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Can habitat surrogates predict the response of target species to landscape change?

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20 Abstract

21 Surrogates are commonly used for monitoring biodiversity under a wide range of scenarios.
22 However, surrogates are not often evaluated under diverse ecological conditions, and this
23 hinders the identification of spatial and temporal boundaries of a surrogate's relationship with
24 its biodiversity metric, including whether a surrogate can predict biodiversity responses to
25 environmental change. We adapted a causal framework from the medical literature and
26 applied this framework to investigate the consistency of a well-established habitat surrogate
27 of arboreal marsupials: hollow-bearing trees. We tested the consistency of the relationship
28 between hollow-bearing trees and arboreal marsupials across four long-term studies (>10
29 years) covering different habitat types and environmental disturbance. We also tested the
30 ability of the change in hollow-bearing trees over time to predict the change in arboreal
31 marsupials over time. We found a somewhat consistent relationship between hollow-bearing
32 trees and relative abundance of arboreal marsupials, but the mechanistic details of this
33 relationship varied both by location and by species of arboreal marsupial. Similarly, the
34 surrogate approach was not able to predict trends over time, a result likely due to differences
35 in natural temporal variation between the surrogate and target species of interest. Our
36 investigation demonstrates that habitat surrogates can be very useful for certain aspects of
37 monitoring programs, but that serious limitations prevail when trying to monitor changes
38 over time, or if information on species-specific responses is required. Our new framework
39 can be readily applied to any biodiversity surrogate with an established mechanistic link
40 between the surrogate and biodiversity metric of interest.

41 Keywords (6): monitoring, surrogate, adaptive management, tree hollow, arboreal marsupial,
42 cavity nest

43

44 1. Introduction

45 Ecological surrogates are widely adopted by ecologists, and sought after by practitioners, as
46 substitutes for the difficult and costly task of measuring wholesale biodiversity (Noss 1990,
47 Dale and Beyeler 2001, Angelstam and Dönz-Breuss 2004, Sarkar et al. 2005, Rodrigues and
48 Brooks 2007, Butchart et al. 2010, Halpern et al. 2012, Noon et al. 2012). In this paper, we
49 define an ecological surrogate as a measure that “reflects the biotic or abiotic state of the
50 environment; represents the impact of an environmental change on a habitat, community or
51 ecosystem; represents the abundance of a particular species; or is indicative of the diversity of
52 a subset of taxa, or of wholesale diversity, within an area” (Lindenmayer et al. 2014).

53 A growing body of literature is dedicated to defining a wide range of ecological
54 surrogates for actions such as designing reserves and monitoring biodiversity and
55 effectiveness of management actions (McGeoch and Chown 1998, Wessels et al. 1999,
56 Lombard et al. 2003, Van Wynsberge et al. 2012, Koch et al. 2013, Kunkel et al. 2013). Yet,
57 many surrogates are not validated or only validated under a narrow range of spatial and
58 temporal conditions. Without subsequent evaluation, the temporal and spatial boundaries of a
59 surrogate’s effectiveness in reflecting the actual variable of interest remain unknown, and this
60 potentially limits its broader application. The lack of an established framework to test key
61 attributes of ecological surrogates in contrasting ecosystems, over time, or after a disturbance,
62 contributes to this critical knowledge gap affecting the usefulness of many surrogates.

63 Few studies of ecological surrogates include a rigorous test of the spatial and temporal
64 aspects of the surrogate relationship. Recent work has evaluated the effectiveness of
65 surrogates in selecting reserve designs based on their ability to reflect the distribution of the
66 patterns of interest, and compared results of different analytical methods to assess surrogacy
67 relationships. For example, (Grantham et al. 2010) evaluated alternate methods (incidental
68 representation, species accumulation index, and summed irreplaceability) for assessing a
69 variety of taxonomic surrogates and found that different methods ranked the effectiveness of
70 surrogates inconsistently.

