1   **Submission of Research Paper for _Biological Conservation_**

2   **Title:** Plantations, not farmlands, cause biotic homogenisation of ground-active beetles in

3   south-eastern Australia

4   **Authors:** Nicole SWEANEY[a*], Don A. DRISCOLL[a1], D. B. LINDENMAYER[a2]

5   and Nicholas, PORCH[b3]

6   [a]ARC Centre of Excellence for Environmental Decisions

7   The NERP Environmental Decisions Hub

8   Fenner School of Environment and Society

9   The Australian National University

10   Canberra, ACT, 0200, Australia

11   [b]School of Life and Environmental Science

12   Deakin University

13   211 Burwood Highway

14   Burwood, Victoria, 3125, Australia

15   * Corresponding author: _Mobile:_ +61 (0) 404822775 _Email:_ nici.sweaney@anu.edu.au

16   [1] Email: don.driscoll@anu.edu.au

17   [2] Email: david.lindenmayer@anu.edu.au

18   [3] Email: nicholas.porch@deakin.edu.au

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Abstract

Following landscape change, species invasions and extinctions may lead to biotic homogenisation; resulting in increased taxonomic and functional similarity between previously distinct biotas. Biotic homogenisation is more likely to occur in landscapes where the matrix contrasts strongly with native vegetation patches. To test this, we examined the distribution of ground-active beetles in a landscape of remnant *Eucalyptus* open woodland patches where large areas of lower contrast matrix (farmland) are being transformed to high-contrast pine plantations in south-eastern Australia. We sampled beetles from 30 sites including six replicates of five categories; 1) remnants adjacent to farmland, 2) remnants adjacent to plantation, 3) farmland, 4) plantation, and, 5) remnants between pine plantation *and* farmland. Community composition in the pine matrix was similar to native patches embedded in pine (ANOSIM, Global R= 0.49, P<0.000), which we suggest is due to biotic homogenisation. Remnant patches with edges of both farmland and pine plantation did not represent an intermediate community composition between patches surrounded by either matrix type, but rather a unique habitat with unique species. Farmland supported the greatest number of individuals (F=9.049, df=25, P<0.000) and species (F=5.875, df=25, P=0.002), even compared to native remnant patches. Our results suggest that matrix transformations can reduce species richness and homogenise within-patch populations. This may increase the risk of species declines in fragmented landscapes where plantations are not only replacing native vegetation patches, but also other matrix types that may better support biodiversity. Our findings are particularly concerning given expanding plantation establishment worldwide.

Keywords

1.1 __Introduction__

Many native species exist in a landscape mosaic that includes native vegetation patches surrounded by human-modified land-cover; the 'matrix' (Lindenmayer et al. 2001). Driscoll et al. (2013) defines the matrix as areas where species of conservation interest cannot form sustainable populations. The matrix can significantly impact the colonisation, persistence and survival of patch-associated species by influencing migration (Kuefler et al. 2010), changing abiotic conditions at patch edges (Lindenmayer et al. 2009), and providing resources to patch-associated species and/or non-patch species (Brady et al. 2011; Driscoll et al. 2013). While each of these effects have consequences for individual species and community composition (Driscoll et al. 2013), the ability of the matrix to foster non-patch species can lead to biotic homogenisation (Olden 2006).

Biotic homogenisation refers to the reduction of species diversity and increase in community similarity between previously distinct biotas (Olden et al. 2004; Dormann et al. 2007). The 'winners' of biotic homogenisation are usually generalist species, with rapid dispersal rates and a high tolerance of human-modified landscapes (McKinney and Lockwood 1999). The 'losers' are often habitat specialists, with low dispersal rates, being dependent on areas characterised by low levels of landscape modification (Robertson et al. 2013). These 'losers' are vulnerable to external perturbations (Olden et al. 2004; Dormann et al. 2007) and are therefore more likely to suffer from local extinction events. Successful generalist species may further expedite the process of biotic homogenisation by exerting competitive dominance over patch-associated species (Robertson et al. 2013).

Patch-associated species are expected to be less vulnerable to biotic homogenisation if they can also exploit the surrounding matrix (Ekroos et al. 2010). Matrices which share structural similarities with habitat patches can increase matrix use and movement for patch-associated species (reviewed in Eycott et al. 2012), which helps protect species against patch isolation

69 and associated extinction risks (Donald and Evans 2006). For example, species associated

70 with open, grass-dominated native vegetation remnants may perceive agricultural pastures,

71 also having open canopies and grasses, as sub-optimal habitat rather than hostile matrix

72 (Bayne and Hobson 1998; House et al. 2012; Sweaney et al. in review). Hence, in some

73 fragmented landscapes, agricultural pastures can be more conducive to edge crossings,

74 dispersal, and resource supplementation than dense closed forest (e.g. Jules and Shahani

75 2003; Pita et al. 2007). Structurally similar matrices can support connectivity and persistence

76 of native patch-associated species (Eycott et al. 2012). In these cases, the potential for

77 widespread generalist species to successfully dominate patch-associated species or colonise

78 patches after local extinctions is limited (Ekroos et al. 2010).

79 In many regions of the world, agricultural matrices are being transformed to tree plantations

80 (Felton et al. 2010; Kröger 2012). Simplified landscapes created by the establishment and

81 maintenance of monoculture plantations can cause a loss of habitat specialists and increase in

82 population isolation, thereby increasing vulnerabilities to extinction risks (Dormann et al.

83 2007; Ekroos et al. 2010). Such landscape transformations may exacerbate and accelerate

84 biotic homogenisation, particularly in areas where the agricultural matrix being replaced was

85 structurally similar to native vegetation remnants.

86 We examined the distribution and abundance of ground-active beetles in a fragmented

87 landscape in south-eastern (SE) Australia. Here, patches of *Eucalyptus* open woodland are

88 surrounded by agricultural pastures (established almost two centuries ago) and extensive

89 areas of pine plantations (established 1998), including areas where the two matrix types meet

90 (Lindenmayer et al. 2008a). Previous research in this study area has shown that butterflies

91 were often found in farmland, but were completely absent in pine plantations (Sweaney et al.

