

Running headline: Soil seed bank along an urbanization gradient

1 Title: Composition of the soil seed bank in remnant patches of grassy woodland along an urbanization
2 gradient in Melbourne, Australia

3 Authors: Amy K. Hahs^{1,2} and Mark J. McDonnell^{1,2}

4 Affiliations: ¹ Australian Research Centre for Urban Ecology, Royal Botanic Gardens Melbourne,
5 Birdwood Avenue, South Yarra, VIC 3141, Australia

6 ² School of Botany, The University of Melbourne, VIC 3010, Australia

7 Corresponding Author: Amy K. Hahs

8 Australian Research Centre for Urban Ecology, c/o School of Botany, The University of Melbourne,
9 VIC 3010, Australia

10 Email: hahsa@unimelb.edu.au

11 Telephone: +613 8344 0116

12 Fax: +613 9347 9123

13

14 **Abstract**

15 Urban areas around the world are rapidly expanding, with flow on consequences for the native plants
16 and animals that inhabit these areas. The impacts of this urban growth are not always immediate, and in
17 the case of the local extinction of plant species may take up to 100 – 150 years. Understanding how
18 urbanization affects ecological patterns and processes may allow us to minimize the loss of species from
19 these areas through better planning and conservation decisions. This study examined the composition of
20 the soil seed bank in remnant patches of grassy woodland along an urbanization gradient in northern
21 Melbourne, Australia, using an ex situ glasshouse germination trial. A total of 108 species emerged
22 from the soil seed bank, although a majority of the seedlings were seeds from 19 non-indigenous
23 monocot species. Species richness per plot of emergent seedlings was best explained by average annual
24 rainfall, rather than the degree of urbanization in the surrounding landscape. This indicates that the
25 existing plant community may be responding to a natural productivity gradient. The persistence of 123
26 indigenous plant species in the existing vegetation, even when the soil seed bank is dominated by non-
27 indigenous monocot species, suggests that these plant communities can exist within urban areas,
28 particularly in combination with appropriate management activities that ensure the continuation of
29 previously occurring natural processes.

30 Key words: indigenous species; non-indigenous species; Bayesian statistics; temperate eucalypt
31 woodlands; urban ecology

32 **Introduction**

33 Over the past 50 years the area occupied by cities and towns has rapidly increased as the world's human
34 population becomes increasingly urbanized (UNFPA 2007). This trend towards increased occupation of
35 new and existing urban areas has had a large influence on the biodiversity of plant and animal species
36 living within these locations (McDonnell et al. 2009). The impacts of urban growth are not always
37 immediate, and in the case of the local extinction of plant species may take up to 100 – 150 years (Hahs
38 et al. 2009). However, this lag time may also provide us with an opportunity to minimize the loss of
39 species from these areas through better planning and conservation decisions. In order to make more
40 informed decisions we need additional information on how urbanization affects ecological patterns and
41 processes (Grimm et al. 2000).

42 Williams et al. (2009) present a conceptual framework for assessing the impact of urban environments
43 on floras and suggest that the composition of soil seeds banks is important to the survival of plant
44 species in fragmented landscapes. The soil seed bank reflects the composition of both the past and
45 present plant communities and can be considered to form part of the site's 'ecological memory'
46 (Schaefer 2009). It's also an indication of the potential future composition of the local area (Simpson et
47 al. 1989), and expands our understanding of the temporal dynamics of the vegetation community. The
48 presence of species in the soil seed bank which are not present in the existing vegetation indicates which
49 species may not have experienced favourable conditions for germination, establishment or growth
50 (Pickett and McDonnell 1989). When these are indigenous species, this information can provide a list of
51 potential local extinctions from the patch, and could guide future research investigating why certain
52 species may be disappearing from remnant patches in urban areas. The presence of non-indigenous
53 species identifies the new plant species that have entered the patch through dispersal, and may germinate
54 and become established under favourable conditions. The abundance of indigenous and non-indigenous

55 species in the soil seed bank could indicate potential shifts in the composition of the future plant
56 community (Gioria et al 2012). Soil seed banks therefore provide an indication of what the future plant
57 community could look like, based on the composition of the past and current plant communities, and the
58 composition of plants in the surrounding landscape (Fenner and Thompson 2005; Leck et al. 1989).

59 The composition of the existing vegetation in the *Eucalyptus camaldulensis* woodlands of northern
60 Melbourne, Australia shows little variability between patches, particularly in the composition of the
61 indigenous plant species (Hahs and McDonnell 2007). The small amount of variability in the richness
62 and abundance of particular groups of species shows a stronger response to the average annual rainfall
63 gradient than to the amount of urbanization in the surrounding landscape (Hahs and McDonnell 2007).
64 The likelihood that these plant communities will remain similar in the future will be partly determined
65 by the ongoing process of recruitment, with new individuals replacing the older individuals as they
66 senesce and die.

67 This study aims to quantify the composition of the soil seed bank within twelve patches of *Eucalyptus*
68 *camaldulensis* woodland, and investigate the influence of urbanisation, rainfall, soil nutrients and patch
69 size on the observed patterns. As the soil seed bank is a relatively good indicator of the potential
70 trajectory for the composition of the plant community, this information will provide useful insights for
71 the preservation and management of these valuable patches of remnant vegetation (Juttila 2003, Bossuyt
72 and Honnay 2008; Albrecht et al 2011).

73 To achieve these goals we asked the following questions:

- 74 1) What is the size and composition of the soil seed bank in patches of *Eucalyptus camaldulensis*
75 woodland?

76 2) What are the main factors contributing to the observed patterns in species richness per plot and
77 seedling abundance per plot?

78 3) How does the composition of the soil seed bank compare to the composition of the existing
79 vegetation?

