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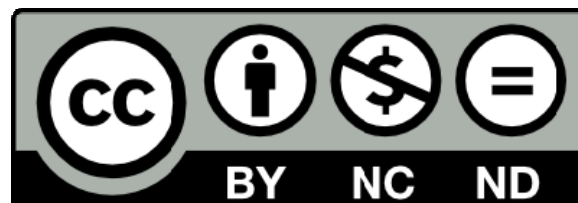
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# Habitat features act as unidirectional and dynamic filters to bat use of production landscapes

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## Abstract

Conserving global biodiversity requires careful management of production landscapes, especially in this era of rapid environmental change. The habitat filtering framework has been used for predicting species responses to land-use changes. Habitat filters are essentially features that may slow, or limit, species use of certain habitats. We wanted to determine if this framework could identify habitat and landscape filters that predicted bat use of restored forest at the species-specific and trait group levels. We surveyed bat activity, vegetation structure, and landscape characteristics at 64 sites over two years in restored northern jarrah (*Eucalyptus marginata*) forests of south-western Australia. Filters to use of restored forest were present for all bats, other than the open space group. We detected dynamic filters to use of restored forest by the open space edge group and unidirectional filters for the closed space edge and closed space groups. Filters to bat use of restored forests were species-specific and related to habitat, rather than landscape, features. In landscapes with relatively low patch-matrix contrast, such as the northern jarrah forest, management actions to reduce filters should focus on habitat features. To

manage for the persistence of specific species within restored forest patches, tree density and midstory cover should aim to be at, or close to, reference forest levels.

**Keywords:** Bat activity; Matrix permeability; Restored forest; Vegetation clutter; Revegetation; South-western Australia

## 1. Introduction

Land-use change is a key driver of the global biodiversity crisis (e.g., Foley et al., 2005), ever increasing the importance of conserving biodiversity in production landscapes. The concept of habitat filtering has been used as a framework for predicting species responses to land-use changes (e.g., Hanspach *et al.*, 2012; Pereira *et al.*, 2004) and thus, can help inform efforts to conserve biodiversity in production landscapes. Conceptually, a habitat filter is a habitat feature whose presence, or absence, renders habitat unsuitable for a species. In essence, filtering identifies habitat features that slow, or limit, species use of certain habitats (Poff, 1997). Filters can be unidirectional, decreasing in magnitude over time, or dynamic, fluctuating in magnitude over time (Craig et al., 2012). In young regrowth forest, number of tree hollows are an example of a unidirectional filter as they are initially absent, which may render habitat unsuitable for hollow dependent species (Goldingay, 2009). However, as hollows form over time (Vesk et al., 2008) the magnitude of this filter decreases. In contrast, tree density may be a dynamic filter whose influence varies over relatively short time frames. In restored northern jarrah (*Eucalyptus marginata*) forests, the abundance of the skink *Morethia obscura* was inversely proportional to overstory (> 3 m) stem densities with both skink abundance and stem density changing over relatively short time frames (Craig et al., 2012).

As restoration is being increasingly used to conserve biodiversity in production landscapes (Suding, 2011), we wanted to determine if the habitat filtering framework could predict use of restored forest by bats, a highly mobile taxa, in a restored landscape. The habitat filter framework is widely applied in restoration ecology for flora (e.g., Wallem et al., 2010), but only two studies have specifically examined habitat filters for fauna in restored areas (Craig *et al.*, 2012; Summerville *et al.*, 2006. Both

studies were restricted to low mobility taxa yet high mobility taxa, such as bats, potentially respond rapidly to filters, as bats can avoid unfavourable habitats, and as such may be susceptible to both habitat and landscape filters (Bender *et al.*, 2015; Chambers *et al.*, 2016; Kalda *et al.*, 2015). Studies have examined filters to bat habitat use in variegated and fragmented landscapes (e.g., Boughey *et al.*, 2011; Farneda *et al.*, 2015; Hanspach *et al.*, 2012; Kalda *et al.*, 2015), but not in restored landscapes. Hence it is unknown whether species in restored landscapes respond to the same filters as species in other landscapes, especially as the relative influence of habitat and landscape filters is likely to differ between landscapes (e.g., Bender *et al.*, 2015). While restored landscapes can also be fragmented, the contrast between restored forest patch and remnant forest matrix is typically less marked than in partially cleared landscapes. This suggests that the relative importance of landscape filters, such as edge and patch density (e.g., Chambers *et al.*, 2016), may be reduced in restored landscapes.

Insectivorous bats possess particular traits (e.g. wing morphology and echolocation call frequency) which influence manoeuvrability, foraging and microhabitat use (Norberg and Rayner, 1987). Bat functional trait groups are typically used to identify filters and predict bat habitat use across a variety of landscapes (Blakey *et al.*, 2016; Hanspach *et al.*, 2012; Müller *et al.*, 2013; Silvis *et al.*, 2016). Large, less manoeuvrable bats tend to have low frequency echolocation calls that allow prey detection at greater distances in open environments (Schnitzler and Kalko, 2001) and are adapted for open space environments, such as forest clearings or above the canopy (Adams *et al.*, 2009; Müller *et al.*, 2013). In contrast, small, more manoeuvrable bats tend to have high frequency echolocation calls that allow prey capture in close, densely vegetated environments (Schnitzler and Kalko, 2001), although most edge space and some closed space adapted species show preference for less densely vegetated environments (e.g., Blakey *et al.*, 2016; Hanspach *et al.*, 2012; Müller *et al.*, 2013). We would expect bats to differentially use restored forest depending on restoration age, as vegetation structure and density changes with age (e.g., Craig *et al.*, 2012), however, whether use of restored forests is consistent among species within a trait group is poorly understood. It is also unclear whether filters for bats in trait groups are consistent between restored landscapes and other fragmented landscapes with differing levels of patch-matrix contrast.