92 in review). These results suggested that pine plantations constitute a high-contrast matrix for

93 patch-associated species, which may make populations in patches surrounded by pine

susceptible to biotic homogenisation. Ground-active beetles are an ecologically important

group in most ecosystems (Werner and Raffa 2000; Gibb et al. 2006b) and are expected to

also be sensitive to matrix transformation (Gaublomme et al. 2008). However, research

examining biotic homogenisation in areas undergoing landscape transformation is limited

(Ekroos et al. 2010), and represents a concerning knowledge gap in the literature.

To address this knowledge gap, we sought to determine if taxonomic and functional

similarities between ground-active beetles in the matrix and native vegetation remnants was

greater in areas where agricultural pastures had been transformed to pine plantations. We

examined overall community composition, as well as the abundance and species richness of

ground-active beetles and groups of beetles with various traits (body size, wing presence and

trophic group). We expected that, because pine plantations in our study area contrast more

strongly with eucalypt patches compared to agricultural pastures, ground-active beetle

populations in patches surrounded by pine will show more signs of biotic homogenisation

than patches adjacent to farmland.

Given that most of the world's new plantations are established on former agricultural pastures

(Felton et al. 2010), understanding species' responses to matrix transformations from

agriculture to plantation is critical to successful biodiversity conservation and the effective

management of plantations. This is particularly important given expectations that plantations

will expand globally from 230 million ha to over 300 million ha by 2020 (FAO 2010).

1.2 **Materials and Methods**

1.2.1 **Study Area**

This investigation was conducted at 'Nanangroe', 10-20 km south-east of Jugiong in NSW

Australia (Lindenmayer et al. 2001; Figure 1). Historically, the area consisted of extensive

stands of temperate *Eucalyptus* open woodlands. Approximately 85% has been cleared for

118   agriculture over the past 170 years (Lindenmayer et al. 2008b). In 1998, large areas of

119   Nanangroe were converted to *Pinus radiata* plantations (Lindenmayer et al. 2008b). Prior to

120   plantation establishment, 52 *Eucalyptus* woodland patches were selected for exemption from

121   conversion (Lindenmayer et al. 2001). These remnant patches are relatively small fragments

122   (most are <5 ha), surrounded by a matrix of agricultural pastures and dense pine plantations,

123   including areas where the two matrices meet (Lindenmayer et al. 2001, Figure 1).
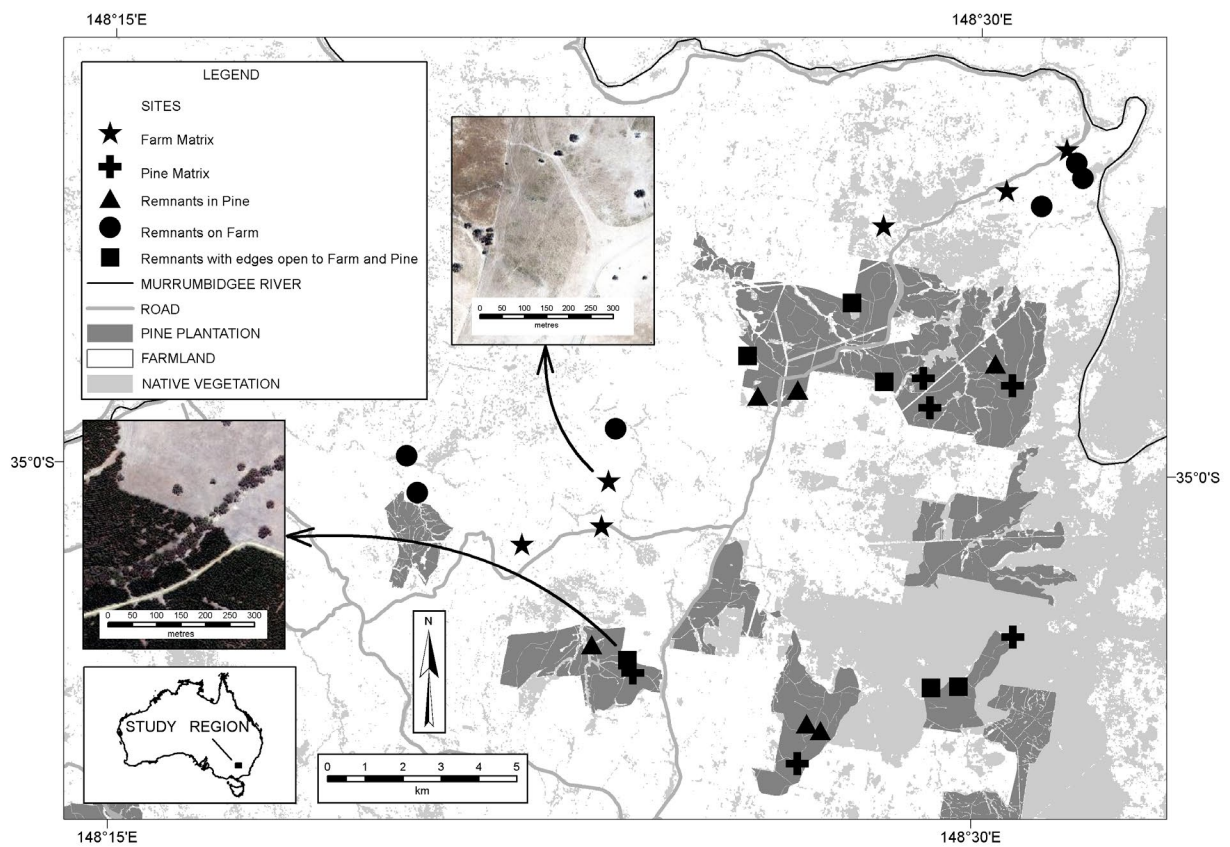
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125   **Figure 1 Map of the study area; Nanangroe, south-west slopes of NSW Australia. Symbols show all thirty**
126   **study sites. Inserts show close-ups of two of our study sites (a eucalypt patch with edges of farm and pine,**
127   **and a farm matrix site).**

128   **1.2.2   Study Sites**

129   We selected 30 study sites, including six replicates of five different site categories; 1)

130   woodland patch adjacent to both pine plantation and farmland (referred to as 'PwB' i.e.