80 **Methods**

81 Melbourne is located at approximately -38° latitude and 145° longitude on the south coast of
82 southeastern Australia and is the capital city of the state of Victoria. Between 1996 and 2001
83 Melbourne's human population increased by 7.2% to 3.2 million people (Australian Bureau of Statistics
84 2003), and the population is predicted to reach 5 million by the year 2036 (Victorian State Government
85 2009). Patterns of urbanization across northern Melbourne have been quantified by Hahs and
86 McDonnell (2006). The climate is Mediterranean, with cool, wet winters and warm, dry summers, and
87 average annual rainfall for a 30 year period up to 2001 varied from 500 mm to 1200 mm over an 80 km
88 distance from west to east (Australian Bureau of Meteorology 2000). To minimize the influence of
89 geology, we restricted our sampling to the Victorian Volcanic Plains bioregion, which extends north and
90 east of the Yarra River on basalt plains formed in the Cainozoic period (Thackway and Cresswell 1995).
91 The soils vary from light grey loams, to dark grey sand over clay and heavy clay on younger basalt (Soil
92 Conservation Authority 2001).

93 This research was conducted in open grassy woodland with an overstory of *E. camaldulensis*,
94 occasionally forming mixed stands with *E. melliodora* or *Acacia* species (Hahs 2006). This community
95 belongs to the Plains Grassy Woodland vegetation class (Oates and Taranto 2001), which once covered
96 28% of the study area, but now only covers 1% due to clearing for urban development and agriculture
97 (Department of Natural Resources and Environment 2002a, b). The remaining remnant areas are

98 generally degraded due to the presence of introduced plant species, changes to the fire regime, and the
99 reduction and loss of the tree canopy due to timber harvesting and stock grazing, although there are
100 scattered remnants that retain a diverse plant community (Department of Conservation and Environment
101 1992).

102 To minimize the influence of geology or rainfall on our study, our patches were confined to the
103 Victorian Volcanic Plains bioregion, and within a minimal rainfall gradient (see Online Resource 1). As
104 we were interested in the effects of urbanisation on the plant community, we ensured that our patches
105 were distributed along a 35 km urbanization gradient that extended from close to the central business
106 district (CBD) out to the surrounding rural landscape, and that the degree of urbanisation in a 1 km² area
107 surrounding each patch was representative of the broader urbanisation gradient that has been quantified
108 for Melbourne (Hahs and McDonnell 2006). Additional selection criteria were: patches had to be
109 greater than 0.5 ha, located in upland areas away from riparian zones or flood plains, and patch
110 boundaries were defined using existing fence lines to minimize the influence of different grazing
111 regimes or other management goals within an individual patch. We were able to obtain permission to
112 access each patch. *Eucalyptus camaldulensis* was present as the dominant overstory tree, saplings of this
113 species were present as evidence of recruitment, and the understory contained indigenous plant species
114 and was not regularly mown (Hahs and McDonnell (2007). The selected patches represent all of the
115 previously recorded localities of this vegetation type that met all of these selection criteria.

116 Within each patch, a stratified random approach was used which weighted the number of plots such that
117 the sampled area represented a minimum of 1% of the entire patch area. Two plots were placed in
118 patches smaller than 4 ha, while the larger patches had between 4 – 8 plots (Online Resource 1). Plot
119 locations were randomly assigned prior to the first visit, and in the larger patches, plots were evenly
120 divided between edge (within 30 m of the patch boundary) and interior.

121 Each plot was divided into four 10x10m quadrants, and the existing vegetation was recorded between
122 October and December 2001. All trees with a diameter at breast height (dbh) > 4 cm were recorded for
123 each plot and the saplings and shrubs were recorded for two randomly assigned 5x5m non-overlapping
124 quadrats within each quadrant. The groundlayer in each quadrant was sampled along three 10m
125 transects that originated at the plot's external corners. This protocol and the analysis of the existing
126 vegetation are described in more detail by Hahs and McDonnell (2007).

127 To examine the soil seed bank in each plot, soil samples were collected over a one week period in March
128 2002 which coincided with the end of the main flowering and seed production season for most of the
129 species in the herb and shrub layers. In each quadrant, three soil cores were randomly collected and
130 combined to form a single soil sample. Thus, four separate soil samples were collected for each plot.
131 The soil cores were 6.5 cm diameter and inserted to a depth of 5 cm. This provide a sampled surface
132 area of 99.6 cm² per quadrant, 398.4 cm² per plot, and a total surface area sampled of 16732.8 cm².

133 The germination rates of several grassy woodland species have been shown to respond to smoke and
134 heat cues (Morgan 1998a). Therefore, a smoke germination cue was applied by circulating fresh wood
135 smoke through an enclosure containing the soil samples for one hour (Hahs 2006). Heat was applied to
136 the soil seed bank samples by placing the aluminium trays containing soil samples in an oven at 100°C
137 for one hour.

138 After cooling overnight, the soil samples were spread out in plastic seedling trays (29 x 34 cm) over 2 to
139 3 cm of washed river sand. To economize on space, each germination tray was divided in half using 5
140 mm thick cardboard, and held two randomly selected soil samples. Trays were assigned random
141 locations within the glass house, and relocated every 14 days. Six control samples of sterilized potting
142 mix were interspersed between the samples to detect the level of contamination from external seed

143 sources. Trays were subjected to natural light levels, and an automatic watering system delivered a fine
144 mist of water for fifteen minutes each day.

145 Seedling emergence was recorded over a 37 week period between 11 March 2002 and 23 November
146 2002. It was limited to a fixed time period as this was duration the greenhouse space was available for.
147 We identified, recorded and removed seedlings as they emerged to minimize the effects of competition.
148 Unknown seedlings were re-potted for later identification. Seedling taxonomy follows Ross and Walsh
149 (2003).