71 Less work has been done to evaluate the effectiveness of ecological surrogates to
72 monitor biodiversity, subgroups such as threatened species, or responses to management
73 actions. Importantly, for a surrogate to be effective for monitoring, similar temporal trends
74 should be present, which requires monitoring both the surrogate and outcome of interest
75 (Favreau et al. 2006). Studies that do assess surrogates in multiple ecological scenarios often
76 focus on only one aspect of the surrogate relationship, such as different spatial scales
77 (Angelstam and Dönz-Breuss 2004, Banks-Leite et al. 2013, Morelli et al. 2013). For
78 example, Drever et al. (2008) found a consistent relationship between woodpecker richness
79 and overall avian richness across 23 sites in British Columbia, yet cautioned that this
80 relationship may break down during insect outbreaks when woodpeckers were likely to
81 respond differently to the overall bird community. Other studies have attempted to test the
82 limits of surrogates in different ways. Although these studies (and several others, e.g.
83 (Warman et al. 2004, Sarkar et al. 2005, Altmooß and Henle 2006, Favreau et al. 2006, Hess
84 et al. 2006, Rodrigues and Brooks 2007, Gollan et al. 2008, Dalleau et al. 2010, Grantham et
85 al. 2010, Lewandowski et al. 2010, Van Wynsberge et al. 2012, Gillison et al. 2013, Di Minin
86 et al. 2014, Lindenmayer et al. 2014)) provide specific examples of surrogate evaluation, they
87 are each done in very different ways. What is lacking in ecology, therefore, is a general
88 approach to the testing and evaluation of surrogacy relationships, and a simple framework to
89 guide surrogacy testing for monitoring purposes.

90 Here, we adapt a causal framework from the medical surrogate literature (sensu
91 (Atkinson et al. 2001)) to provide a stepwise process to guide the assessment of the
92 relationships between a surrogate and variables of interest (hereafter termed targets) (Fig. 1)
93 (Barton et al. in review). In this framework, a mechanistic link between a potential surrogate
94 and a target is identified (Fig. 1m); the relationship between the surrogate and target is tested
95 in a variety of environmental conditions, such as different habitat types (Fig 1A); the
96 surrogate's response to disturbance is evaluated under a range of treatment types (Fig 1B);
97 the target's response to disturbance is evaluated under the same treatment types (Fig 1B); and
98 the relationship between the temporal trend of the surrogate and the temporal trend of the
99 target is tested (Fig 1C). By quantifying the relationship between the surrogate and the target
100 under a range of spatial and temporal conditions, the strengths and limitations of the full
101 surrogate model are able to be more fully understood. Critical to this framework, however, is
102 a known mechanistic link between the surrogate and the target (Fig 1m). Habitat surrogates
103 often have a clear mechanistic link to the biodiversity metric being measured (Koch et al.
104 2013), and this provides the basis for why a consistent response to landscape change might be
105 expected by both the surrogate and the biodiversity metric of interest.

106 Hollow-bearing trees have a clear mechanistic link with cavity-dwelling vertebrates
107 globally, including birds, bats, invertebrates and a variety of terrestrial mammals through
108 provision of shelter and nesting resources (Fischer and McClelland 1983, Rose et al. 2001,
109 Gibbons et al. 2002, Ranius et al. 2005), and thus are considered a keystone structure for
110 biodiversity (Remm and Löhms 2011). Furthermore, hollow-bearing trees are an established
111 habitat surrogate for arboreal marsupials, which rely on hollows for roosting (Gibbons et al.
112 2002). Globally, numbers of hollow-bearing trees are declining in many forests and
113 agricultural areas (Lindenmayer et al. 2012) often resulting in declines in the fauna dependent
114 on hollows (Ranius et al. 2009). For this reason, they are monitored in different parts of the
115 world to provide information about their associated fauna (Fischer and McClelland 1983,
116 Lindenmayer and Wood 2010, Edworthy et al. 2012). We therefore expected a strong
117 relationship between the availability of hollow-bearing trees and the presence and relative
118 abundance of arboreal marsupials to persist under wide temporal and spatial conditions.

119 We tested the broader potential of hollow-bearing trees to act as a surrogate for
120 arboreal marsupial presence and abundance using the causal framework outlined in Fig. 1.
121 We used four long-term studies, each in a contrasting ecosystem, that have been monitored
122 for both hollow-bearing trees and arboreal marsupials for at least 10 years. Each of these
123 studies also included either fire or fragmentation as a distinct ecological disturbance during
124 the monitoring period. Thus, we had an unparalleled opportunity to test the framework over a
125 large spatial (~ 1000km) and temporal scale (> 10 years) on a key group of species that are of
126 conservation concern (e.g. endangered Leadbeater's possum (*Gymnobelideus leadbeateri*),
127 and the vulnerable squirrel glider (*Petaurus norfolcensis*) and yellow-bellied glider (*Petaurus*
128 *australis*)) to identify the boundaries of the surrogacy relationship. Using our large datasets,
129 and the framework shown in Fig 1, we addressed the following questions:

130 Q1) Are hollow-bearing trees (or hollows) consistently a surrogate for the occurrence
131 of arboreal marsupials (Fig. 1A)? In this context, we define "consistent" to be a repeated
132 observation of a significant correlative relationship between the surrogate and target. We
133 predicted that a relationship between the abundance of hollow-bearing trees and arboreal
134 marsupials will occur consistently across space and time given the dependence of arboreal
135 marsupials on hollows for daily roosting.