131   patches with *both* types of edge), 2) farmland matrix ('F'), 3) woodland patch adjacent to

6

132 farmland ('PF'), 4) woodland patch adjacent to dense pine plantation ('PPi'), and, 5) pine

133 matrix ('Pi') (Figure 1).

134 Pine plantations ('Pi' sites) in Nanangroe are thinned every 12-15 years and clearfelled after

135 25 years (Lindenmayer et al. 2008b). At the time of our study, the pine plantation was mature

136 (>12 years old) and densely stocked (i.e. had not been thinned). The ground cover of all pine

137 matrix sites was comprised almost exclusively of fallen pine needles.

138 The agricultural pastures ('F' sites) studied are subject to fertilizer application, chemical

139 spraying, and intensive grazing by domestic livestock (Lindenmayer 2009). Our farmland

140 sites supported sparse clusters of woodland trees and shrubs. Farmlands also were

141 characterised by several species of native and introduced grasses.

142 *Eucalyptus* open woodland patches ('PwB', 'PF' and 'PPi') are dominated by an overstorey

143 of several species of eucalypt (Fischer et al. 2008). Overstorey trees are widely spaced, and

144 tree canopies rarely touch. The understorey and ground cover are simple; mostly

145 characterised by short native, and some exotic, species of grass.

146 **1.2.3   Field Surveys**

147 To sample ground-active beetles, we used pitfall traps (Driscoll and Weir 2005). We set 10,

148 275 ml pitfall traps on each of our 30 study sites. Traps were arranged in two lines of five.

149 The lines of traps were 2 m apart, and the traps within a given line were separated by 1 m. In

150 *Eucalyptus* patches, the traps were placed approximately in the middle of a site. Depending

151 on the shape of the patch, this left an average of 20 m from traps to patch edges. Matrix areas

152 were much larger than remnant native vegetation patches, so traps were at least 20 m away

153 (158 m) from patch edges.

154 Pitfall traps were protected from rain and falling debris by a round, clear plastic lid held

155 above the trap using wooden skewers. Our traps contained 100 ml of saturated salt solution

156 (70g/L NaCl) as a preservative (Driscoll et al. 2010). We left our traps open for three weeks

157 during March 2013. The average daily maximum temperature over the survey period was

158 28°C (SD = 4°C), with a low of 15°C (SD = 1.15°C) overnight (AccuWeather 2013). The

159 traps were checked half way through the sampling period, and topped up with salt solution if

160 necessary. While we acknowledge that many beetle species are most active during summer

161 months (Archer and Elgar 2003), wildfires in January and February 2013 prohibited access to

162 the study region before March 2013.

163 We recorded vegetation variables for each site. We estimated the percentage of ground

164 covered by grass, shrubs and trees in 10 m x 10 m quadrats at 0 m, 100 m and 200 m along

165 transects previously established at each of our sites (see Lindenmayer et al. 2001). These

166 values were averaged across the three quadrats to give an average value of grass, shrub and

167 tree cover for each site.

1.2.4 Species Identification

169 Samples of ground-active beetles were identified by one of the authors (Nicholas Porch), who

170 has extensive experience with the beetle fauna of the study region. All individuals were

171 identified to genus level (at least) and then assigned a morphospecies.

172 We selected three species traits shown to be linked to species responses to environmental

173 variables for inclusion in our data analyses. These were: wing presence (Driscoll and Weir

174 2005; Gibb et al. 2006a), body length (Blackburn et al. 1990) and trophic level (Didham et al.

175 1998).

176 We recorded body length from an approximately median-sized individual (chosen by

177 Nicholas Porch). Trophic group was assigned based on the genus of each species (Lawrence

178 and Slipinski 2013), as species-specific information is rarely available.

1.2.5 Statistical Analyses

In our analyses, 'site type' refers to the five different categories that each of our 30 study sites were assigned to (PwB, F, PF, PPi, or Pi, see section 1.2.2).

1.2.5.1 Community Structure

We investigated relationships between the beetle community sampled and site type using non-metric multidimensional scaling (nMDS). We produced a Bray and Curtis (1957) distance matrix that included the abundance of all beetle species sampled. We used non-standardized data to preserve site-specific characteristics and responses (Lassau and Hochuli 2008). We plotted two-dimensional ordinations using nMDS, and performed analysis of similarity (ANOSIM; Clarke and Warwick 2001) with 10000 permutations to test for significant differences in multivariate community structure between site types. We used R packages 'MASS' (Venables and Ripley 2002) and 'vegan' (Oksanen et al. 2013) to perform nMDS.

1.2.5.2 Abundance and Species Richness (including Species Traits) Analyses

Before we performed analyses involving total abundance, species richness and species traits, we examined all explanatory variables (site type, average tree, shrub and grass cover for each site, elevation and easting and nothing) for possible correlations. We found a strong correlation (correlation co-efficient $\geq \pm 0.7$) between tree and grass cover (correlation co-efficient = -0.71, Appendix A) and tree cover and northing (correlation co-efficient = -0.82, Appendix A). We therefore excluded grass cover and northing from the analysis. We did not find any other strong correlations between covariates (Appendix A).

Our statistical models initially fitted each response variable (total abundance, species richness, and each species trait group) against our explanatory variables (excluding grass cover and northing). We eliminated explanatory variables from our models using a backwards-stepwise approach (Wohlgemuth 1998). Explanatory variables that did not return

204 a significant P value (i.e. where P≤0.05) were dropped one at a time from each of our models

205 until only statistically significant explanatory variables remained.