150 The data from the soil seed bank samples were amalgamated for analysis at the level of the plot (N = 42)
151 and the patch (N = 12). To accommodate the uneven sampling design, all of the analyses presented in
152 this paper were conducted at the plot scale (N=42), unless otherwise stated. The overall characteristics
153 of the soil seed bank were also examined by pooling the data for all of the soil samples. Non-metric
154 multidimensional scaling (NMDS) ordinations were performed in the software package PAST (Hammer
155 et al. 2001) to examine trends in species composition between plots, and to compare similarities between
156 the emergent seedlings and the existing vegetation. The importance value [relative frequency + relative
157 density] for each species per plot were used to construct a Bray-Curtis similarity matrix, which was used
158 as input for the ordination. The ordinations were also run using presence/absence data.

159 Similarities between the emergent seedlings and the existing vegetation at the patch scale were
160 calculated using Sørensen's Index of Similarity (Eq. 1):

$$161 \quad S_s = \frac{2c}{a+b} \quad (\text{Eq. 1})$$

162 where a is the number of species emerging from the soil seed bank, b is the number of species recorded
163 in the existing vegetation and c is the number of species in both the soil seed bank and the existing

164 vegetation (Kent and Coker 1992). Sørensen's Index of Similarity quantifies the percent of the total
165 species that were recorded in both the existing vegetation and as emergent seedlings. The uneven
166 sampling design between patches is not expected to influence the values as i) this is a relative measure,
167 ii) the existing vegetation and the soil seed bank were recorded from the same plots within each patch,
168 and iii) we do not conduct any further analyses to examine trends with patch area or any other factor.

169 We used Bayesian statistics to determine the main factors contributing to the observed patterns in
170 species richness per plot and abundance per plot in the emergent seedlings, as this approach has a better
171 ability to handle small sample sizes, unbalanced, hierarchical sampling designs and non-normal
172 distributions of data (Holl et al. 2003; McCarthy 2007). The models were developed to investigate
173 responses at the patch scale (N=12), however, to accommodate our uneven sampling design between
174 patches, the actual response variables we modelled were the average species richness per plot and
175 average seedling abundance per plot. This removed the area bias from the estimates of species richness
176 and seedling abundance although the number of plots used to calculate the average would vary between
177 patches.

178 The competing models we used to examine the factors contributing to the observed patterns were
179 Average Annual Rainfall, Patch Size, Available Inorganic Phosphorous in the soil, Soil C:N ratio, and
180 four relatively independent measures of urbanisation which are described in more detail in Online
181 Resource 1. While several of our factors were highly correlated, the relationships were not perfect so
182 we retained all of the potential models in order to assess their relative strength in describing the
183 observed patterns of seedling emergence. We also tested a null model, which essentially predicts no
184 difference in the response observed between patches.

185 Centered linear regression models were developed to examine the strength of the relationship between
186 environmental and spatial variables and species richness or seedling abundance, using the program
187 WinBUGS (version 1.4.1; © MRC and Imperial College of Science, Technology and Medicine,
188 London). Each model was calibrated for 100,000 iterations and then run for a second set of 100,000
189 iterations, during which time the model variables were monitored and recorded. The uniform prior
190 distribution for the model of seedling abundance had a mean value of 0 and a variance of 100, as this
191 allowed our analysis to proceed without being influenced by the constraints of a more informative prior.
192 As species richness per plot data are based on simple integers to represent counts, we used a Poisson
193 distribution to model the expected response. Seedling abundance per plot varied between plots by an
194 order of magnitude so the data were square root transformed [$\sqrt{(\text{Abundance} + 0.5)}$] prior to analysis, and
195 a normal distribution was used to model their response. The mean and credible interval from the
196 Bayesian models for seedling abundance per plot was converted back to a raw-data equivalent by using
197 the inverse of the square root transformation function.

198 Deviance Information Criterion (DIC) were calculated for each model to obtain a measure of parsimony
199 between the input data and the prediction (Spiegelhalter et al. 2002). DIC values indicate the relative
200 support between competing models, and can only be compared between models that used the same input
201 data. Models with DIC values more than 3 units smaller are considered to be superior (Spiegelhalter et
202 al. 2002). Models that differ by less than 2 DIC units are considered to be equivalent. To examine the
203 best models in more detail, this paper presents predictions from the superior models, or if the models are
204 equivalent the model with the lowest DIC value is presented in order to allow for discussion around
205 model accuracy and the fit with the existing data.

206 **Results**

207 One hundred and eight species from 32558 seedlings were recorded from the germinable soil seed bank.
208 Both the total species richness and total abundance of seedlings were dominated by non-indigenous
209 species (Table 1). The majority of seedlings were non-indigenous monocot species such as
210 *Anthoxanthum odoratum*, *Vulpia bromoides*, *Aira caryophylleaea*, *Lolium rigidum*, *Briza maxima* and *B.*
211 *minor*. Close to 40% of seedlings belonged to a group of *Cyperaceae* species whose taxonomy was
212 unable to be resolved further as many of the seedlings were removed relatively quickly due to their
213 abundance, prior to discovering that they represented multiple species. Other dominant species were the
214 non-indigenous *Plantago lanceolata*, *Trifolium* spp., and the indigenous *Crassula decumbens* var.
215 *decumbens*. Forty-three indigenous species were recorded in the soil seed bank, the majority of which
216 were perennial dicots such as *Hypericum gramineum* and *Dichondra repens*. Twelve (28%) of these
217 indigenous species were not recorded in the existing vegetation plots (Hahs and McDonnell 2007),
218 although some may have been incidentally observed in the patches.

219 Species composition of seedlings in each plot showed no clear trends between patches (Fig. 1). One plot
220 in Patch 4 fell as an outlier due to the presence of three species which were rarely recorded in any other
221 samples, and was excluded to improve the stress value. Transforming the input data and using
222 presence/absence did not improve the stress values of the ordinations. The main trends across the
223 ordination space were for increasing patch size from left to right, increasing rainfall towards the upper
224 right corner, and increasing people per unit urban land-cover towards the lower right corner (Fig.1).