136 Q2) Do hollow-bearing trees and arboreal marsupials respond similarly, in terms of
 137 both biological and statistical significance, to landscape disturbance (i.e., a treatment such as
 138 fire) (Fig. 1B)? We predicted that a disturbance that primarily affects the roosting resource of
 139 arboreal marsupials (hollow-bearing trees) will result in similar responses (e.g., effect size
 140 and direction) of arboreal marsupials and hollow-bearing trees. However, a disturbance that
 141 affects other resources such as the availability of food resources may affect arboreal
 142 marsupials and hollow-bearing trees differentially.

143 Q3) Does the temporal trend in hollow-bearing trees predict the trend in arboreal
 144 marsupials (Fig. 1C)? Given the strong dependence on hollows for daily roosting activities,
 145 we predicted that overall trends in the abundance of hollow-bearing trees will predict overall
 146 trends in the abundance of arboreal marsupials.

147 The advantages of using our new framework include explicit identification of the
 148 spatial and temporal boundaries of the established surrogate relationship. Our study provides
 149 specific details of the limitations of the surrogate relationship between hollow-bearing trees
 150 and arboreal marsupials in southeastern Australia, but has much broader implications to the
 151 study of surrogates in ecosystems worldwide. This study provides a starting point for
 152 evaluating limitations on the use of hollow-bearing trees as a surrogate for hollow-dependent
 153 species, which are crucial for a wide variety of fauna globally (Fischer and McClelland 1983,
 154 Gibbons et al. 2002, Ranius et al. 2005). More broadly, the general framework presented can
 155 be applied to test any surrogate relationship that is based on a mechanistic link between the
 156 potential surrogate and the target of interest. Importantly, by providing a worked example of
 157 how to implement our stepwise framework, we demonstrate a new approach that will
 158 facilitate a more rigorous evaluation of other kinds of habitat surrogates.

159

160 2. Materials and Methods

161 2.1 Study sites

162 **Jervis Bay (JB)** – The Jervis Bay long-term monitoring study is located in Booderee National
 163 Park, Jervis Bay Territory, Australia (Fig. A1). Booderee National Park is characterized by a
 164 wide variety of habitat types, ranging from dry heathland to temperate rainforest, with fire
 165 being a common form of disturbance in the landscape (for details see (Lindenmayer et al.
 166 2008a)). Given the prevalence of fire in this landscape, we tested the treatment effect of
 167 recovery after recent fire, using three categories that describe how long it has been since the
 168 site burned: fire since 2000, fire since 2002, and fire since 2003.

169 We identified 107 sites, each with a 100m permanent transect, that had repeated
 170 surveys of both arboreal marsupials and hollow-bearing trees over time (Table 1; see
 171 Lindenmayer et al. 2008a for more details). Briefly, spotlighting was used for all arboreal
 172 marsupial counts except for common brushtail possums as this species was most often caught
 173 in wire cage traps (Lindenmayer et al. 2008b). Spotlighting entails an observer walking the
 174 100m permanent transect and recording the number of each arboreal marsupial species seen
 175 within 50m of the transect. Trapping was done for 3 day sessions, with cage traps set at the
 176 0m and 100m point along the 100m transect, in February 2004 and December 2012. Only
 177 initial captures were used as an index of relative abundance as it is most similar to
 178 spotlighting data. Hollow-bearing trees were counted in two 20 x 20 m vegetation plots
 179 located at the 20 m and 80 m points of the permanent transect; estimates used were the
 180 combined total of these counts.

