenberger, Drew *et al.*, 2008; Cunningham,
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50 Lindenmayer, Crane *et al.*, 2008; Freudenberger & Harvey, 2004; Lindenmayer, Knight,
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52 Crane *et al.*, 2010).
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3 Our 203 field sites comprised 72 sites of old growth woodland, 65 restoration
4 plantings, and 66 areas of naturally regenerated woodland (hereafter termed regrowth). The
5 patches of old growth woodland in our study were dominated by large old scattered trees,
6 typically 200 or more years old and comprising the following tree species: white box
7 (*Eucalyptus albens*), yellow box (*E. melliodora*), Blakely's red gum (*E. blakelyi*), grey box
8 (*E. microcarpa*), red stringybark (*E. macrorhyncha*), mugga ironbark (*E. sideroxylon*) and
9 red box (*E. polyanthemos*). Other key attributes of old growth sites are summarized by
10 Montague-Drake, Lindenmayer & Cunningham (2009) and Ikin *et al.* (2015).
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21 The 65 planted native vegetation sites were characterized by a mix of local endemic
22 and exotic Australian ground cover, understorey and overstorey plant species. Most plants
23 were typically spaced 2 m apart, but there was not a standard set of spacing and plant species
24 composition protocols applied in revegetation efforts. The majority of plantings were 7–30
25 years old and were established to mitigate problems associated with soil erosion and/or
26 salinity or act as shelter belts for domestic livestock.
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34 The 66 patches of regrowth in our study were woodland recovering after disturbance
35 by fire, clearing or both, or regrowth established from seeds germinating after being dropped
36 by overstorey trees. As in the case of our plantings sites, the stands of regrowth we selected
37 exceeded 7–30 years old, although there was often a clear mix of trees of different ages,
38 including occasional scattered large old trees.
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45 **Field surveys**

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47 We surveyed each of our field sites for arboreal marsupials using a 50 W hand-held
48 spotlight and walking at an average speed of 3 km/h. Each site was a 200 m long transect
49 with one transect per site surveyed for 20 minutes. We surveyed sites in 2002, 2003, 2008,
50 2009 and 2011. We commenced spotlighting surveys 1 hour after dusk and terminated 4
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3 hours later to reduce observer fatigue and potential bias in detectability. Spotlighting was
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5 conducted in winter of each of the five survey years.
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7 **Key study species**

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9 Field surveys based on trapping and spotlighting over the past 20 years have revealed
10 there are four species of arboreal marsupials in the temperate woodland of the South West
11 Slopes of New South Wales (Lindenmayer, Michael, Crane *et al.*, 2016c). These species are
12 the Common Brushtail Possum, the Common Ringtail Possum, the Sugar Glider (*Petaurus*
13 *breviceps*) and the Squirrel Glider (*Petaurus norfolcensis*). The latter two species are
14 comparatively rare and this paper is focused on the Common Brushtail Possum and the
15 Common Ringtail Possum.
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25 The Common Brushtail Possum is large non-gliding phalangerid marsupial weighing
26 up to 3 kg. It has an omnivorous diet that includes foliage, flowers, fruit, and bird eggs and
27 nestlings. The breeding system of the species varies from monogamous to polygamous, with
28 overlapping ranges of male-female pairs or small groups of individuals. The Common
29 Brushtail Possum is dependent on cavities in large old trees for nesting and denning
30 (Goldingay & Jackson, 2004).
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38 The Common Ringtail Possum is a medium-sized non-gliding pseudocheirid
39 marsupial weighing up to 900 grams. The species' diet includes flowers, fruit, and the foliage
40 of a wide range of plants. The breeding system is thought to be polygamous, with animals
41 living in pairs or small groups. The Common Ringtail Possum uses hollows in trees for
42 nesting and denning but is also capable of building a nest comprised of sticks and leaves in
43 the understorey or overstorey canopy (Goldingay & Jackson, 2004; Lindenmayer,
44 MacGregor, Welsh *et al.*, 2008).
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54 **Covariates used in statistical modelling**