206 We analysed total abundance as well as species richness of all beetles with each particular

207 trait (i.e. all ground-active beetles that were predators) for our species trait analyses. We

208 grouped beetles into three categories for body size analysis; small (1-3mm, 47 species),

209 medium (3.5-7.5mm, 43 species) and large (8-25mm, 39 species). This grouping provided

210 similar numbers of species in each body size class.

211 We used Quasi-Poisson (to account for over dispersion; Wedderburn 1974) Generalized

212 Linear Models (GLMs) to investigate the relationship between site type and; total abundance,

213 each of the four trophic groups, wing presence/absence and the three body size classes.

214 We used Gaussian GLMs (McCullagh and Nelder 1989) to investigate relationships between

215 site type and beetle species richness, as these gave approximately normally distributed errors.

216 We also adjusted species richness by rarefaction (Hurlbert 1971), because measures of

217 diversity may be sensitive to sample size, and analysed these values to look for possible

218 relationships with site type. We calculated rarefied species richness values using the rarefy

219 function in the R package 'vegan' v2.0-2 (Oksanen et al. 2013). We analysed both raw and

220 rarefied species richness because rarefaction alone does not account for the fact that

221 distributions of species abundance between the various sampling locations may be

222 intrinsically different (Fleishman et al. 2006).

223 We performed the post-hoc Tukey-Kramer Honestly Significance Difference test (HSD) for

224 all statistical tests that returned a significant result (i.e. where P≤0.05) to identify which

225 group(s) were statistically different from each other (Jaccard et al. 1984)

226 We performed all statistical analysis using R 3.01 (R Core Team 2013).

1.3 Results

We collected a total of 562 ground-active beetles representing 130 morphospecies from 28 families. Of the 130 morphospecies identified, 47 were predators, 36 herbivores, 33 detritivores and 14 fungivores (Appendix B). Only eight morphospecies were exotics, the remainder were native species.

1.3.1 Community Structure

We found the community structure of ground-active beetles sampled was similar between patches in pine and the pine matrix, whereas other site types had distinct communities (ANOSIM, Global R= 0.49, P<0.000, Figure 2a). Patches with edges of both farm and pine matrix were not intermediate in community composition between patches completely surrounded by either matrix type (Figure 2a). We found relatively large numbers of species were unique to each site type, particularly in the farm matrix and patches with edges of both matrix types (Figure 2b).
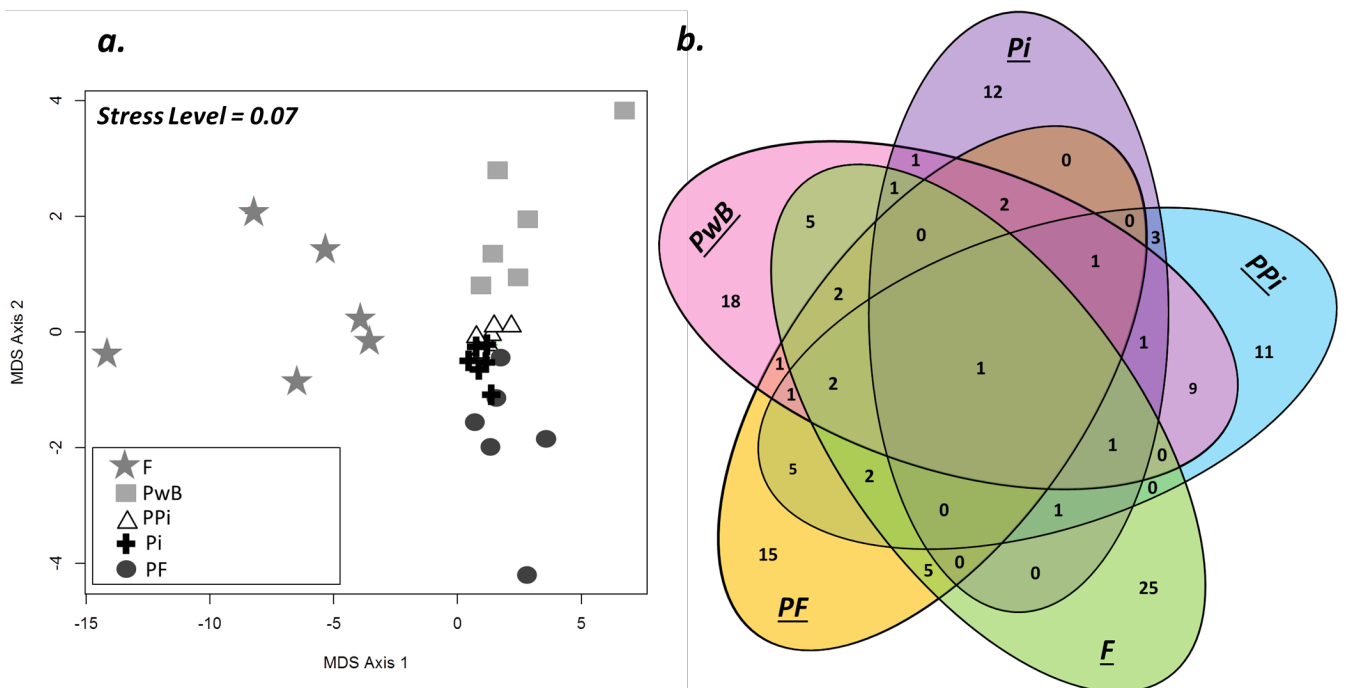
Figure 2 (a) Non-metric multidimensional scaling (two dimensions, Bray-Curtis distance matrix) of beetle species abundance classified by site type (stress level = 0.07). (b) Occurrence of all beetle species among the five site types. Numbers show the total of unique species (i.e. occur there and nowhere else) for that site type or combination of site types.