225 The average number of indigenous seedlings present in the soil seed bank was generally very low, with
226 fewer than 100 seedlings on average recorded for plots in 11 of the 12 patches. The most abundant
227 indigenous species recorded were grasses such as *Austrodanthonia* spp., *Poa labillardieri* var.
228 *labillardieri*, *Themeda triandra* and *Microlaena stipoides*. Indigenous herbs which commonly
229 germinated included *C. decumbens* var. *decumbens*, *H. gramineum*, *D. Repens*, *Poranthera microphylla*,

230 *Lythrum hyssopifolia*, and *Drosera* spp. The composition of non-indigenous species in the soil seed
231 bank was more variable in terms of the dominance of a species, rather than the actual species present,
232 although plots from the same patch tended to be dominated by the same species.

233 Only 987 seedlings of nine species of trees or shrubs germinated from the soil seed bank. Overstory
234 species were not recorded in the soil seed bank of 11 plots from five patches. The overstory species
235 recorded were five species of *Acacia*, one *Eucalypt*, and three non-indigenous shrub species: *Genista*
236 *monspessulana*, *Rubus anglocandicans* and *Ulex europaeus*. Due to the relatively small number of
237 overstory species, the relationship with environmental gradients is not presented here.

238 The soil seed bank contained 16 species (7.1 %) that were not recorded in the existing vegetation,
239 although some of these species were incidentally observed in the vicinity of the plots. The mean
240 Sørensen's index of similarity between the existing vegetation and the soil seed bank was 43.8% for all
241 species, with the maximum similarity being 60.5 % for an individual patch (non-indigenous species in
242 Patch 11) and 66.2% for non-indigenous species in all patches (Online Resource 3). Sørensen's index of
243 similarity was particularly low for the tree and shrub layer, with 5 patches having a similarity of 0
244 (Online Resource 3). The low similarity between the soil seed bank and the existing vegetation is
245 reflected in the ordination which shows a distinct separation between these two groups of plots (Online
246 Resource 4).

247 Total species richness per plot and the richness of indigenous and non-indigenous species per plot at
248 each patch were all best predicted by average annual rainfall (Online Resource 2). In each case, the DIC
249 value was at least 4 DIC points lower than the next best model, indicating a superior fit to the data. This
250 strong model support is reflected in the strong similarity between the predicted model, and the actual
251 data used to develop the models (Fig. 2a-c). These models predicted that as average annual rainfall

252 increased from 590 mm to 770 mm, the total number of species in the soil seed bank would increase
253 from 20 to 31 species, with the indigenous and non-indigenous components increasing from 3 to 7 and
254 17 to 24 species respectively (Fig. 2a-c). The predictive ability of these models is expected to be
255 relatively strong, as the credible intervals around the predicted model are relatively tight.

256 All models for the abundance of seedlings per plot had similar DIC values suggesting that all models
257 were essentially equivalent (Online Resource 2). Models with the lowest DIC values are presented for
258 discussion around the recorded seedling abundance per plot Fig. 2d-f). Average annual rainfall had the
259 lowest DIC value for both total seedling abundance per plot and non-indigenous seedling abundance per
260 plot, while landscape shape index had the lowest DIC value for indigenous seedling abundance per plot.
261 However, the actual data for each patch showed great variability within patches, and were widely scatter
262 around the predicted model. The wide credible intervals around the predicted model are also indicative
263 of a relatively poor predictive ability.

264 **Discussion**

265 The soil seed bank of these urban woodland remnants were dominated by seeds of non-indigenous
266 monocots, despite there being only 19 species of this functional group in the soil seed bank, compared to
267 35 species in the standing vegetation. This prevalence may also indicate that the vegetation in all of
268 these patches have been degraded to some degree. Soil seed banks dominated by a relatively small
269 number of non-indigenous species have also been recorded for other grassy plant communities in
270 Australia (Lunt 1990; Carroll and Ashton 1965; Odgers 1994; Morgan 1998b), as well as in remnant
271 vegetation in other cities around the world (Kostel-Hughes et al. 1998; Lunt 1990; King and Buckney
272 2001; Odgers 1994). Higher reproductive outputs of non-indigenous plant species, their wide dispersal
273 ability, suggests these species may form an ubiquitous seed rain across the landscape (Guntenspergen

274 and Levenson 1997; Bastin and Thomas 1999), while the positive response to disturbance, release from
275 potential predators and the presence of suitable germination sites are additional hypotheses proposed for
276 the successful establishment and expansion of non-indigenous species within remnant plant
277 communities (Lake and Leishman 2004; Baker 1974; Rejmánek 1996; Lodge 1993; Howard et al. 2004).
278 These characteristics also explain the high Sørensen's index of similarity between the soil seed bank and
279 the existing vegetation for non-indigenous species (Online Resource 3).

280 Only one eucalypt seedling was recorded in the soil seed bank, as would be expected from a genus that
281 largely stores seed in the canopy (Grant and MacGregor 2001; Yates et al. 1994), although it may also
282 be due to predation of seeds within the soil seed bank (Yates et al. 1995). The soil seed bank did contain
283 a number of seeds of *Acacia* spp., even where they were not recorded in the existing vegetation (Patches
284 6, 7 and 10). The presence of *Acacia* seedlings at these patches suggests that a lack of fire may be
285 restricting the opportunities for the recruitment of these species. This may be redressed in the future at
286 Patches 6 and 7 which experience an active ecological burning program, but is likely to persist in Patch
287 10 which is on private land that would only experience fire during a wildfire event.