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3 We calculated values for four explanatory variables potentially influencing temporal
4 patterns of occupancy:
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7 **(1)** Patch type, categorised as old growth, regrowth or planting.
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10 **(2)** Amount of tree cover in the 78.5 ha circle (equivalent to a circle with a radius of 500 m)
11 around the centroid of each site (calculated for each survey year). We selected a 500 m circle
12 because it was broadly consistent with the movement patterns and home range size of groups
13 of individuals of the various species of arboreal marsupials in our study area. Our source data
14 were the time series grids of Forest Extent and Change (version 9), produced by the
15 Australian Government Department of Environment (National Carbon Accounting System,
16 [http://pandora.nla.gov.au/pan/102841/20090728-](http://pandora.nla.gov.au/pan/102841/20090728-0000/www.climatechange.gov.au/ncas/reports/tech09.html)
17 [0000/www.climatechange.gov.au/ncas/reports/tech09.html](http://pandora.nla.gov.au/pan/102841/20090728-0000/www.climatechange.gov.au/ncas/reports/tech09.html)). We used Landsat satellite
18 imagery to discriminate between forest and non-forest cover at a grid resolution of 25m.
19 Forest allocation to a grid cell occurred where there was cell occupancy of at least 20 % of
20 vegetation with potential to reach 2 m high, over a minimum area of 0.2 ha.
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24 **(3)** Increase in tree cover within the 78.5 ha circle since the beginning of the study in 2002,
25 using the above dataset. On average, the amount of native vegetation cover in the landscapes
26 in which our sites were located has increased by approximately 3-4% over the past 11 years.
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29 **(4)** Mean topographic wetness index (TWI), which is an indirect measure of productivity
30 reflecting the relative position of a site in the landscape, and thus potential water distribution
31 (Moore & Hutchinson, 1991). Calculation of TWI requires a Digital Elevation Model that has
32 hydrological integrity, and we used the ANUDEM 5.2 algorithm to generate a DEM of our
33 study region at a grid resolution of 20 m. For each cell, the size of the catchment that flows to
34 it was divided by its width, adjusted geometrically by the aspect of inflow direction. This
35 ‘specific catchment’ was then divided by the cell’s local slope. Lower values indicate ridges
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3 and upper slopes that have no, or small, contributing catchment, with values then increasing
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5 through lower slopes, valley flats, and drainage lines.
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8 As part of preliminary analyses conducted as a prelude to this study, we calculated
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10 values for other potential explanatory variables including patch shape, number of patch
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12 edges, mean edge length, mean patch size, number of patches, and patch size variation.
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14 However, each of these was highly correlated with total vegetation cover. We therefore
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16 elected to analyse data on total vegetation cover because it both explained the most variation
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18 in our data and is also a measure easily calculated and understood by land managers. In
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20 addition, it was not possible to fit stand age as a potential explanatory variable in the
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22 modelling because it was not possible to estimate the age of old growth woodlands or for
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24 regrowth woodland (due to the mixture of trees belonging to different age cohorts).
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27 **STATISTICAL MODELLING**

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29 We fitted multiple season occupancy models (McKenzie, Nichols & Hines, 2003) to
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31 account for imperfection in species detection, which is a major source of bias in studies of
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33 mammals (Mortelliti & Boitani, 2007). In addition to controlling for false absences, multiple
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35 season occupancy models allow the estimation of the turnover of local populations
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37 (colonization and extinction probability). We divided the spotlighting transect conducted at
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39 each of our 203 sites into two segments (0–100 m and 100–200m) and considered each
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41 segment as a visit to a site following the methods of (Mortelliti, Crane, Okada *et al.*, 2015).
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43 We assumed populations to be closed between visits occurring in the same year, but open to
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45 colonization/extinction between years.
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50 We adopted the following three-step protocol for fitting models (see also Mortelliti *et al.*,
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52 2015):

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54 STEP 1. We commenced our analyses by first modelling the probability of detection (p). We
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56 fitted three detectability models: categorical year (i.e. year specific variation), numerical year
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3 (i.e. implying a trend in detectability), and constant across years/sites (see Appendix 1). We
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5 selected the best relative model using the Akaike Information Criterion (AIC) (Burnham &
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7 Anderson, 2002). We retained the variable included in the top ranking detection model in all
8
9 the following steps.

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11 STEP 2. We selected the most important variables influencing the probability of a site being
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13 occupied in the first year of the study (Ψ_I). We modelled Ψ_I as a function of: **(a)** tree cover in
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15 the 78.5 ha circle around the centroid of each site, **(b)** patch type (regrowth, old growth or
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17 planting) and **(c)** TWI. We retained the variables included in the top ranking occupancy
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19 model in Step 3.