1.3.2 Abundance and Species Richness (including Species Traits)

We found, through backwards-stepwise elimination, that vegetation (tree and shrub cover) and position (elevation and easting) did not contribute significantly to any of our statistical models, and therefore excluded them from further analyses. Thus, all results we present here are for analyses examining relationships between abundance or species richness (overall total and for each species trait) and site type.

Table 1 Summary of statistical models. All response variables (listed under model) fitted against site type. Significant results (where P≤0.05) are unshaded. (b) Results of Post-Hoc Tukey-Kramer Honestly Significance Difference tests (HSD) for differences in total abundance ("Abund.") and species richness ('Sp. Rich") of ground-active beetles with various species traits between each site type. Significant results (where P≤0.05) are unshaded.

a.

| Model	F	df	P
Species Richness	5.875	25	0.002
Total Abundance	9.049	25	<0.000
Detritivore Abundance	7.924	25	0.000
Detritivore Species Richness	5.886	25	0.002
Fungivore Abundance	5.557	25	0.002
Fungivore Species Richness	4.427	25	0.008
Herbivore Abundance	4.661	25	0.006
Herbivore Species Richness	4.074	25	0.011
Predator Abundance	1.411	25	0.259
Predator Species Richness	1.168	25	0.349
Winged Beetle Abundance	12.300	25	<0.000
Winged Beetle Species Richness	5.380	25	0.003
Flightless Beetle Abundance	4.261	25	0.009
Flightless Beetle Species Richness	7.439	25	0.000
Small Beetle Abundance	10.530	25	<0.000
Small Beetle Species Richness	5.882	25	0.002
Medium Beetle Abundance	9.788	25	<0.000
Medium Beetle Species Richness	6.645	25	0.001
Large Beetle Abundance	8.137	25	0.000
Large Beetle Species Richness	7.992	25	0.000

b.

Model		All Beetles		Detritivores		Fungivores		Herbivores		Winged		Flightless		Small-Bodied		Medium-Bodied		Large-Bodied	
Group 1	Group 2	Abund.	Sp.Rich	Abund.	Sp.Rich	Abund.	Sp.Rich	Abund.	Sp.Rich	Abund.	Sp.Rich	Abund.	Sp.Rich	Abund.	Sp.Rich	Abund.	Sp.Rich	Abund.	Sp.Rich
Pi	F	**0.000**	**0.004**	**0.000**	**0.001**	0.946	0.986	**0.005**	**0.009**	**0.000**	**0.013**	**0.009**	**0.040**	0.923	0.904	**0.000**	**0.004**	**0.000**	**0.001**
Pi	PPi	0.916	0.632	0.945	0.766	0.149	0.066	0.988	0.990	0.995	0.477	0.929	1.000	0.342	0.334	1.000	1.000	0.997	0.981
Pi	PF	0.168	0.097	0.537	0.246	0.802	0.553	0.698	0.502	**0.011**	0.679	0.787	**0.001**	**0.045**	0.427	1.000	0.984	0.191	**0.006**
Pi	PwB	**0.035**	**0.005**	0.267	0.082	**0.021**	0.111	0.251	0.502	0.094	**0.004**	0.138	0.477	**0.000**	**0.014**	0.963	0.743	0.210	0.077
F	PPi	**0.001**	0.098	**0.001**	**0.017**	**0.032**	**0.021**	**0.018**	**0.026**	**0.000**	0.355	0.054	**0.040**	0.079	0.068	**0.000**	**0.004**	**0.001**	**0.004**
F	PwB	0.157	0.999	**0.034**	0.354	**0.004**	**0.038**	0.408	0.262	**0.017**	0.992	0.717	0.645	**0.000**	**0.002**	**0.001**	0.070	0.060	0.383
F	PF	**0.032**	0.632	**0.010**	0.131	0.373	0.276	0.104	0.262	0.137	0.209	0.108	0.645	**0.007**	0.098	**0.000**	**0.001**	0.067	0.958
PF	PwB	0.938	0.689	0.986	0.976	0.208	0.843	0.926	1.000	0.863	0.091	0.692	0.073	0.342	0.427	0.963	0.432	1.000	0.808
PF	PPi	0.575	0.743	0.923	0.879	0.699	0.708	0.926	0.777	**0.026**	0.997	0.997	**0.001**	0.811	0.999	1.000	0.984	0.325	**0.023**
PwB	PPi	0.911	0.117	0.679	0.556	0.886	0.999	0.502	0.777	0.195	0.172	0.488	0.477	**0.045**	0.529	0.987	0.743	0.352	0.217

259 *1.3.2.1 Total abundance and species richness*

260 We found that species richness was significantly lower in the pine matrix compared with

261 farm and patches with edges of both matrix types (Figure 3a, Table 1b). When we adjusted

262 species richness by rarefaction, these results remained the same (P=0.002).

263 We found more beetles on farm sites compared to all other areas, although abundance did not

264 differ significantly between farms and patches with edges of both matrices (Figure 3b, Table

265 1b).