Our study area was a production landscape in the northern jarrah forest of south-western Australia that had been restored post-mining (Fig. 1). Alcoa of Australia (hereafter ‘Alcoa’) clears, mines and restores ~ 600 ha of jarrah forest annually with the aim of restoring a self-sustaining jarrah forest ecosystem (Koch, 2007a). Alcoa has mined bauxite in the northern jarrah forest for > 40 years and, due to the spatial distribution of bauxite, the study area (~ 15,000 ha) is a mosaic of restored forest patches within an unmined forest matrix. Similar to restored forest elsewhere (e.g., Cristescu et al., 2012) faunal community composition within restored forest rarely converges on unmined forest communities (Craig *et al.*, 2015; Craig *et al.*, 2012). The jarrah forest supports nine bat species, all insectivorous (Webala et al., 2011). Our aims were to: (i) determine if unidirectional or dynamic filters to bat use of restored forest were present; (ii) if present, determine the relative importance of habitat and landscape filters; (iii) identify the filters; and (iv) determine if individual species responses were generalizable to trait groups. We predicted that habitat, rather than landscape, features would act as filters to bat use of restored forest due to the low contrast between restored and unmined forest. We also predicted that members of trait groups would respond to the same filters and that these filters would be the same as in landscapes with greater patch-matrix contrast. Specifically, we predicted dynamic filters for open space (OS) and open space edge (OSE) trait species with higher activity in newly restored forest, akin to clearings, and unmined forest, with natural openings, than densely vegetated older restored forests. Conversely, we predicted unidirectional filters for edge space (ES) and closed space (CS) trait species with low activity in young restored forest but increasing activity with the increasing vegetation density of maturing restored and unmined forest.

## **2. Material and methods**

### **2.1. Study area and experimental design**

We surveyed bats at Alcoa's Huntly minesite (32°36'S, 116°07'E), located ~ 90 km SSE of Perth, Western Australia. The region has a Mediterranean climate with cool, wet winters and hot, dry summers with annual rainfall from 1990 to 2012 averaging 1180 mm. The first year of the study

(2010) was exceptionally dry and received half the average rainfall (630 mm) while the second year (2011) received average rainfall (1205 mm). Both forest types have an overstory dominated by two eucalypt species, jarrah and marri (*Corymbia calophylla*). Restored forests have similar plant species compositions to unmined jarrah forest, although dryland rush and sedge species are less common (Koch, 2007b).

We surveyed bats in five forest types: four restored forest age classes representing different stages of vegetation succession within restored forest (0–4, 5–9, 10–14 and > 15 years; Norman et al., 2006) and unmined forest. Alcoa monitors mine-pits nine months post-restoration and categorizes them as desirable or dense based on eucalypt stem densities (500–2500 and > 2500 stems ha<sup>-1</sup>, respectively; Grant, 2006). To capture tree density variation we selected sites with both dense and desirable densities in all restored forest ages (restored forest < 5 years old only had desirable densities). Eight sites were selected in each of eight treatments (desirable 0–4, desirable 5–9, dense 5–9, desirable 10–14, dense 10–14, desirable > 15, dense > 15 and unmined forest) for a total of 64 sites. However, we found no differences in eucalypt stem densities between desirable and dense treatments of similar age: (5–9,  $t_{14} = -1.40$ ,  $p = 0.184$ ; 10–14,  $t_{14} = -0.35$ ,  $p = 0.786$  and > 15,  $t_{14} = -0.84$ ,  $p = 0.416$ ) so we pooled desirable and dense restored sites of the same age into a single age class. Sites were all > 4 ha size, with at least one edge bordered by unmined forest. Bat detectors were > 500 m apart and were > 80 m from other ages of restored or unmined forest.

## **2.2. Bat surveys**

Bat surveys were conducted four times at each of the 64 sites between October and March in both 2010/2011 and 2011/2012 for a total of 512 survey nights. Each site was surveyed using ultrasonic detectors (Anabat, Titley Electronics), to record bat echolocation calls, and were set to record from 30 min before sunset until 30 min after sunrise. We deployed eight detectors each survey night to simultaneously survey each forest type/density treatment and evenly distribute any potential bias. All sites were surveyed once before being re-surveyed and we did not survey on nights with rain or high winds. Detectors were placed 1.5 m above the ground and angled at 45°, facing a vegetation gap to minimise call attenuation (Patriquin et al., 2003), and oriented towards the closest unmined forest

edge. All work was conducted under Murdoch University Animal Ethics Committee (W2347/10) and Department of Parks and Wildlife (CE002999, CE003726, SF007648 and SF008894) permits.

### **2.3. Vegetation surveys**

Vegetation structure was assessed at each site each field year, between April and July 2011 and 2012, following bat surveys. Vegetation surveys consisted of sampling vegetation characteristics in five  $5 \times 5$  m quadrats at each site, one at detector locations and four 30 m from detector locations in each cardinal direction. We initially considered vegetation in each quadrat as belonging to four strata: canopy ( $> 15$  m), midstory (5 to 15 m), shrub (0.75 to 5 m) and ground ( $< 0.75$  m). We measured maximum strata height, using a tape measure for ground and shrub strata and a tree vertex for the midstory and canopy strata, the latter calculated as the average height of the five tallest plants (even when  $< 15$  m tall)  $< 10$  m from the centre of all quadrats. We visually estimated percent midstory, shrub, ground, log (coarse woody debris  $> 5$  cm diameter at largest end) and litter cover in each quadrat. We took digital photographs at the four corners of quadrats, with a camera pointed vertically upwards 1.5 m above the ground, and used gap fraction analysis (Macfarlane et al., 2007) to calculate canopy cover, although this often included cover in the midstory stratum and occasionally the shrub stratum as well. Tree (plant  $> 5$  m in height) density was measured only in the second year of bat surveys by measuring the distance from detector locations, and points 10, 20 and 30 m from detector locations in each cardinal direction, to the nearest trees and calculating densities using the formula  $(10,000 / 2 * x^2)$  where  $x$  is the average of the nearest tree distances).