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21 STEP 3. We modelled the probability of colonization (γ) and the probability of extinction (ε)
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23 as functions of the following variables: **(a)** tree cover, **(b)** numerical year, **(c)** patch type, and
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25 **(d)** increase in tree cover since the beginning of the study.
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29 We acknowledge that planting age may be an important variable affecting the occurrence
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31 of animals in plantings (Selwood, Mac Nally & Thomson, 2008). However, we were unable
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33 to find a way to include an ‘age’ covariate for planting sites only (the value zero in the other
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35 patch types would not be meaningful).
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39 Following Burnham & Anderson (2002), we reported models within 2 Δ AIC. Model
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41 predictions were based on model averaging and goodness of fit was measured using
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43 Nagelkerke’s R^2 (Nagelkerke, 2004). Because of the nested structure of our design (i.e.
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45 multiple patches within the same farm), we checked for spatial autocorrelation (i.e. spatial
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47 dependence) in the residuals of the most parameterised model by using a spline correlogram
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49 (Zuur, Ieno, Walker *et al.*, 2009). We calculated correlograms for each of the five years and
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51 for the average values across years. However, we found no evidence of spatial
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53 autocorrelation for either of the target species. Occupancy models were fitted using the
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55 *unmarked* package for R (Fiske & Chandler, 2011).
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Results

We obtained sufficient data for the analyses of two species of arboreal marsupials, the Common Ringtail Possum (248 detections overall) and the Common Brushtail Possum (248 detections overall). Other species such as the Sugar Glider (7 detections overall) and the Squirrel Glider (24 detections overall) were too rare to enable detailed statistical analysis.

Question 1. Are initial occupancy, colonization and extinction of patches influenced by the broad structural vegetation type?

We found that the probability of a patch being occupied during the first survey (ψ) by both the Common Ringtail Possum and the Common Brushtail Possum was highest in old growth woodland and almost zero in plantings. Occupancy of regrowth patches was intermediate between plantings and old growth (Table 1, Figs. 2a and 3a).

Question 2. Are initial occupancy, colonization and extinction of patches influenced by the amount of native vegetation cover in the surrounding landscape?

Our analyses revealed that the amount of surrounding tree cover influenced the colonization probability (γ) of old growth and regrowth woodland patches by the Common Ringtail Possum and the Common Brushtail Possum (Table 1, Figs. 2b and 3b). That is, patches characterized by a large amount of surrounding tree cover had a greater chance of being colonized by the Common Ringtail Possum and the Common Brushtail Possum than patches with low amounts of surrounding tree cover. We tested for interactions between patch type and the amount of surrounding tree cover but found little support for this relationship.

Question 3. Are colonization and extinction linked to temporal increases in the amount of native vegetation cover in the landscape?

We found no evidence to indicate that the colonization probability of patches by the Common Ringtail Possum and the Common Brushtail Possum was affected by a temporal increase in tree cover surrounding patches (Table 1).

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3 Finally, we found no clear effects of the predictor variables on the probability of
4 extinction possibly due to lack of statistical power in estimating this parameter. In the case of
5 the Common Ringtail Possum, extinction was constant in the top ranked model but all other
6 variables were included within 2 Δ AIC, whereas in the case of the Common Brushtail
7 Possum, parameter estimates were considered unreliable (standard errors larger than the
8 parameter).

16 **DISCUSSION**

18 The success of attempts to restore degraded land is dependent on the colonization of
19 restored areas by target species (Barrett *et al.*, 2008; Catterall, Freeman, Kanowski *et al.*,
20 2012; Dobson, Bradshaw & M., 1997; Munro, Lindenmayer & Fischer, 2007; Reay &
21 Norton, 1999; Standish, Cramer, Wild *et al.*, 2007). However, medium- to long-term
22 effectiveness of restoration efforts is often not quantified (Barrett *et al.*, 2008; Crouzeilles *et*
23 *al.*, 2016; Hilderbrand, Watts & Randle, 2005; Mossman, Brown, Davy *et al.*, 2012). Given
24 this, we have sought to answer three key questions associated with patch occupancy and
25 patch colonization by arboreal marsupials in agricultural landscapes in south-eastern
26 Australia.