288 Half the species recorded in the existing vegetation were present in the soil seed bank, leading to
289 relatively low similarity measures between the existing vegetation and the soil seed bank (Online
290 Resource 3) and their separation within an ordination space (Online Resource 4). This is similar to the
291 findings of other studies examining the soil seed bank and the composition of the existing vegetation,
292 and is largely due to the higher diversity of species in the existing vegetation compared to the soil seed
293 bank (Bossuyt et al. 2002; Kostel-Hughes et al. 1998; Lunt 1990). Most of the plant species recorded in
294 the soil seed bank were also present in the existing vegetation, but less than half of the species recorded
295 in the existing vegetation were recorded in the soil seed bank. This suggests that the soil seed bank does
296 not play a major role in maintaining species diversity within patches, as has been observed from studies

297 of herbaceous plants from grassland communities elsewhere in Victoria (Morgan 1998a, b; Clarke et al.
298 2000; Scott and Morgan 2012a).

299 The lack of a persistent soil seed bank suggests that direct seeding or planting would be a more
300 successful strategy for increasing indigenous plant diversity in these patches, rather than relying upon
301 regeneration from the soil seed bank (Morgan 1998b; Lunt 1990, 1997; Scott and Morgan 2012a). The
302 dominance of non-indigenous monocot seeds in the soil seed bank is another reason why the soil seed
303 bank may not be an effective option for increasing biodiversity within these patches (Lunt 1990;
304 Bossuyt et al. 2002). However, the indigenous species recorded may be an useful indicator of which
305 species could potentially be reintroduced.

306 Average annual rainfall increased the number of species recorded for each plot from the soil seed bank
307 for all of the combinations of understory species investigated. This strong response to the rainfall
308 gradient was also observed in the existing plant community (Hahs and McDonnell 2007), and may be
309 related to a productivity gradient. Plants growing in the patches with higher average annual rainfall may
310 experience lower moisture stress, and may be able to partition more energy into reproductive efforts than
311 similar individuals growing in lower rainfall areas. However, if average annual rainfall is the dominant
312 driver behind patterns of plant community composition, this plant community may be threatened by
313 changes to the local weather patterns associated with global climate change as rainfall in this area is
314 forecast to decrease by up to 13% by 2050 (Howe et al. 2005).

315 The abundance of seedlings per plot were not strongly related to rainfall, patch size, soil nutrients or
316 urbanisation, with all models having a DIC value similar to that for the null model. This suggests that
317 there may be other factors influencing the observed responses which were not captured by this study.

318 The soil seed bank in *E. camaldulensis* woodlands near Patches 11 and 12 was investigated in 1964 and
319 was dominated by *Anthoxanthum odoratum*, *Plantago lanceolata*, *Briza minor* and *Hypericum* sp.
320 (Carroll and Ashton 1965), species that were also frequently recorded in the current study. The
321 continued presence of many indigenous plant species in these patches, thirty years after large numbers of
322 non-indigenous species were recorded in the soil seed bank, indicates that these plant communities
323 continue to maintain viable populations of indigenous plant species in the long-term, even though these
324 species may only compose a small proportion of the total soil seed bank.

325 *In situ*, the seedlings that germinate may only a subset of the species that germinated under more
326 favourable glasshouse conditions (Jutila 2003). However, *ex-situ* germination may miss out on some
327 viable seeds as dormancy may not have been broken or the correct conditions for germination and
328 establishment may not have been met for all species (Jutila 2003). Therefore the composition of the soil
329 seed bank is merely an indication of the species which could germinate *in situ*.

330 While the soil seed bank can hold some of the ‘ecological memory’ of a site, this memory is likely to be
331 incomplete. Many different factors influence a successful seed set, including pollination, seed growth
332 and development, and finally the release and dispersal of those seeds to the soil seed bank (Pickett and
333 McDonnell 1989). This study has shown there are reasons to be optimistic about the persistence of this
334 plant community within the urban landscape. While the majority of the emergent seedlings were non-
335 indigenous monocots, the soil seed bank also contained seedlings of 43 indigenous species (39.8 %).
336 The persistence of 123 indigenous plants in the existing vegetation (Hahs and McDonnell 2007), even
337 when the soil seed bank appears to have been dominated by non-indigenous monocot species for over
338 thirty years (Carroll and Ashton 1965), indicates that these plant communities can be resilient to changes
339 in the landscape associated with urbanization; particularly when accompanied by management activities

340 that are able to ensure the continuation of previously occurring natural processes and minimize how
341 much of the extinction debt is realised over the next 50-100 years.

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349 **References**

- 350 Albrecht H, Eder E, Langbehn T, Tschiersch C (2011) The soil seed bank and its relationship to the
351 established vegetation in urban wastelands. *Landsc Urb Plan* 100: 87–97
- 352 Australian Bureau of Meteorology (2000) Average annual rainfall across greater Melbourne. Bureau of
353 Meteorology, Melbourne
- 354 Australian Bureau of Statistics (2003) Melbourne- A Social Atlas 2001- 2030. 2 edn. Australian Bureau
355 of Statistics, Canberra
- 356 Baker HG (1974) The evolution of weeds. *Annu Rev Ecol Syst* 5:1-24
- 357 Bastin L, Thomas CD (1999) The distribution of plant species in urban vegetation fragments. *Landsc*
358 *Ecol* 14 (5):493-507
- 359 Bossuyt B, Heyn M, Hermy M (2002) Seed bank and vegetation composition of forest stands of varying
360 age in central Belgium: consequences for regeneration of ancient forest vegetation. *Plant Ecol*
361 162 (1):33-48