181 **The Victorian Central Highlands (VCH)** – The Victorian Central Highlands forest
 182 management study is located in central Victoria (Fig. A1) primarily in montane ash forests
 183 dominated by Mountain Ash (*Eucalyptus regnans*), Alpine Ash (*Eucalyptus delegatensis*), or
 184 Shining Gum (*Eucalyptus nitens*) (for details, see Lindenmayer (2009)). Long-term datasets
 185 from these sites have previously been used to establish that hollow-bearing trees are a viable
 186 habitat surrogate for arboreal marsupials in undisturbed study sites (Lindenmayer et al. 2014).
 187 In 2009, a large fire occurred and burned approximately half the study sites. This provided a
 188 ‘natural experiment’ in which to evaluate the before/after treatment effect of fire on both
 189 arboreal marsupials and hollow-bearing trees.

190 We identified 124 1-ha sites with repeated surveys of both arboreal marsupials and
 191 hollow-bearing tree data, 68 of which burned in 2009 (Table 1). Arboreal marsupials were
 192 counted by stag-watching (Lindenmayer et al. 1991), where hollow-bearing trees (i.e. stags)
 193 are watched for one hour, starting 15 minutes prior to dusk, to observe arboreal marsupials
 194 emerging from hollows. The abundance of hollow-bearing trees was counted on the same
 195 sites; trees >0.5 m dbh were visually examined for cavities using binoculars and trees with
 196 hollows were marked and GPS locations recorded so that the same trees could be resurveyed
 197 (Lindenmayer and Wood 2010).

198
 199 **Nanangroe (NAN)** –The Nanangroe study is a longitudinal investigation designed to assess
 200 landscape matrix effects on fauna in eucalypt woodland remnants. Woodland remnants vary
 201 in size from 0.5 – 9.7 ha and are surrounded by either an agricultural matrix or a matrix of
 202 recently planted softwood plantations (*Pinus radiata*; planted in 1998-2000) (for details see
 203 Lindenmayer et al. (2001)). We tested the treatment effect of the change in the landscape
 204 matrix on the relationship between arboreal marsupials and tree hollow availability within
 205 woodland remnants.

206 We identified 105 sites that had temporal surveys completed (Table 1). Spotlighting
 207 surveys were used to count the number of each species of arboreal marsupial seen within 50
 208 m of permanent 200 m transects. The abundance of hollows (as opposed to hollow-bearing
 209 trees) was estimated as the average from three 20 m x 20 m vegetation plots located at the 0,
 210 100, and 200 m locations of a permanent 200 m transect.

211 **Southwest Slopes (SWS)** – The Southwest Slopes study is a longitudinal investigation
 212 established to monitor the effects of revegetation of agricultural landscapes on wildlife (for
 213 details see Cunningham et al. (2007)). Study sites are located within farms in the southern
 214 region of the southwest slopes of NSW (Fig. A1). We tested the treatment effect of differing
 215 restoration methods; some sites are naturally revegetated and some are planted vegetation.

216 We identified 157 sites with repeated sampling for both arboreal marsupials and
 217 hollow-bearing trees. Spotlighting surveys were used to count the number of each species of
 218 arboreal marsupial seen within 50m of the permanent 200 m transect. The abundance of
 219 hollow-bearing trees per ha was estimated by taking the average of the number of trees with
 220 hollows counted in each of three 20 x 20 m vegetation plots located at the 0, 100 and 200 m
 221 points along the transect and then multiplying this average by 25.

222

223 2.2 Statistical Analysis

224 To address the three key questions specified in the Introduction, we used a sequence
 225 of generalized linear models (GLMs) that each examined the relationships outlined in Fig.1.

226 Generalized linear models are commonly used in the surrogacy literature to assess the
 227 relationship between a potential surrogate and the variables that they may represent (e.g.,
 228 (Kirkman et al. 2012, Banks-Leite et al. 2013). Response variables in the form of count data
 229 were best suited to models with Poisson distributions, with a dispersion parameter estimated
 230 from the data to account for overdispersion. Response variables in the form of estimated
 231 trends were analysed using Gaussian distributions. Standard model-checking procedures were
 232 used to check the appropriateness of these distributions, in particular assessing the residuals
 233 of fitted models. All analyses were performed in GenStat 16 (VSN International 2013). In all
 234 cases, we used the total number of arboreal marsupials (including all species observed) as an
 235 index of relative abundance of arboreal marsupials. We evaluated the relative abundance of
 236 individual arboreal marsupial species as response variables when enough data were present (>
 237 20 observations).