### **2.4. Landscape variables**

To investigate potential landscape filters we used GIS (Esri ArcMap v10.1, USA) to derive eight variables. For patch complexity we divided the restored forest patch edge length by the patch area. As unmined forest was the matrix habitat and, hence, did not have a patch size, we considered unmined forest sites as circular patches with a 250 m radius resulting in all unmined forest sites having a patch complexity of 0.008. Slope (ordinal variable with four levels:  $0-3^\circ$ ,  $3-6^\circ$ ,  $6-9^\circ$  and  $9-12^\circ$ ), distance to nearest stream, and distance to nearest restored/unmined forest edge were derived directly from

available GIS layers. We divided the actual by the theoretical maximum amount of unmined forest within four radii (250, 500, 1000 and 1500 m) from detector locations at each site to determine the proportion of unmined forest within each radii.

## 2.5. Data analysis

Prior to analysis we excluded four bat surveys when detectors failed, leaving 508 surveys. We quantified bat activity as numbers of bat call files per night; call files contained a group of echolocation pulses recorded within 15 s, which we assumed belonged to one individual bat (O'Farrell et al., 1999). Bat call files were downloaded using CFCRead software (C. Corben/Titley Electronics) and processed using Anlook version 3.8 (C. Corben; <http://hoarybat.com>). All call files were filtered to remove extraneous noise and extract echolocation call parameters for subsequent identification. Three *Nyctophilus* species (*N. geoffroyi*, *N. gouldi*, *N. major*) in the study region have calls that are indistinguishable when recorded using Anabat detectors (Adams et al., 2010) and calls from these species were pooled as *Nyctophilus* spp. Bat calls were automatically identified to species, or species group, using a random forest model within the R caret package (Kuhn, 2008). See Burgar (2014) for details of the automation process.

To determine jarrah forest bat species trait groups we first plotted aspect ratio and characteristic echolocation call frequency values for 26 other Australian and European bat species, grouping species by guilds defined in the literature (Adams et al., 2009; Blakey et al., 2016; Müller et al., 2013), and then plotted the same values for jarrah forest bat species to determine their placement in these trait groups (Fig. A.1). Because of discrepancies in nomenclature between studies and overlap between edge and closed space species we also ran a principal component analysis (PCA; Fig. A.2) on four traits (aspect ratio, characteristic frequency, characteristic slope, and forearm length) for the jarrah forest bat species to tease apart the groupings (Table A.1). *Austronomus australis* sat well apart from all other species and has been categorized as both above canopy (Adams et al., 2009) and open space (Blakey et al., 2016). We followed Fullard et al. (1991) and placed *A. australis* in the open space (OS) trait group. *Chalinolobus gouldli*, *Falsistrellus mackenziei*, and *Mormopterus kitcheneri* fell between open space and closed space edge so we categorized them as open space edge (OSE) to reflect this.



The closed space edge (CSE) group comprised *C. morio* and *Vespadelus regulus* while the three *Nyctophilus* species comprised the closed space (CS) group.

## **2.6. Statistical analysis**

Prior to running analyses we excluded highly correlated variables by checking variance inflation factors (VIFs). For vegetation variables, we excluded litter cover (correlated with canopy cover; Fig. A.3). Canopy cover had a VIF greater than the recommended value of three (4.6; Zuur et al., 2009), but we retained this variable as we felt it might be an important habitat filter. For landscape variables, we excluded the proportion of unmined forest within 250 m (correlated with distance to unmined forest and the proportion of unmined forest within 500 m) and 1000 m (correlated with the proportion of unmined forest within 1500 m; Fig. A.4). We retained 13 variables: canopy, midstory, shrub, ground and log cover, canopy height, tree density, shape complexity, slope, distance to stream, distance to unmined forest and proportion of unmined forest within 500 and 1500 m.

We took a model-based approach to test effects of field year and forest type on vegetation structure, using the function `manyglm` in the R package `mvabund` (Wang et al., 2012). This approach uses a multivariate generalized linear model (GLM) to make inferences by fitting separate GLMs to each variable, with a common set of explanatory variables, and testing significance through resampling-based hypothesis testing (Wang et al., 2012). We ran negative binomial GLMs with a two-dimensional matrix of vegetation structure variables as the response variable and both field year, forest type, and their interaction as explanatory variables. Reference categories were the first field year and unmined forest, respectively. *p*-Values were calculated using 999 resampling iterations via PIT trap resampling. To determine whether landscape characteristics differed between forest types we used the same approach as above, but with only forest type as the explanatory variable and unmined forest as the reference category.

## **2.7. Filters to bat use of restored Forest**

To determine the presence of habitat or landscape filters we ran negative binomial generalized linear mixed models (GLMMs) with bat activity for individual species/species grouping as the response

variable, field year, forest type, and their interaction as fixed factors and site as a random factor, to account for spatial autocorrelation. We considered a dynamic filter present for a species/species grouping when activity levels differed between years of the same restored forest type or when there was lower activity levels in older, but not younger, restored forest compared to unmined forest. We considered a unidirectional filter as one when activity levels were lower in either all or younger, but not older, restored forest compared to unmined forest. GLMMs were run using the R package `glmmADMB` (Fournier et al., 2012) and used Laplace likelihood approximations and type III sum of squares.