37 **Are initial occupancy, colonization and extinction of patches influenced by broad** 38 **structural vegetation type?**

39 We found strong empirical evidence of a gradient in occupancy levels from old growth,
40 regrowth and through to plantings (which remained largely unoccupied). In addition,
41 plantings were not occupied by arboreal marsupials at the outset of our investigation and
42 were rarely colonized throughout the 11 years of our investigation. There are marked
43 differences in the structure of the three different broad vegetation types examined in this
44 study (Ikin *et al.*, 2015) with key stand attributes such as the abundance of large old hollow-
45 bearing trees being rare or absent in plantings. Their paucity of such structures may explain
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3 the absence of the cavity-dependent Common Brushtail Possum from plantings. However, the
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5 Common Ringtail Possum is a facultative cavity user that is also capable of constructing its
6
7 own nests or dreys (Lindenmayer *et al.*, 2008). At the outset of this investigation, we
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9 anticipated that the species may build dreys in plantings as hollow-bearing trees were absent,
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11 but this did not occur. Dreys are readily observed both during the daytime and in night-time
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13 spotlighting but none were found in plantings or indeed in other vegetation types. Dreys
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15 provide only limited insulation and the Common Ringtail Possum is known to be heat-
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17 sensitive (Pahl, 1984). It is therefore possible that high summer temperatures in our study
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19 region may preclude the species from occurring in areas such as plantings where shelter sites
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21 within tree hollows are lacking.
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25 If access to hollow-bearing trees is a factor limiting the colonization of plantings by
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27 arboreal marsupials, it is possible that this problem might be rectified through the provision
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29 of artificial cavities such as nest boxes (Goldingay, Rueegger, Grimson *et al.*, 2015; Smith &
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31 Agnew, 2002; Smith, Hogan, Franks *et al.*, 2015). Indeed, recent work in restored woodlands
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33 has shown that suitably designed nest boxes are occupied by arboreal marsupials such as the
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35 Common Ringtail Possum and the Common Brushtail Possum (Lindenmayer, Crane,
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37 Blanchard *et al.*, 2016a). Moreover, comparisons between the results of the work reported
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39 here indicating that plantings are not colonized by arboreal marsupials and studies of
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41 plantings where nest boxes are occupied (Lindenmayer *et al.*, 2016a) do indeed suggest that a
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43 paucity of cavities is limiting the occupancy of plantings by these animals.
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47 **Are initial occupancy, colonization and extinction of patches influenced by the amount**
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49 **of native vegetation cover in the surrounding landscape?**
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52 We uncovered evidence of strong positive relationships between the probability of
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54 colonization of old growth and regrowth woodland patches and the amount of native
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56 vegetation cover in the surrounding landscape (Table 1, Figs. 2b and 3b). Such effects were
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1
2
3 not observed for plantings. Several factors may independently or in combination explain why
4
5 the amount of native vegetation had an important influence on patch colonization. For
6
7 example, large suitable areas of native vegetation surrounding a patch may support a larger
8
9 pool of dispersers readily able to colonize a given patch (Driscoll, Banks, Barton *et al.*,
10
11 2013). In addition or alternatively, larger areas of suitable native vegetation surrounding a
12
13 patch also may have an enhanced connectivity function, thereby facilitating patch
14
15 colonization. Third, larger areas of native vegetation may support larger amounts of suitable
16
17 food resources and, in turn, influence patterns of breeding success and ultimately long-term
18
19 patch occupancy – an affect that has been demonstrated for birds in Australian temperate
20
21 woodland landscapes (Zanette, Doyle & Tremont, 2000). Notably, recent studies of woodland
22
23 patch colonization in Radiata Pine plantation-dominated landscapes showed that the same
24
25 species of arboreal marsupials as analysed in the work reported here also responded
26
27 positively to the amount of native vegetation cover surrounding a patch (Mortelliti *et al.*,
28
29 2015). This suggests a commonality of mechanisms and responses in markedly different
30
31 landscape contexts (i.e. between the agro-ecological landscapes studied here and plantation-
32
33 dominated landscapes examined by Mortelliti *et al.* (2015)).
34
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38 **Are colonization and extinction patterns linked to temporal increases in the amount of**
39 **native vegetation cover in the landscape?**
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42
43 We found no evidence for positive (or negative) relationships between the
44
45 colonization of patches by arboreal marsupials and temporal increases in the amount of native
46
47 vegetation cover in the landscapes surrounding our study sites. The reasons for this result
48
49 remain unclear but they may be associated with the fact that much of the temporal increase in
50
51 vegetation cover in our study area has occurred through deliberate planting of woodland
52
53 vegetation, but such areas are currently of limited direct habitat value for arboreal marsupials
54
55 (Figs. 3a and 3b). In addition, earlier work (see Cunningham, Lindenmayer, Crane *et al.*,
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1
2
3 2007) showed that most replanting of woodland vegetation (and where the increase in
4
5 vegetation cover has been greatest) was on heavily cleared farms where much of the original
6
7 cover of old growth woodland was removed. Nevertheless, other analyses in our investigation
8
9 suggest that attempts to increase vegetation cover are not without value as colonization of old
10
11 growth and regrowth patches is significantly influenced by the amount of woody vegetation
12
13 cover in the surrounding landscape (Table 1).
14
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16 We acknowledge that our analyses were based on a post-hoc application of multiple
17
18 season occupancy models (McKenzie *et al.*, 2003); that is, the models were developed after
19
20 the beginning of our project so we could not adapt our established protocol. Consequently,
21
22 we had to use spatial replication instead of temporal replication to be able to generate
23
24 detection history data. This is not ideal and we acknowledge that temporal replication (i.e.
25
26 multiple visits of the same transect on different days) would have been preferable. Indeed, we
27
28 opted to employ this approach as the advantages of being able to take into account
29
30 uncertainty in species detection are higher than the disadvantages (Vojta, 2005).
31
32 Nevertheless, we believe that our approach is sound and sections of the transect were
33
34 relatively independent because: **(1)** The transect was likely to cross multiple home-ranges
35
36 (also supported by the fact that we often recorded multiple individuals within the transect).
37
38 **(2)** Multiple individuals within the section of the transect counted as a single detection. **(3)**
39
40 We recorded the position of each individual so it was extremely unlikely to record the same
41
42 individual on multiple occasions or in different sections of the transect. And, **(4)** We
43
44 emphasize that we have followed the same approach in other studies (e.g. Mortelliti *et al.*,
45
46 2015).
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51 **Management implications**