266 We found total abundance and species richness did not differ significantly between the pine

267 matrix and patches in pine (Figure 3, Table 1b).
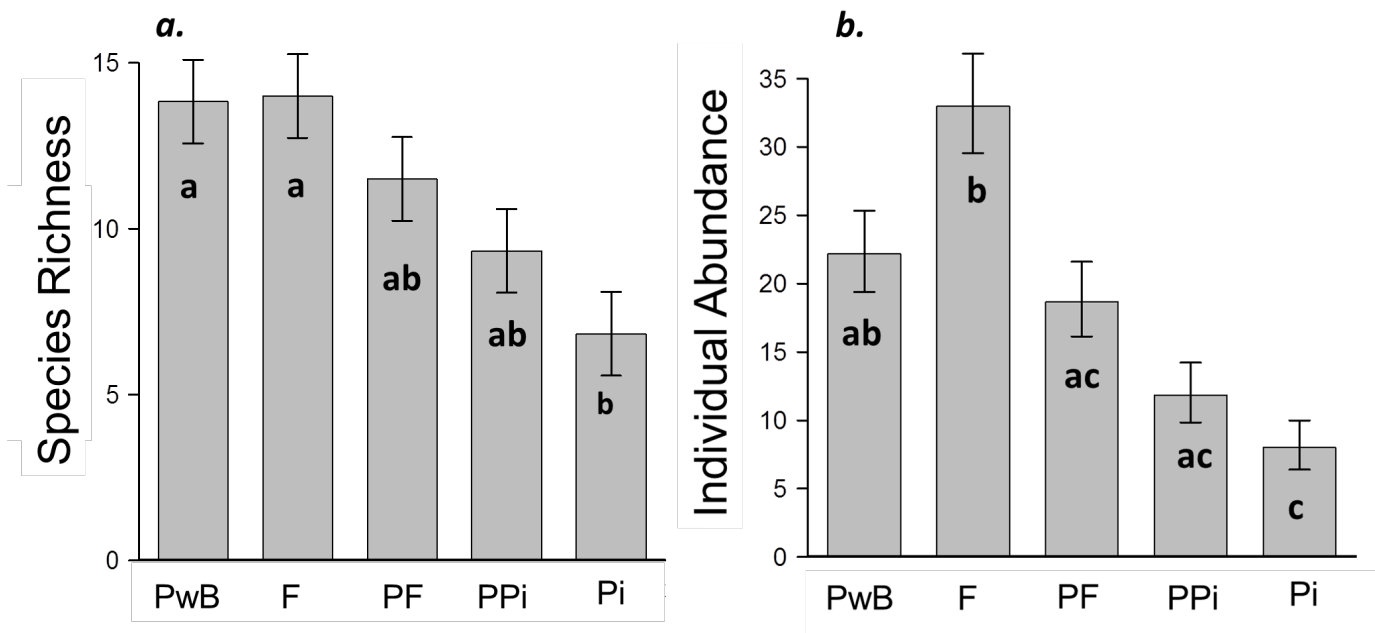
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269 **Figure 3 Differences in (a) species richness and (b) total abundance of ground-active beetles between site**
270 **types. Values are shown as predicted means and error bars indicate standard errors. Letters on bars indicate**
271 **which sites are statistically similar, and which are different.**

1.3.2.2   Species Traits

Trophic Groups

We found the abundance of detritivorous and herbivorous beetles was highest in farmland compared to all other site types (Table 1b, Figure 4a&c). We found species richness of detritivores and herbivores was similar between farmland and all patches that shared edges with farmland (Table 1b, Figure 4a&c). We also found detritivore and herbivore abundance and species richness was significantly lower in pine and patches embedded in pine compared to other site types (Table 1b, Figure 4a&c).

We found that both matrix types supported fewer fungivores (total abundance and species) compared to eucalypt patches, although this difference was not significant between the pine matrix and patches in pine (Table 1b, Figure 4b1-2).

We did not find a significant relationship between the abundance and species richness of predators and site type (Table 1a).

Wing Presence

We found that farm sites, and patches with edges of farmland, generally supported more winged and flightless beetles than the pine matrix and patches in pine (Table 1b, Figure 4d1&4e1). We found lower species richness of flightless beetle species in patches surrounded by pine and in the pine matrix compared to other sites (Figure 4e2). We also found species richness of winged beetles was not significantly different between the farm matrix and patches with edges of farmland, but was significantly lower in the pine matrix (Table 1b, Figure 4d2).

293 *Body Size*

294   Generally, we found fewer small beetles (both abundance and species richness) in both

295 matrix types compared with eucalypt patches, particularly patches which had edges of both

296 farm and pine matrices (Table 1b, Figure 4f1-2). We found more medium-sized beetles in

297 farmland compared to other sites (Table 1b, Figure 4g1-2). We observed the same pattern for

298 species richness of medium sized species, although there was no significant difference

299 between farm matrix and patches open to both matrix types (Table 1b, Figure 4g2). We found

300 more individuals and more species of large bodied beetles in the farm matrix compared to the