Once we determined the presence of a filter, we identified potential species-specific habitat or landscape filters to bat use of restored forest by modelling bat activity against vegetation and landscape variables for restored sites. Employing an information-theoretic approach to model selection (Burnham and Anderson, 2002) we constructed 22 separate models: a null (intercept only) model, a full model with all variables (including original and quadratic forms for all vegetation variables, to test linear and quadratic relationships, respectively), two models for each vegetation variable (its original form and both original and quadratic forms) and one model each for the six landscape variables (their original form). We ran negative binomial GLMMs for each species/species group with bat activity as response variables, habitat features and landscape characteristics as explanatory variables and both site and survey period as random factors. Due to small sample sizes we could not run models for *F. mackenziei*. Models were ranked based on Akaike's information criterion (AIC) scores and AIC weights using the R package `MuMIn` (Barton, 2014). We considered models with the highest AIC weights as the most plausible model(s) describing filters to bat use of restored forest, calculating parameter estimates using model averaging (Burnham and Anderson, 2002). We conducted deviance tests to assess the goodness of fit of each most plausible model and calculated evidence ratios (ER; Anderson, 2008) to weigh support for each variable as filters to bat use of restored forest. Evidence ratios are summed AIC weights of models including that variable divided by summed AIC weights of models not including that variable. All statistical analyses were performed in R (R Core Team, 2013).

### 3. Results

We recorded 31,347 bat call files over both field years of which 22,520 were identified to species/species group. More call files were recorded in the second field year than the first (13,821 vs 8699; Table A.2). *V. regulus* was detected most frequently (15,833 call files) and *F. mackenziei* least frequently (167 call files).

#### 3.1. Vegetation structure and landscape features

Vegetation structure was highly variable across forest types (Fig. A.5; Table A.2). Overall vegetation structure differed significantly between unmined forest and each restored forest age (all  $p = 0.001$ ) but not between field years ( $p = 0.574$ ). There was a significant interaction between forest type and year for restored forest < 10 years ( $R < 5$  – unmined  $p = 0.001$ ;  $R$  5–9 – unmined  $p = 0.015$ ) but not for restored forest  $\geq 10$  years ( $R$  10–14 – unmined  $p = 0.079$ ; unmined –  $R > 15$   $p = 0.363$ ). Analyses of individual variables revealed log cover and canopy height were predominantly driving these differences while remaining variables were similar between restored and unmined forest for some restored forest ages, but not others (Fig. A.5; Table A.2). There was significantly more canopy ( $p = 0.010$ ), midstory ( $p = 0.003$ ) and log cover ( $p = 0.021$ ) in < 5 year old restored forest during the second, compared to first, field year. Log cover was also greater, albeit marginally so, in 5–9 year old restored forest during the second, compared to the first, field year ( $p = 0.042$ ). As restored forest aged, vegetation structure became more similar to unmined forest. Five of six vegetation structure variables differed between < 5 year old restored and unmined forest ( $p \leq 0.017$ ) with one less variable with each increasing restored forest age category ( $R$  5–9 – unmined, four variables  $p \leq 0.007$ ;  $R$  10–14 – unmined, three variables  $p = 0.001$ ,  $R > 15$  – unmined, two variables  $p = 0.001$ ). Landscape characteristics were similar across restored forest types (Fig. A.6). Overall landscape differed significantly between unmined forest and each restored forest age (Table A.3;  $R$  0–4  $p = 0.005$ ,  $R$  5–9  $p = 0.029$ ;  $R$  10–14 and  $R > 15$   $p < 0.001$ ). Differences between restored and unmined forest were driven by the proportion of unmined forest surrounding sites, particularly at the 500 m scale (all  $p < 0.014$ ).

### 3.2. Detecting filters

Bat activity was highly variable within and between forest types and years, ranging from  $< 1$  to  $> 70$  calls per night depending on species and forest type (Fig. 2; Table A.1). Bat activity levels were higher in the second, compared to first, field year, for *A. australis*, *C. gouldii* (both  $p < 0.001$ ), and *Nyctophilus* spp. ( $p = 0.014$ ).

We did not detect any filters for *A. australis* (OS) while dynamic filters were detected for the three OSE bats (Table A.4). Compared to unmined forest, *A. australis* had significantly higher activity levels in  $< 5$  and 5–9 year old restored forest ( $p = 0.001$  and 0.022, respectively), but not  $\geq 10$  year old restored forest, in the first field year, and no difference in activity levels between any forest type in the second field year. Activity levels for OSE bats suggested that filters developed as restored forest aged, with similar activity levels between young restored forest and unmined forest but significantly lower activity levels in older restored forest (*F. mackenziei*: R 10–14,  $p = 0.020$ , R  $> 15$ ,  $p = 0.035$ , and *M. kitcheneri*: R  $> 15$ ,  $p = 0.010$ ). For *C. gouldii* the magnitude of this dynamic filter changed between field years; the significant interaction between 5 and 14 year old restored forest and field year suggested a filter to *C. gouldii* use of this restored forest age in the second field year (R 5–9,  $p = 0.015$  and R 10–14,  $p = 0.002$ ), but not the first.

For ES and CS bats we detected unidirectional filters (Table A.4). All species had significantly lower activity levels in  $< 5$  year old restored forest, compared to unmined forest (*C. morio*  $p = 0.020$ , *V. regulus* and *Nyctophilus* spp.  $p < 0.001$ ). Although the filter was only present for *C. morio* in  $< 5$  year old restored forest, *V. regulus* and *Nyctophilus* spp. activity levels were consistently lower in restored forest, compared to unmined forest (all  $p \leq 0.024$ ). The magnitude of the filter in older ( $> 15$  year old) restored forest depended on the year for *V. regulus* with similar activity levels in older restored forest and unmined forest during the second field year.