52 Our findings have at least four significant implications for vegetation management for
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54 the conservation of arboreal marsupials in Australian agricultural landscapes. First, in
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3 common with previous work on birds and reptiles (see Cunningham *et al.*, 2007;
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5 Lindenmayer *et al.*, 2012b; Michael, Cunningham & Lindenmayer, 2011; Michael *et al.*,
6
7 2014), we have found that old growth woodland, regrowth woodland and plantings have
8
9 different values as habitat for vertebrate biota and support different assemblages of species.
10
11 In this study of arboreal marsupials, we have found that plantings were rarely occupied over
12
13 the duration of our study. This suggests there may be significant time lags (*sensu* Vesk *et al.*,
14
15 2008) between when areas are first restored and when they might become suitable habitat for
16
17 arboreal marsupials. The plantings in our study were typically 20-30 years old and
18
19 considerably more time may be required for plantings to become suitable for arboreal
20
21 marsupials such as the Common Ringtail Possum and Common Brushtail Possum. Older
22
23 plantings were not available for monitoring in this study to determine when (or indeed if)
24
25 colonization by arboreal marsupials takes place.
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29
30 The time lag between planting establishment and colonization by arboreal marsupials
31
32 might be prolonged given that it can take a century (and sometimes much longer) for trees to
33
34 develop cavities suitable for occupancy by these animals (Gibbons & Lindenmayer, 2002;
35
36 Manning, Gibbons, Fischer *et al.*, 2013). It is possible that lags between when the time when
37
38 plantings are established and when they become suitable for arboreal marsupials may be
39
40 reduced by installing nest boxes (Lindenmayer *et al.*, 2016a). This might facilitate patch
41
42 colonization by species like the Common Brushtail Possum and the Common Ringtail
43
44 Possum which appear to be relatively common in the landscape (Lindenmayer *et al.*, 2016a).
45
46 However, nest boxes may not create suitable nesting resources for other, rarer and more
47
48 specialised arboreal marsupials such as the Squirrel Glider. These species only infrequently
49
50 (if ever) use nest boxes in our study region (Crane *et al.*, unpublished data).
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54 A second important implication of our work was that it has confirmed the importance
55
56 of old growth woodland for arboreal marsupials in agricultural landscapes. This conclusion
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2
3 was underscored by the differences in the probability of occupancy between the old growth
4
5 woodland and the other vegetation types. Our results further suggest that offsetting
6
7 approaches (Maron, Gordon, Possingham *et al.*, 2015) in which clearing of old growth
8
9 woodland on a farm is compensated for by establishing plantings elsewhere on a farm or
10
11 landscape may be highly problematic (Gibbons & Lindenmayer, 2007). Hence, we argue that
12
13 clearing of old growth vegetation should not occur in temperate woodland, especially as so
14
15 much clearing has already taken place in these environments (Lindenmayer, Bennett &
16
17 Hobbs, 2010) and replanted vegetation appears to remain unsuitable for prolonged periods of
18
19 time after establishment.
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23 Third, we found regrowth woodland was characterized by levels of patch occupancy
24
25 that were significantly greater than plantings. This underscores the fact that regrowth has
26
27 habitat value for arboreal marsupials and therefore should not be subject to widespread
28
29 clearing. This is in marked contrast to communications by peak farm lobby groups seeking to
30
31 relax vegetation clearing legislation (Victorian Farmers Federation, 2011).
32
33