301 pine matrix and patches in the pine (Table 1b, Figure 4h1-2).
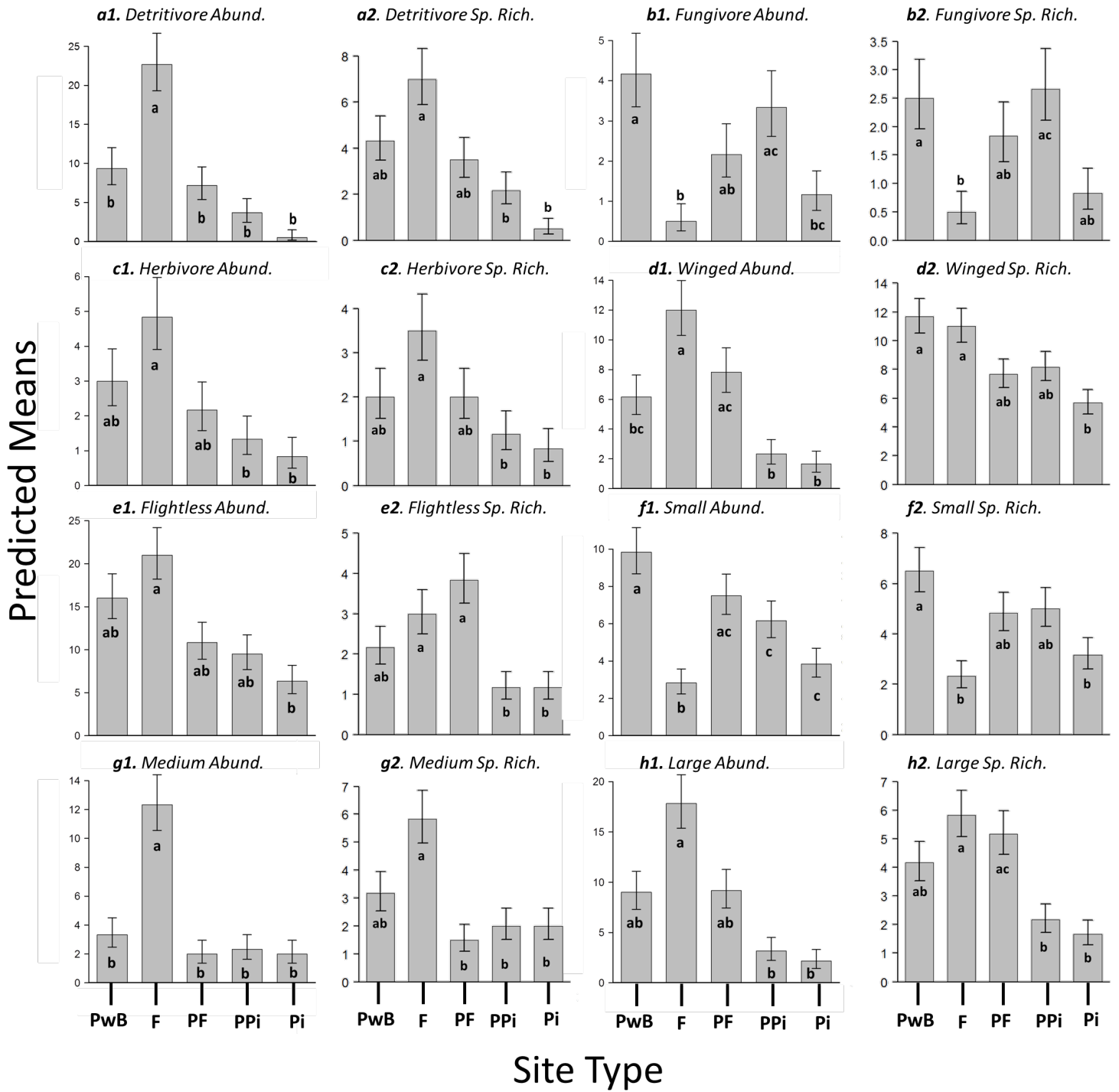
Figure 4 Differences in total abundance (*'Abund.'*) and species richness (*'Sp. Rich'*) for ground-active beetles with various species traits between site types. Graphs (a)-(c) show results for trophic groups, (d)&(e) flight ability and (f)-(h) categories of body size. Values are shown as predicted means and error bars indicate standard errors. Letters on bars indicate which sites are statistically similar, and which are different.

1.4   <u>Discussion</u>

Our results suggest replacing agricultural pastures with plantations in areas characterised by open native vegetation patches may negatively affect patch-associated species and others that occur more broadly across the landscape. While farmland communities of ground-active beetles shared some similarities with those in native vegetation patches, community composition was still distinct. Conversely, the establishment of pine plantations appeared to enhance the process of biotic homogenisation, which is likely to have a range of negative ecological, evolutionary and social costs (Moritz 2002; Olden 2006). Supporting landscapes with heterogeneous or mixed matrix types may enable unique patch-associated species to persist. Our findings have broad implications for the successful conservation of other taxa worldwide in areas where lower-contrast matrices are being transformed to homogenous, high contrast matrix types.

1.4.1   Biotic homogenisation between pine plantations and patches surrounded by pine

The taxonomic and functional similarity between ground-active beetles sampled in the pine matrix and patches surrounded by pine (Figure 2&4) provides compelling evidence that biotic homogenisation has occurred between these habitats. We suggest this is due to two possible, congruent mechanisms; a loss of vulnerable species from patches in pine and the pine matrix, and an inability of ground-active beetles outside the pine matrix to recolonise patches within the pine.

We found significantly fewer species of flightless beetles and lower abundance and species richness of larger-bodied beetles in pine and patches embedded in pine compared to all other sites in our study (Figure 4). These groups of beetles are known to have low dispersal ability (Cole et al. 2012) and to be sensitive to environmental change (Rusch et al. 2013). Our results suggest that the establishment of pine plantations has led to a loss of these vulnerable species

in the pine matrix and patches surrounded by pine, which is expected to enhance the process

of biotic homogenisation (Olden et al. 2004; Ekroos et al. 2010).

If patch-associated species cannot recolonise patches left empty by local extinctions of

vulnerable species, this will further exacerbate the process of biotic homogenisation (Ekroos

et al. 2010). Dispersal ability of beetles in grassland and cultivated pastures can be greatly

reduced by taller and more structurally complex matrix types (i.e. shrubs and forest) in other

systems (Kareiva 1985; Jonsen et al. 2001). Our results support the suggestion that pines may

be limiting effective dispersal, as patches within pine did not share taxonomic or functional

similarities with other patch types (e.g. Figure 2a, the abundance of small-bodied beetles and

species richness of larger-bodied beetles, Figure 4). More research will be needed, perhaps

employing mark/recapture (Dávalos and Blossey 2011) or direct tracking methods (Goodwin

and Fahrig 2002), to understand the effects of the matrix on dispersal behaviour and

consequences for recolonisation efforts by ground-active beetles in our study area.

1.4.2   Abiotic conditions influencing community divergence

Abiotic conditions experienced at edges of patches can influence within-patch communities

(Jules and Shahani 2003; Farmilo et al. 2013). Closed canopy plantations experience more

stable temperature gradients, decreased drying of top soil layers (Butterfield 1999), less wind

and direct sunlight, and moister soil (Karen et al. 2008) compared to open habitats. These

conditions influence beetle assemblages in other systems around the world (Barbosa and

Marquet 2002; Perner and Malt 2003; Koivula 2011), and may be contributing to the ground-

active beetle community divergence between patches surrounded by pine and other eucalypt

remnants in our study.