### 3.3. Identifying filters

We identified one most plausible model to describe bat use of restored forest for *M. kitcheneri*, *C. morio* and *C. gouldii* and two most plausible models (original and quadratic

forms of the same variable) for *A. australis* and *Nyctophilus* spp. (Table A.5). For *V. regulus* no model was significantly better at explaining activity than the null model (Table A.6). Tree density, canopy height, and midstory cover were the best predictors of bat activity in restored forest for all species/species group where most plausible models were identified. There was no evidence to support landscape variables as important to bat use of restored forest; all landscape variables modelled had AICc weights and relative importance values  $< 0.01$  (*A. australis*, *C. gouldii* and *M. kitcheneri*) or  $< 0.1$  (*C. morio*, *V. regulus* and *Nyctophilus* spp.).

For *A. australis*, tree density was the best predictor of bat activity in restored forest (Table A.6), displaying a negative curvilinear relationship with highest activity levels at low tree densities ( Fig. 3). The best predictor for OSE activity in restored forest was tree density for *C. gouldii* and canopy height for *M. kitcheneri* (Table A.6), in both cases the relationship was negatively linear ( Fig. 3). Midstory cover was the best predictor of *C. morio* activity (Table A.6), with activity levels increasing with cover until cover reached  $\sim 15\%$  and then decreasing (Fig. 3), however there was only weak support for this habitat feature as a filter ( $ER < 1.0$ ; Table 1). In contrast, there was strong support ( $ER = 15.33$ ) for midstory cover predicting *Nyctophilus* spp. activity in restored forest, with peak activity at  $\sim 15\text{--}30\%$  cover (Fig. 3; Table 1).

## 4. Discussion

### 4.1. Presence of filters

All jarrah forest bat species/species groups were recorded in all ages of restored and unmined forest. Similar to other fauna studies (Craig *et al.*, 2012; Summerville *et al.*, 2006) we detected filters to faunal use of restored forest at the local scale for all but *A. australis*. This OS bat preferred  $< 10$  year old restored forest compared to unmined forest but there was no difference in activity levels between older restored and unmined forest, suggesting that young restored forest may be more suitable to navigating and foraging *A. australis* than unmined forest. Our results supported our predictions for the presence of dynamic filters to bat use of restored forest for large, less manoeuvrable species and

unidirectional filters to use of restored forest for small, more manoeuvrable species. The three species of OSE bats had similar activity levels in < 5 years old restored forest and unmined forest but lower activity in one or two age groups of restored forest  $\geq 5$  years old. The filter was especially dynamic for *C. gouldii*, only occurring in the second field year. In contrast *V. regulus*, *C. morio* (ES) and *Nyctophilus* spp. (CS) unidirectionally avoided restored forest. The filter to *C. morio* use of restored forest was relatively short-lived, dissipating once restored forest was  $\geq 5$  years old. Comparatively *V. regulus* and *Nyctophilus* spp. had reduced activity in all ages of restored forest except during the second field year when the filter dissipated for *V. regulus* once restored forest was > 15 years. Our findings corroborate other bat studies in production landscapes across Australia and in North America, showing differing bat activity levels in managed, compared to remnant sites (e.g., Law and Chidel, 2006; Silvis *et al.*, 2016; Webala *et al.*, 2011).

#### **4.2. Habitat, rather than landscape, features as filters**

As predicted, habitat, not landscape, features acted as filters to bat use of restored forest. Our study area has a relatively permeable matrix with high connectivity between preferred habitat patches; all restored sites were < 200 m from an unmined forest edge and more than half of the forest within 500 and 1500 m of detector locations was unmined forest. Synthesizing our findings with bat studies that also examined site and landscape features, we found our results to be comparable to studies in landscapes with low patch-matrix contrast, such as selectively logged landscapes, where habitat features predominantly drive bat use (e.g., Bender *et al.*, 2015; Farneda *et al.*, 2015). In contrast, landscape features, particularly at the 1000 m scale, are important to bats in landscapes with a high patch-matrix contrast, such as urban and agricultural landscapes (e.g., Chambers *et al.*, 2016; Kalda *et al.*, 2015). The lack of a relationship between bat activity and distance to stream was likely due to the fact that all streams were < 1 km from detector locations, within the foraging range of most species in this study (Burgar *et al.*, 2015). The restored forest landscape likely provides enough heterogeneity within a bats home range that landscape features do not exert a strong influence on their activity levels across the landscape. Future studies should examine filters at broader spatial

scales to determine if landscape characteristics exert a stronger influence on bat habitat use at larger spatial scales than the ones we studied (e.g., Chambers et al., 2016).

#### **4.3. Species-specific responses not generalizable to trait group**

Our finding that *A. australis* (OS) bat activity was higher in young restored (< 10 year old), compared to unmined, forest and negatively associated with tree density corroborates other studies with similar patch-matrix contrast where OS bats prefer structurally simplified sites, i.e., open sites with few if any trees, over unharvested forest (e.g., Morris et al., 2010). In eastern Australia (Blakey et al., 2016) and the southern jarrah forest (Webala et al., 2011) *A. australis* activity did not differ across logging treatment types but these studies did not have such structurally simplified sites and the patch-matrix contrast was lower than in our study. The negative association of *C. gouldii* and *M. kitcheneri* activity with tree density and canopy height, respectively, aligns with studies elsewhere where OSE bats respond positively to local effects of habitat openings (Blakey et al., 2016; Müller et al., 2013). In the restored jarrah forest canopy height is typically < 15 m, often without a gap in vegetation between the different strata; we speculate that canopy height itself may not have limited *M. kitcheneri* activity but that it was a proxy for a correlated, but unmeasured, habitat feature. Echolocation calls of bats flying above the canopy may have also been attenuated due to the dense vegetation within older restored forest (Patriquin et al., 2003; Surlykke and Kalko, 2008). ES and CS bats are typically the most tolerant of increasing vegetation density (Adams et al., 2009; Müller et al., 2013), but we found that *C. morio* and *Nyctophilus* spp. were only tolerant of increasing midstory cover to a point. The small effect size of these relationships warrants cautious interpretation; future studies could use experimental manipulation to determine if changes in midstory cover are causative as well as correlative. Our inability to identify a filter for *V. regulus* (ES) contrasts with research elsewhere in Australia and Europe where vegetation structure predicts ES bat activity (Adams et al., 2009; Blakey et al., 2016; Müller et al., 2013; Webala et al., 2011). The discrepancy between studies and the low support for individual features as filters to ES and CS use of restored forest indicates that filtering is complex and may relate to overall vegetation structure, rather than single features (e.g., Craig et al., 2015). We acknowledge that our pooling of *Nyctophilus* spp. restricted our ability to

find species-specific filters for the CS group and that studies in areas with greater numbers of bat species may find increased heterogeneity in species-specific responses within trait groups.