34 Fourth, we found that landscapes with high levels of vegetation cover are important
35
36 for arboreal marsupials, particularly when that cover includes patches of old growth
37
38 woodland. This was highlighted by our results showing the probability of patch colonization
39
40 was greatest in patches surrounded by large amounts of native vegetation cover. We therefore
41
42 suggest that efforts to increase vegetation cover might be best focussed around existing areas
43
44 of old growth and natural regrowth woodland which have significantly higher levels of patch
45
46 occupancy than plantings.
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48

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Table 1. Top ranked occupancy models. Model ranking according to ΔAIC (delta Akaike Information Criterion); only models <2 are shown. Ψ = probability of a site being occupied during the first survey, Y =probability of colonization; ϵ =probability of extinction, p =detection probability; PT= patch type (plantings, vs regrowth vs old growth); TC=tree cover in the 78.5 ha circle, ITC= increase in tree cover since 2002, TWI= mean topographic wetness index (site productivity); Y=year (categorical covariate); R^2 = Nagelkerke's coefficient of determination; (.)= constant model (no covariate).

Species	Scientific name	Model	ΔAIC	R^2
Common Ringtail	<i>Pseudocheirus</i>	$\Psi(PT)Y(TC+PT)\epsilon(.)p(Y)$	0.000	0.258
Possum	<i>peregrinus</i>	$\Psi(PT)Y(TC+PT)\epsilon(ITC)p(Y)$	0.245	0.265
		$\Psi(PT)Y(TC+PT)\epsilon(TC)p(Y)$	1.027	0.262
		$\Psi(PT)Y(TC+PT)\epsilon(TWI)p(Y)$	1.566	0.260
		$\Psi(PT)Y(TC*PT)\epsilon(.)p(Y)$	1.869	0.266
Common Brushtail	<i>Trichosurus</i>	$\Psi(PT)Y(TC)\epsilon(.)p(.)$	0.000	0.253
Possum	<i>vulpecula</i>			