- 362 Carroll EJ, Ashton DH (1965) Seed storage in soils of several Victorian plant communities. *Vic Nat*
363 82:102-110
- 364 Clarke PJ, Davison EA, Fulloon L (2000) Germination and dormancy of grassy woodland and forest
365 species: effects of smoke, heat, darkness and cold. *Aust J Bot* 48 (6):687-700
- 366 Department of Conservation and Environment (1992) Draft conservation program for native grasslands
367 and grassy woodlands in Victoria. Department of Conservation and Environment, Melbourne
- 368 Department of Natural Resources and Environment (2002a) Ecological Vegetation Classes. Department
369 of Natural Resources and Environment, Melbourne
- 370 Department of Natural Resources and Environment (2002b) Ecological Vegetation Classes pre-1750.
371 Department of Natural Resources and Environment, Melbourne
- 372 Fenner M, Thompson K (2005) *The Ecology of Seeds*. Cambridge University Press, Cambridge
- 373 Grant CD, MacGregor CM (2001) Topsoil seed banks in grazed and ungrazed eucalypt woodlands at
374 Newholme, Armidale, New South Wales, Australia. *New Zeal J Bot* 39:471-481
- 375 Grimm NB, Grove JM, Pickett STA, Redman CA (2000) Integrated approaches to long-term studies of
376 urban ecological systems. *BioScience* 50 (7):571-584
- 377 Guntenspergen GR, Levenson JB (1997) Understorey plant species composition in remnant stands along
378 an urban-to-rural land-use gradient. *Urban Ecosys* 1 (3):155-169
- 379 Hahs AK (2006) Measures of urbanisation and the ecology of remnant woodlands along an urban-rural
380 gradient. PhD, The University of Melbourne, Melbourne
- 381 Hahs AK, McDonnell MJ (2006) Selecting independent measures to quantify Melbourne's urban-rural
382 gradient. *Landsc Urban Plann* 78 (4):435-448. doi:10.1016/j.landurbplan.2005.12.005.
- 383 Hahs AK, McDonnell MJ (2007) Composition of the plant community in remnant patches of grassy
384 woodland along an urban-rural gradient in Melbourne, Australia. *Urban Ecosys* 10 (4):355-377

- 385 Hahs AK, McDonnell MJ, McCarthy MA, Vesk PA, Corlett RT, Norton BA, Clemants SE, Duncan RP,
386 Schwartz MW, Thompson K, Williams NSG (2009) A global analysis of plant extinction rates in
387 urban areas. *Ecol Lett* 12 (11):1165-1173. doi:10.1111/j.1461-0248.2009.01372.x
- 388 Hammer Ø, Harper DAT, RyanPD (2001) PAST: Paleontological Statistics Software Package for
389 Education and Data Analysis. *Palaeontologia Electronica* 4(1): 9pp
- 390 Holl KD, Crone EE, Schultz CB (2003) Landscape restoration: Moving from generalities to
391 methodologies. *BioScience* 53 (5):491-502
- 392 Howard TG, Gurevitch J, Hyatt L, Carreiro M, Lerdau M (2004) Forest invasibility in communities in
393 southeastern New York. *Biological Invasions* 6:393-410
- 394 Howe C, Jones RN, Maheepala S, Rhodes B (2005) Melbourne Water climate change study-
395 Implications of Potential Climate Change for Melbourne's Water Resources. A collaborative
396 Project between Melbourne Water and CSIRO Urban Water and Climate Impact Groups,
397 Melbourne
- 398 Jutila HM (2003) Germination in Baltic coastal wetland meadows: similarities and differences between
399 vegetation and seed bank. *Plant Ecol* 166 (2):275-293
- 400 Kent M, Coker P (1992) *Vegetation description and analysis: A practical approach*. CRC Press, Ann
401 Arbor, MI
- 402 King SA, Buckney RT (2001) Exotic plants in the soil-stored seed bank of urban bushland. *Aust J Bot*
403 49:717-720
- 404 Kostel-Hughes F, Young TP, McDonnell MJ (1998) The soil seed bank and its relationship to the above
405 ground vegetation in deciduous forests in New York City. *Urban Ecosys* 2 (1):43-61
- 406 Lake JC, Leishman MR (2004) Invasion success of exotic plants in natural ecosystems: the role of
407 disturbance, plant attributes and freedom from herbivores. *Biol Conserv* 117 (2):215-226

- 408 Leck MA, Parker VT, Simpson RL (eds) (1989) Ecology of Soil Seed Banks. Academic Press, Inc., San
409 Diego, CA
- 410 Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evol 8 (4):133-137
- 411 Lunt ID (1990) The soil seed bank of a long-grazed *Themeda triandra* grassland in Victoria.
412 Proceedings of the Royal Society of Victoria 102 (1):53-58
- 413 Lunt ID (1997) Germinable soil seed banks of anthropogenic native grasslands and grassy forest
414 remnants in temperate south-eastern Australia. Plant Ecol 130:21-34
- 415 McCarthy MA (2007) Bayesian methods for ecology. Cambridge University Press, Cambridge
- 416 McDonnell MJ, Hahs AK, Breuste JH (eds) (2009) Ecology of Cities and Towns: A comparative
417 approach. Cambridge University Press, Cambridge
- 418 Morgan JW (1998a) Comparative germination responses of 28 temperate grassland species. Aust J Bot
419 46 (2):209-219
- 420 Morgan JW (1998b) Composition and seasonal flux of the soil seed bank of species-rich *Themeda*
421 *triandra* grasslands in relation to burning history. J Veg Sci 9 (2):145-156
- 422 Oates A, Taranto M (2001) Vegetation mapping of the Port Phillip and Westernport Region. Arthur
423 Rylah Institute for Environmental Research, Melbourne
- 424 Odgers BM (1994) Seed banks and vegetation of three contrasting sites in an urban Eucalypt forest
425 reserve. Aust J Bot 42 (4):371-382
- 426 Rejmánek M (1996) A theory of seed plant invasiveness: the first sketch. Biol Conserv 78:171-181
- 427 Ross JH, Walsh NG (2003) A census of the vascular plants of Victoria. 7th edn. Royal Botanic Gardens,
428 South Yarra, Victoria