Our results suggest that vegetation structure > 5 m influences bat use of restored forest, but the exact mechanism is species-specific. We found that tree density, canopy height, or midstory cover were the best predictors of bat use of restored forest, similar to fragmented landscapes with similar patch-matrix contrast (e.g., Farneda et al., 2015). In variegated landscapes in south-eastern Australia where tree density varies continuously, effectively eliminating patch-matrix contrast, bat activity peaks around 20–50 stems ha<sup>-1</sup> (Hanspach et al., 2012), which likely allows OS and OSE bats room to navigate while still providing adequate cover for ES bats. In timber harvested landscapes in North America, with patch-matrix contrast similar to our study area, bats also prefer less dense, unmanaged forest where tree densities average 180 stems ha<sup>-1</sup> (Morris et al., 2010). A vegetation density, or clutter, threshold of 1100 stems ha<sup>-1</sup> has been suggested for insectivorous bats in Australia and the United States (Adams *et al.*, 2009; Blakey *et al.*, 2016). Bats in the northern jarrah forest navigate through patches of exceptionally high tree densities (mean densities across all restored and unmined forest sites in this study were 2112 ± 141 and 1601 ± 152 stems ha<sup>-1</sup>, respectively), which suggests jarrah forest bats have the ability to navigate dense vegetation, even though the energetic costs of doing so likely outweigh the benefits (Sleep and Brigham, 2003). One benefit of high, compared to low, density patches may be increased prey availability. In eastern Australia insect biomass was greater in dense regrowth compared to open forest (Blakey et al., 2016). However, in the southern jarrah forest food availability did not influence bat activity (Webala et al., 2011). Future studies are needed to elucidate prey availability and accessibility in restored jarrah forests. Our results highlight the importance of region specific studies as bat responses to habitat features varies between different ecosystems.

#### **4.4. Management implications**

Our study suggested that the importance of habitat and landscape features as filters to bat use of production landscapes depends on the patch-matrix contrast. In landscapes with relatively low patch-matrix contrast, such as the northern jarrah forest, management actions should focus on habitat



features. Specifically, tree density and midstory cover should aim to be at unmined forest levels to facilitate bat use of restored forest patches. In landscapes with high patch-matrix contrast, managers may also need to manage for landscape features such as connectivity and patch density (e.g., Chambers et al., 2016). In the northern jarrah forest the proportion of unmined forest surrounding restored forest may need to be maintained at current levels; further research is required to determine if there is a threshold effect of habitat loss on the persistence of bat species populations (e.g., Muylaert et al., 2016). Bats species grouped in the same trait group had the same type (i.e. unidirectional or dynamic) of filter, but the feature acting as the filter was species-specific, underscoring the importance of modelling filters at the species-level. Our study area had a limited number of species and areas with increased species richness may yield increased heterogeneity in species-specific responses. Even when species richness is low grouping species in trait groups can bias management decisions towards the most frequently occurring species. The implications of disregarding species-specific responses may be particularly problematic when managing for ES and CS species, as filters are typically unidirectional and can persist for decades. Equally important are longitudinal studies as the magnitude of filters can vary between years, as we found for two species. Our findings have important implications for conserving biodiversity in production landscapes facing land-use changes and will ultimately improve our ability to conserve global biodiversity.

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Fig. 1. Map showing spatial arrangement of the 64 sites at Alcoa's Huntly minesite in south-western Australia. Light grey lines denote streams and black lines denote sealed roads. In the legend R = restored forest and Unmined = unmined forest. Inset map with arrow pointing to the location of the northern jarrah forest (filled circle).