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3 **Figure 1.** The South-west Slopes study region of southern New South Wales, south-eastern
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5 Australia. The circles correspond to farms where old growth, regrowth or planted sites are
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7 located.
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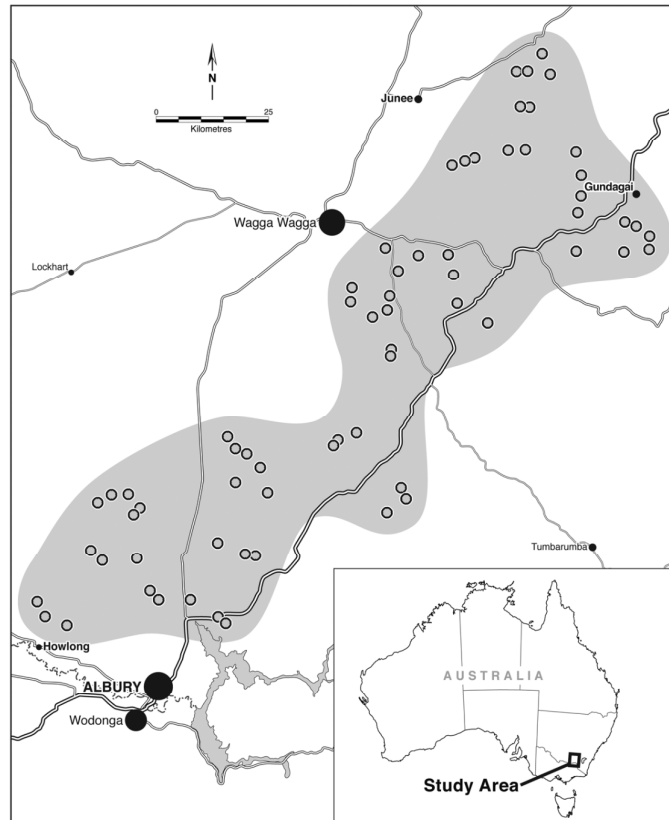
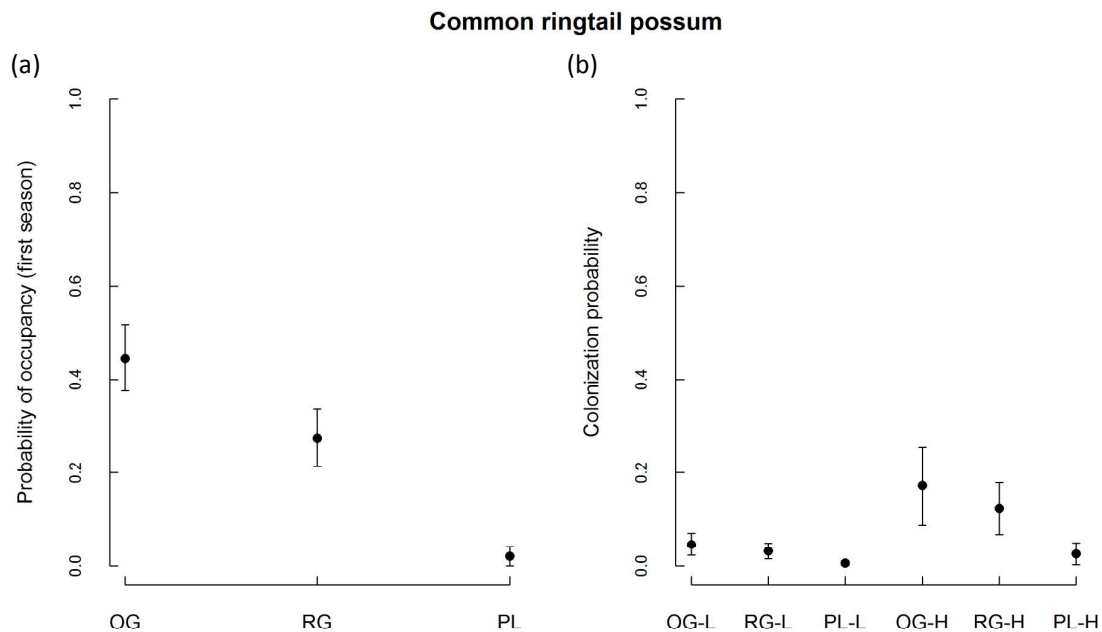
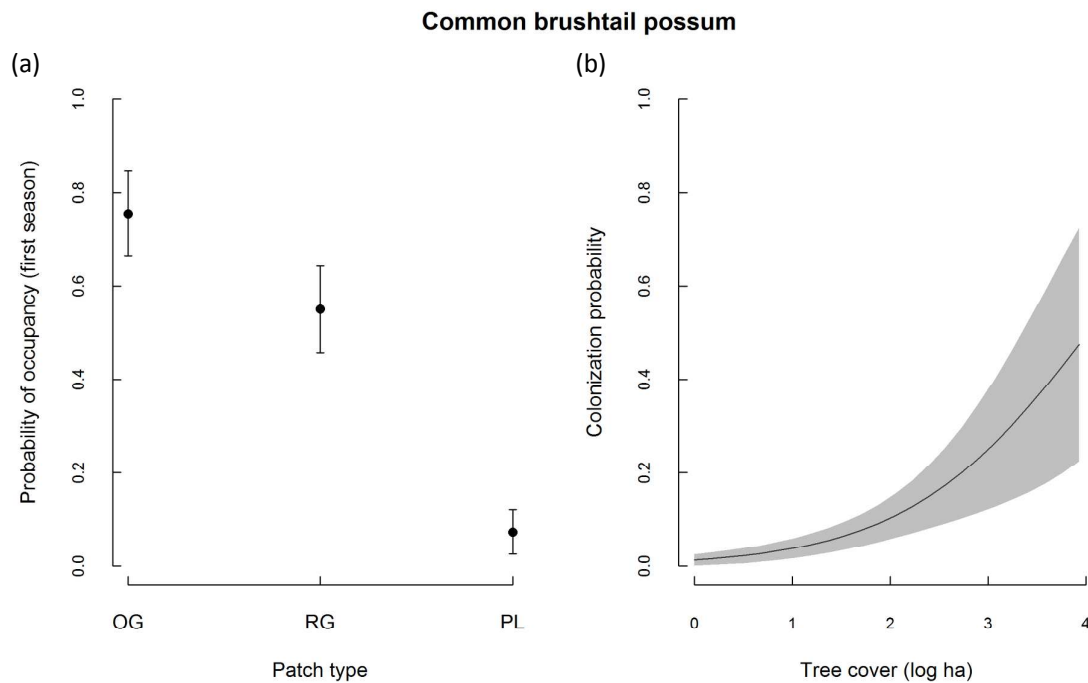