238 We purposefully designed one simplistic model per question and applied them to
 239 multiple datasets collected from four long-term studies to test the consistency of the
 240 relationship between the surrogate and outcome of interest across time and space, without
 241 potential knowledge of the effect of covariates that also likely vary in space and time. While
 242 adding covariates to the models may improve their overall predictive capabilities, our goal
 243 was focused on evaluating the consistency of the surrogate – outcome relationship across
 244 space and time, as opposed to selecting the best predictive model in each study. This
 245 approach allows us to determine if the relationship between the surrogate and outcome is
 246 consistent enough for the surrogate to be applied in new systems without testing for the
 247 effects of new potential covariates over time. Our logic is that if covariates dominate the
 248 predictive relationship, then a direct measurement approach may be more efficient than
 249 seeking to use a surrogate relationship that requires measurement of covariates in conjunction
 250 with the surrogate. Here, we describe the details of each analysis and any modifications
 251 specific to each long-term study.

252 **Are hollow-bearing trees (or hollows) consistently a surrogate for arboreal marsupials?**

253 To address this question, we used a GLM with a Poisson distribution and a logarithm link and
 254 estimated the dispersion parameter to account for overdispersion. In each study, we used the
 255 abundance of hollow-bearing trees (hollows in Nanangroe) as an explanatory variable and the
 256 relative abundance of arboreal marsupials as a response variable (Fig 1A). We also used
 257 individual species as response variables when sufficient individuals were observed (> 20
 258 observations).

259 **Do hollow-bearing trees and arboreal marsupials show a similar response to landscape 260 disturbance, in terms of both biological and statistical significance?**

261 To address this question, we tested the effects of a treatment (e.g. fire), as an explanatory
 262 variable, on hollow-bearing trees and arboreal marsupials, each as response variables in
 263 separate models, to determine if these variables had similar responses to the same treatment
 264 in each study location. As both response variables are count data, we used a GLM with a
 265 Poisson distribution and a logarithm link and estimated a dispersion parameter to account for
 266 overdispersion. We began with a simple model that had the environmental change or
 267 treatment (Table 1) as the explanatory variable and the abundance of hollow-bearing trees as
 268 the response variable (Fig.1B). The next set of models tested a treatment effect on the relative
 269 abundance of all arboreal marsupials as well as individual species with sufficient
 270 observations (Fig. 1c). All the sites (except those in the Victorian Central Highlands) were
 271 exposed to a constant treatment between the two time-points. In the Victorian Central

272 Highlands, the treatment (the fire of 2009) affected some of the sites between the two time-
 273 points; we therefore used as response variables the change in the abundance of hollow-
 274 bearing trees and the change in the relative abundance of arboreal marsupials between the
 275 two time-points (Fig. 1B). We modelled these changes with a Gaussian distribution and
 276 identity link in the GLM. We evaluated biological significance using model coefficients as
 277 effect sizes and used $P < 0.05$ as the criterion for statistical significance.

278 **Does the trend in hollow-bearing trees predict the trend in arboreal marsupials?**

279 Finally, we tested whether the change in the relative abundance of arboreal marsupials could
 280 be explained by the change in the abundance of hollow-bearing trees under a range of
 281 environmental conditions and treatments (Fig 1C). We calculated the change in both the
 282 abundance of hollow-bearing trees and arboreal marsupials by calculating the difference
 283 between the most recent count and the initial count at each site:

$$284 \Delta_N = N_{t2} - N_{t1}$$

285 We used a linear regression (a GLM with a Gaussian distribution and identity link) to
 286 evaluate the relationship between the change in the relative abundance of arboreal marsupials
 287 and the change in the abundance of hollow-bearing trees.

288

289 3. Results

290 **Are hollow-bearing trees (or hollows) consistently a surrogate for arboreal marsupials?**

291 In all four study areas, the abundance of hollow-bearing trees was a significant variable in
 292 explaining the relative abundance of all arboreal marsupials recorded on the site. Effect sizes,
 293 expressed as percentages because we used a log-link in analyses, ranged from 1-32%, with
 294 Nanangroe showing the largest effect size (Fig. 2, Table 2). These effect sizes represent the
 295 increases in expected abundance of arboreal marsupials for each extra hollow-bearing tree (or
 296 hollow).

297 At Jervis Bay, estimates of relative abundance of arboreal marsupials included
 298 observations of the sugar glider, greater glider, common ringtail possum (*Pseudocheirus*
 299 *peregrinus*), and common brushtail possum (*Trichosurus vulpecula*); the last three had
 300 sufficient data to evaluate individually. The greater glider and the common brushtail possum
 301 exhibited a significant relationship with the abundance of hollow-bearing trees, with the
 302 greater glider showing the largest effect size (25%; Fig. 2).