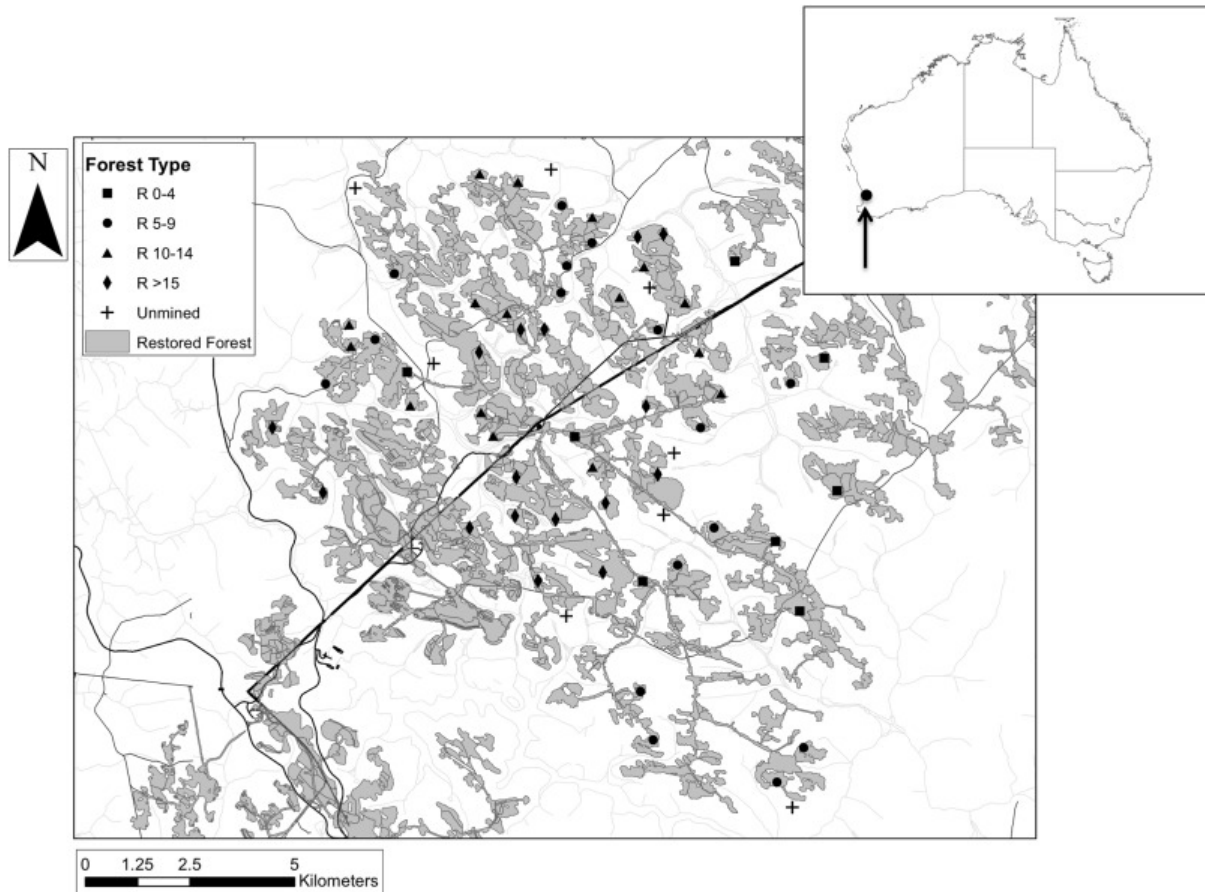


Fig. 2. Mean ( $\pm$  SE) nightly bat activity for the northern jarrah forest, by species/species group. Dark grey bars indicate the first field year while white bars denote the the second field year. Note the different scales along the y-axis. For the x-axis R = restored forest and Unmined = unmined forest. Bat species trait groups as in Table 1.

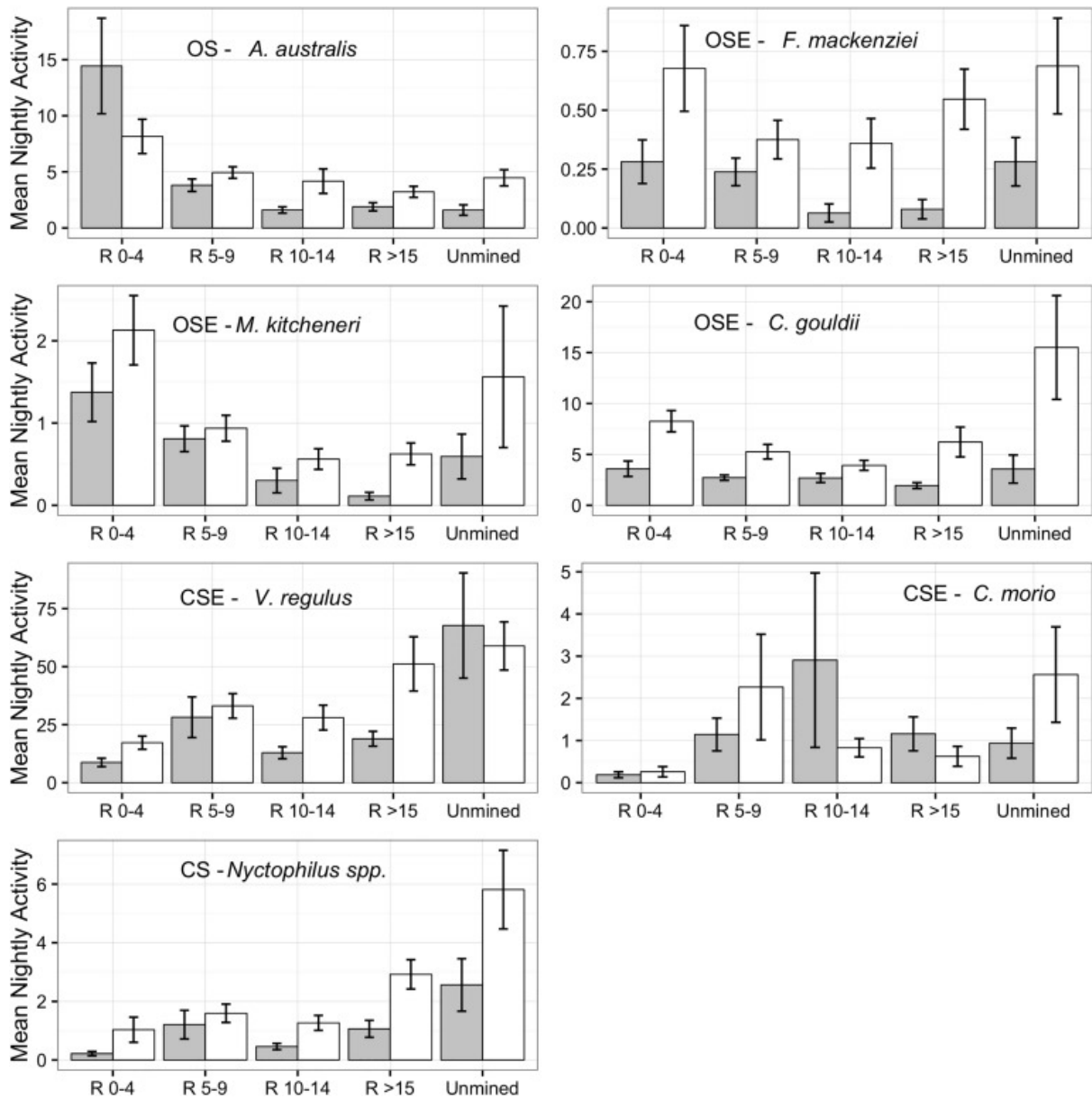


Fig. 3. Species/species group specific relationships between nightly bat activity and the habitat feature that best explained use of restored northern jarrah forest. The solid line depicts the regression line, dashed line depicts the 95% confidence interval boundaries, and the grey open circles are the observed data. Note the different scales along the y-axis.