Figure 2. Probability of a site being occupied during the first sampling season (Ψ) and colonization probability (including SE) based on model averaged estimates of top ranking models ($\Delta AIC < 2$) for the Common Ringtail Possum. In the case of the colonization probability, we made predictions using the 1st and 3rd quartile of tree cover in the surrounding landscape to provide an overview of how predictions varied as function of both patch type and tree cover. Predictions with 1st quartile are labelled as L (low) whereas predictions with 3rd quartile are labelled as H (high). OG=old growth, RG=regrowth, PL= plantings.



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3 **Figure 3.** Probability of a site being occupied during the first sampling season (Ψ) and
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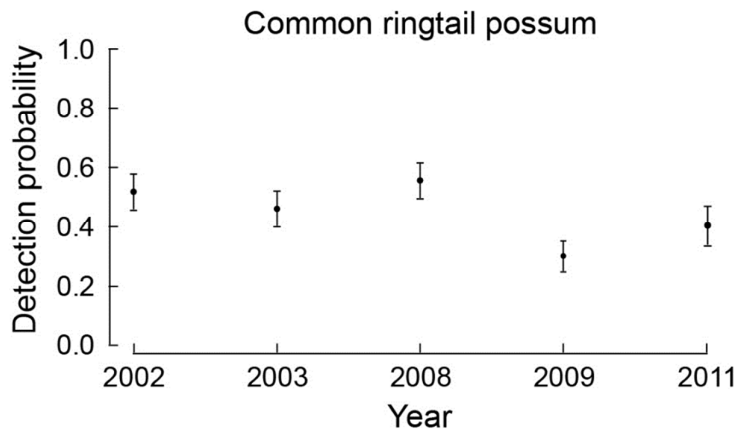
APPENDICES

Appendix 1. Images of spotlighting, the Common Brushtail Possum and dense planting (Photo credits D Michael, L O'Loughlin and D Blair)



Appendix 2. Detection probability analysis.

Fig. S1. We found that the detection probability for the Common Ringtail Possum varied each year. By contrast, the detection probability of the Common Brushtail Possum was constant (data not shown).



Appendix 3. Number of hollow-bearing trees in 3 major broad vegetation types

Year	Regrowth	Old growth	Planting
2002	12.75 ± 1.33	24.19 ± 2.12	0.33 ± 0.19
2008	8.39 ± 1.21	17.80 ± 2.04	1.70 ± 0.86

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Remnant native vegetation cover in Australian temperate agricultural landscapes includes old growth woodland, regrowth woodland, and planted (restored) woodland. We quantified occupancy and colonization probability of these kinds of woodland by arboreal marsupials over an 11 year period. Occupancy levels were highest in old growth, approached zero in plantings, with regrowth intermediate between these two vegetation types. Plantings were not occupied at the outset of our investigation and only rarely colonized throughout the subsequent 10 years, most probably as a result of a lack of shelter sites in large old hollow-bearing trees. The probability of colonization was positively related to the amount of vegetation cover in the landscape surrounding a patch but not influenced by a temporal increase in woody vegetation cover. Our findings emphasize the value of old growth woodland for arboreal marsupials and suggest that restoration efforts be targeted around old growth and regrowth woodland patches. Image:

Common Brushtail Possum (Photo by D. Blair)

91x62mm (300 x 300 DPI)