- 429 Simpson RL, Leck MA, Parker VT (1989) Seed banks: General concepts and methodological issues. In:
430 Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, Inc., San
431 Diego, CA, pp 3-8
- 432 Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A (2002) Bayesian measures of model complexity
433 and fit. *J Roy Stat Soc B* 64 (Part 4):583-639
- 434 Thackway R, Cresswell ID (1995) An Interim Biogeographic Regionalisation for Australia: a
435 framework for setting priorities in the National Reserves System Cooperative Program. Reserve
436 System Unit, Australian Nature Conservation Agency, Canberra
- 437 UNFPA (2007) State of the World Population 2007: Unleashing the potential urban growth. United
438 Nations Population Fund, New York
- 439 Victorian State Government (2009) Victoria in Future 2008: Victorian State Government Population and
440 Household Projections 2006–2036. Second Release: September 2009 edn. Victorian State
441 Government, Melbourne
- 442 Yates CJ, Hobbs RJ, Bell RW (1994) Factors limiting the recruitment of *Eucalyptus salmonophloia* in
443 remnant woodlands. I. Pattern of flowering, seed production and seed fall. *Australian Journal of*
444 *Botany* 42:531-542
- 445 Yates CJ, Taplin R, Hobbs RJ, Bell RW (1995) Factors limiting the recruitment of *Eucalyptus*
446 *salmonophloia* in remnant woodlands. II. Post-dispersal seed predation and soil reserves. *Aust J*
447 *Bot* 43:145-155
- 448
- 449

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451 Table 1. Total species richness and seedling abundance recorded for the soil seed bank. The proportion of the
 452 total number is shown in parentheses. The high number of seedlings of uncertain origin is largely due to the
 453 Cyperaceae species agglomeration, which contains both indigenous and non-indigenous species.

	Species Richness (%)	Seedling Abundance (%)
Total	108	32 558
Indigenous	43 (39.8 %)	1 827 (5.6 %)
Non-Indigenous	55 (50.9 %)	16 659 (51.2 %)
Uncertain Origin	10 (9.3 %)	14 072 (43.2 %)
Monocots	35 (32.4 %)	24 551 (75.4 %)
Dicots	70 (64.8 %)	7 989 (24.4 %)
Ferns	3 (2.8 %)	18 (0.1 %)

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455

456 **Figure Captions**

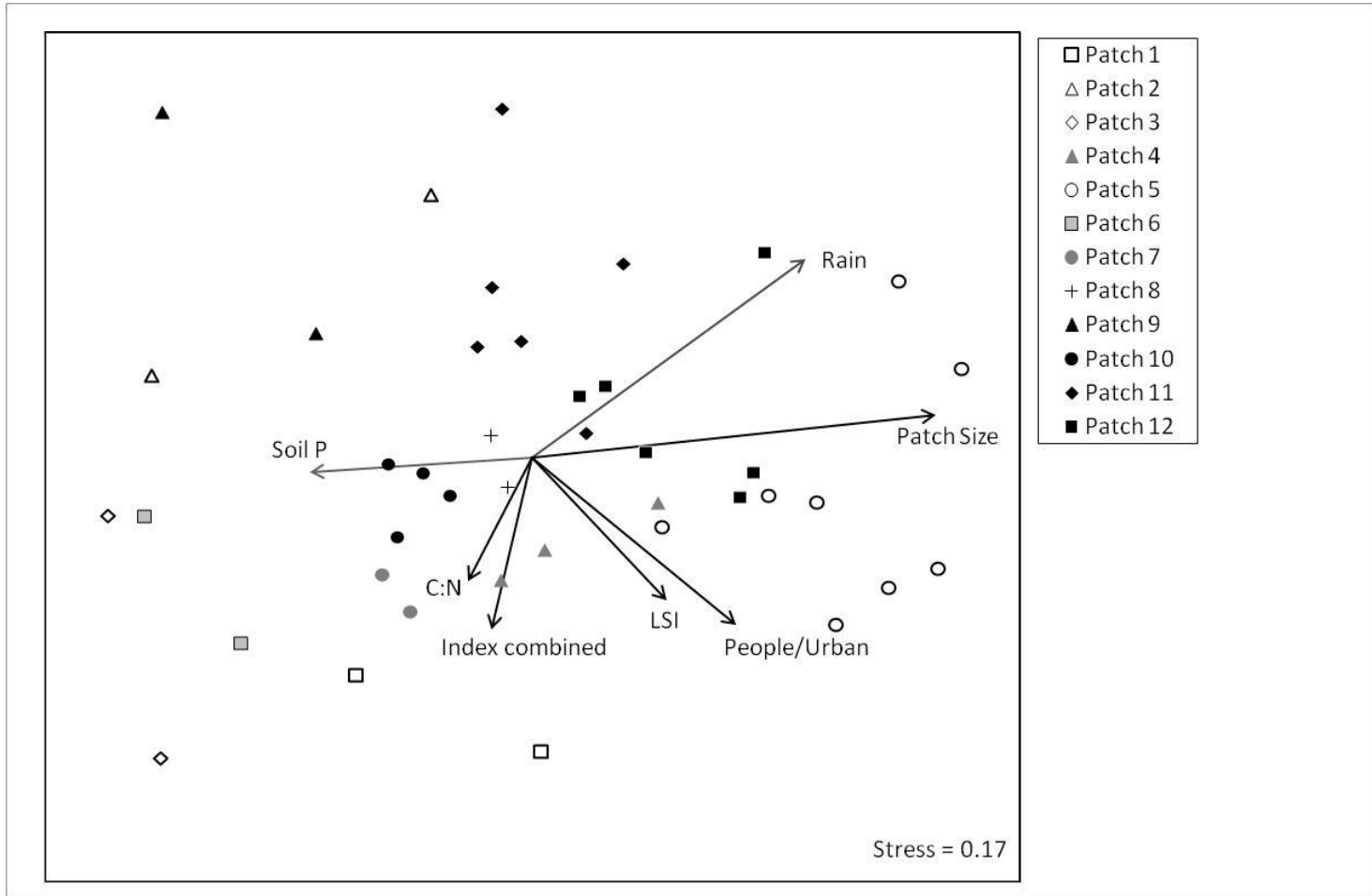
457 **Fig. 1** Non-metric multidimensional scaling ordination plots representing the composition of emergent
458 seedlings in each plot (N = 42). (□) Patch 1, (△) Patch 2, (◇) Patch 3, (▲) Patch 4, (○) Patch 5, (▣)
459 Patch 6, (●) Patch 7, (+) Patch 8, (▲) Patch 9, (●) Patch 10, (◆) Patch 11, (■) Patch 12. The vectors
460 represent the trends across the ordination space of for average annual rainfall (Rain), patch size (Patch
461 Size), Soil Carbon: Nitrogen Ratio (C:N), Available Inorganic Phosphorous (Soil P), Landscape shape
462 index (LSI), Index of urbanization combined (Index combined) and People per unit urban land cover
463 (People/Urban).