1.4.3   The effect of farmland on within-patch communities

The farmland matrix in our study supported the largest number of ground-active beetle

individuals and species (Figure 3), even compared to native vegetation patches. This result

358   contrasts with those of other studies (Driscoll and Weir 2005; Hendrickx et al. 2007). Our

359   nMDS analysis showed farmlands supported a unique community of ground-active beetles,

360   with many species found solely on farmlands (Figure 2). These results were not driven by an

361   influx of exotic species, as our analysis yielded the same results even when exotic species

362   (n=8) were removed from our dataset. Rather, we suggest that since farmland establishment

363   (over 100 years ago), species sensitive to this change in land-cover use (from native

364   vegetation to agricultural pasture) may have already become locally extinct (Jellinek et al.

365   2004). Nanangroe may now be inhabited by many ground-active beetle species that are well

366   adapted to agricultural pastures (Jellinek et al. 2013). As the pine plantation at Nanangroe is

367   comparatively new (approx.15 years old), our study may be highlighting the impact of this

368   recent change in land-cover. Watson et al. (2013) suggest that repeated land-cover change

369   can further simplify community composition of various taxa. Our results indicate that with

370   further replacement of farmland with plantations, there could be a large shift in the ground-

371   active beetle assemblage, including the loss or reduction in abundance of many species.

372   ### 1.4.4   Patches with mixed matrix edges

373   Interestingly, our nMDS analysis did not show patches with edges of both farm and pine

374   matrix as being intermediate in community composition between the two other patch types

375   (Figure 2a). This is unexpected as other studies have shown intermediate community

376   structure in patches surrounded by matrices undergoing land-cover change (Drapeau et al.

377   2000). Our species trait analysis highlights some intermediate properties of these patches,

378   such as abundance of winged beetles and species richness of flightless and large-bodied

379   beetles (Figure 4). However, patches with edges open to both matrix types also supported

380   relatively large numbers of unique beetle species (Figure 2b), which would influence

381   community divergence. Two species in particular, belonging to the Families Anobiidae and

382   Sphinididae, were present in almost every patch with edges of both matrix types, but nowhere

383   else in our study area. While pine plantations appear to negatively impact ground-active

384   beetle communities generally, this result suggests that patches with edges of mixed matrix

385   types and therefore more heterogeneous edges, represent a unique habitat. This has broader

386   implications for the management of fragmented landscapes, as it suggests that increasing

387   edge heterogeneity may enable unique patch-associated species to persist (Dauber et al. 2003;

388   Slancarova et al. 2014). Further research is needed to identify what patch-level variables are

389   influencing the high levels of species uniqueness we observed between the various site types.

390   **1.4.5   Effect of plantation cycle**

391   Our investigations may have yielded different results if surveys had been conducted at other

392   times of the year, especially following pine thinning or clearfelling. Clearfelled plantations

393   may support just as many beetle species as native vegetation patches (Butterfield et al. 1995),

394   and more species than densely stocked forests (Lenski 1982; Fahy and Gormally 1998).

395   However, clearfelling and thinning are temporary habitats, and as such may not be stable

396   enough to provide the resources for rare species, longer-lived species, or those with poor

397   dispersal abilities (Bengtsson et al. 2000; Koivula et al. 2002). Therefore, clearfelling may

398   not, for example, prove beneficial for increasing the occurrence or abundance of the flightless

399   and larger-bodied species in our study that appeared to be negatively impacted by plantation

400   establishment.

401   **1.4.6   Management Implications**

402   Our findings suggest that expansions of plantations in areas where they contrast strongly with

403   native vegetation patches may increase the risk of species declines in fragmented landscapes,

404   particularly if they completely replace other matrix types. Therefore, altering homogenous,

405   high-contrast matrices to increase the structural and compositional similarity to native

406   vegetation patches should be a priority for management concerned with enhancing

407   biodiversity conservation in patchy networks (Hodgson et al. 2009; Eycott et al. 2012). In

408 Nanangroe, this may be achieved through a few simple changes to plantation management,

409 including; lowering tree density (Kleintjes et al. 2004; Waltz and Wallace Covington 2004)

410 and/or planting or regenerating corridors of native trees or understorey vegetation (Hartley

411 2002). These strategies have improved matrix permeability and use for a range of patch-

412 associated invertebrates in other systems (Kleintjes et al. 2004; Waltz and Wallace Covington

413 2004; Eycott et al. 2012).

1.4.7 Conclusions

415 Our results show that agricultural areas support a diverse population of ground-active beetles.

416 However, the expansion of plantation establishment worldwide (FAO 2010; Nahuelhual et al.

417 2012) will often be at the expense of agricultural pastures (Felton et al. 2010). Matrix

418 transformations from agriculture to pine plantation can have a significant impact on the

419 ground-active beetle community inhabiting not only the matrix, but also adjacent native

420 vegetation remnants. We suggest that densely stocked plantations may cause taxonomic and

421 functional biotic homogenisation of ground-active beetles. This process is expected to also

422 affect a range of other taxa, particularly species with low dispersal capabilities or those

423 vulnerable to environmental change. Efforts to increase matrix permeability and use by

424 patch-associated species should be a key management objective for successful biodiversity

425 conservation in fragmented landscapes (Hodgson et al. 2009; Eycott et al. 2012; Öckinger et

426 al. 2012).

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Appendix A. Correlation co-efficient scores between explanatory variables. Dark grey shows strong correlations (> ±0.7), while light grey shows moderate (> ± 0.4) correlations. Weak correlations are unshaded. Where two variables were strongly correlated we excluded one of them from analysis (average grass cover and northing were excluded).

	Site Type	Av. Tree	Av. Shrub	Av. Grass	Elevation	Easting	Northing
Site Type	-						
Av. Tree	0.06	-					
Av. Shrub	0.36	-0.12	-				
Av. Grass	0.02	-0.71	-0.29	-			
Elevation	0.17	0.33	0.40	-0.59	-		
Easting	-0.06	0.16	-0.02	-0.24	0.05	-	
Northing	-0.12	-0.82	-0.46	0.40	-0.62	0.44	-

Appendix B. Summary of all ground-active beetles sampled, grouped by trophic group and then further separated into body size and wing presence.