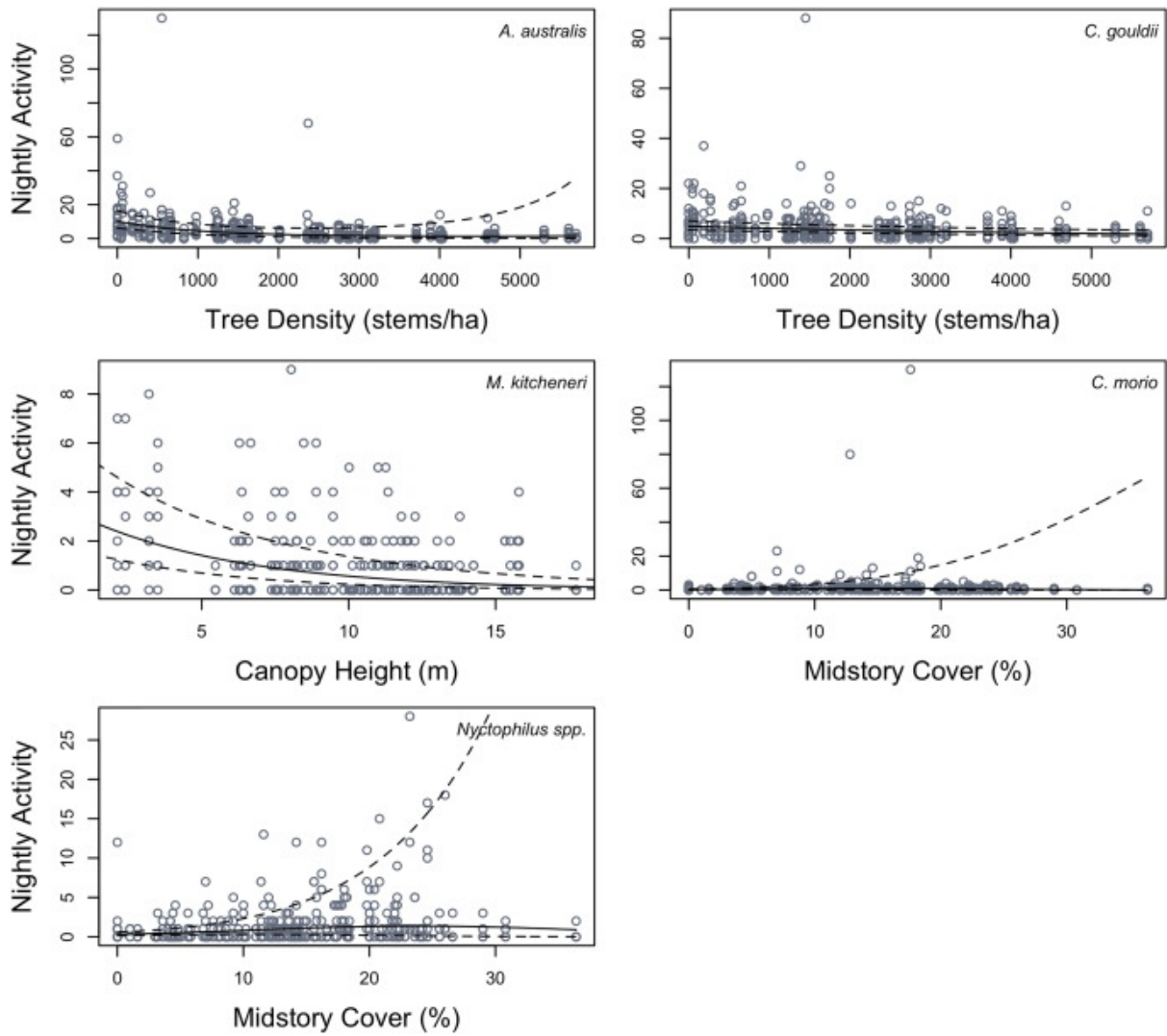




Table 1. Drop in deviance ( $D_{\text{drop}}$ )  $p$  values for the full model to the most plausible model and the most plausible model to the null model for each species/species group. Evidence ratio (ER) values for the habitat feature in each most plausible model is provided.

Species/species group	Trait group	Habitat feature	$p$ of $D_{\text{drop}}$ to full model	$p$ of $D_{\text{drop}}$ to null model	ER
<i>A. australis</i>	Open space (OS)	Tree density <sup>2</sup>	0.06	< 0.001	6.69
<i>C. gouldii</i>	Open space edge (OSE)	Tree density	0.078	< 0.001	2.03
<i>M. kitcheneri</i>	Open space edge (OSE)	Canopy height	0.956	< 0.001	48.5
<i>C. morio</i>	Edge space (ES)	Midstory cover <sup>2</sup>	0.713	0.016	0.79
<i>V. regulus</i>	Edge space (ES)	Log cover	0.375	0.065	0.34
<i>Nyctophilus</i> spp.	Closed space (CS)	Midstory cover <sup>2</sup>	0.016	< 0.001	15.33