464

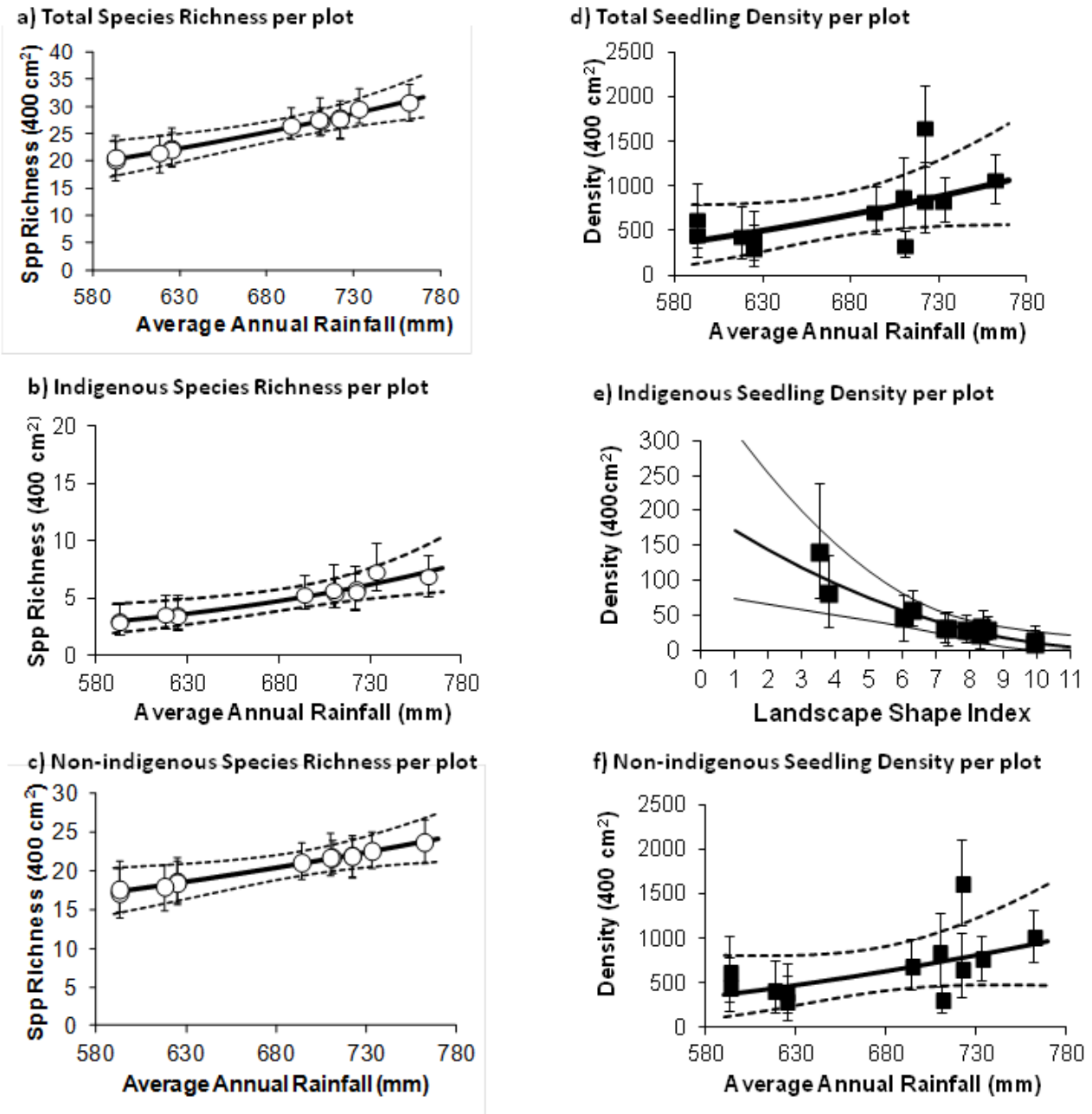
465 **Fig. 2** Graphs showing the predicted response of the best linear regression models developed at the
466 patch scale for species richness per plot using a) all species, b) indigenous species, and c) non-
467 indigenous species; and the linear regression models with the lowest DIC values for seedling abundance
468 per plot using d) all seedlings, e) indigenous seedlings, and f) non-indigenous seedlings. Species
469 richness per plot and seedling abundance per plot were averaged for each patch. The solid line
470 represents the predicted relationship between the predictor variable and the response variable. The
471 dashed lines represent the 95% credible intervals around the prediction, and are an indication of the
472 confidence around the model prediction, with tighter credible intervals representing greater reliability.
473 The actual data used to develop the models are shown as open circles (○) to represent the mean species
474 richness per plot for each patch, and as black squares (■) to represent the mean seedling density per plot
475 for each patch. The vertical bars represent the 95% credible interval on the estimate for the mean, and
476 are an indication of the variability observed between plots in the original data.

477

478



480 **Fig. 1**



481

482 **Fig. 2**