303 In the Victorian Central Highlands, estimates of relative abundance of arboreal
 304 marsupials included observations of the feathertail glider (*Acrobates pygmaeus*), yellow-
 305 tailed glider, eastern pygmy possum (*Cercartetus nanus*), Leadbeater's possum, greater glider
 306 (*Petauroides volans*), sugar glider, and mountain brushtail possum (*Trichosurus*
 307 *cunninghami*); of which the last four had sufficient data to evaluate independently. We found
 308 a significant relationship between the abundance of hollow-bearing trees and the relative
 309 abundance of each individual species (Table 2). The greater glider and sugar glider showed
 310 the largest effect size (8%) and Leadbeater's possum had the smallest effect size (4%; Fig. 2).

311 At Nanangroe, estimates of relative abundance of arboreal marsupials included
 312 observations of the sugar glider, squirrel glider (*Petaurus norfolcensis*), common ringtail
 313 possum, and common brushtail possum; the last two had sufficient data to evaluate

314 independently. However, only the common ringtail possum exhibited a significant
315 relationship with the abundance of hollows, with a large effect size (32%; Fig. 2).

316 At Southwest Slopes, estimates of relative abundance of arboreal marsupials included
317 observations of the squirrel glider, the common ringtail possum, and the common brushtail
318 possum; the last two species had sufficient data to evaluate independently. There was a
319 significant relationship between the abundance of hollow-bearing trees per ha and the relative
320 abundance of both the common ringtail possum and the common brushtail possum (Table 2).
321 However, these relationships all had very low effect sizes (2-3 %; Fig. 2).

322 **Do hollow-bearing trees and arboreal marsupials show a similar response to landscape** 323 **disturbance, in terms of both biological and statistical significance?**

324 Across all studies, we found that hollow-bearing trees and arboreal marsupials had similar
325 responses to treatment effects (Fig. 3, Table 3). In addition, relationships between treatment
326 and arboreal marsupials and between treatment and hollow-bearing trees were either both
327 significant or both non-significant within each study (Table 3).

328 In the Victorian Central Highlands, we examined how fire affected the change in
329 hollow-bearing trees and arboreal marsupials over time since the treatment occurred after
330 initial surveys. Both hollow-bearing trees and arboreal marsupials were significantly affected
331 by fire, showing similar effect sizes (Fig. 3). This relationship appears to be driven by
332 Leadbeater's possum (Table 3) and other rare observations of species included in the relative
333 abundance of arboreal marsupials. The greater glider and the mountain brushtail possum did
334 not show a significant response to the 2009 fire (Table 3).

335 At Jervis Bay, all three categories of time since fire responded similarly, so we
336 present only the treatment 'fire since 2000'. The relative abundance of arboreal marsupials
337 did not respond significantly to recent fire (Table 3). The effect on abundance of hollow-
338 bearing trees was marginally non-significant ($P = 0.086$), and the greater glider showed a
339 significant response to recent fire (Table 3).

340 At Nanangroe, the effect on the abundance of hollows was not significant ($P = 0.057$),
341 but our results suggest that a negative relationship between pine matrix surrounding the
342 remnant woodland patches and the abundance of hollows may exist (Table 3). Arboreal
343 marsupials did not exhibit a significant response to matrix type (Table 3).

344 At Southwest Slopes, we found highly significant responses of all variables to
345 restoration method, which is planting new vegetation, as well as very large positive effect
346 sizes associated with the naturally revegetated patches (Fig. 3; Table 3).

347 **Does the trend in hollow-bearing trees predict the trend in arboreal marsupials?**

348 We found no significant relationships between $\Delta_{\text{hollow-bearing trees}}$ and $\Delta_{\text{arboreal marsupials}}$, indicating
349 that the change over time in the abundance of hollow-bearing trees does not predict the
350 change in relative abundance of arboreal marsupials (Table 4). However, in the Victorian
351 Central Highlands, there was a weak relationships between $\Delta_{\text{hollow-bearing trees}}$ and Δ_{arboreal}
352 marsupials ($P = 0.087$). There was large variation in the change over time in both hollow-bearing
353 trees and arboreal marsupials, which does not appear to be associated with treatments (Fig.
354 4). If the relative abundance of arboreal marsupials consistently increased or decreased with
355 the abundance of hollow-bearing trees, we would expect to see a pattern of responses that is
356 restricted to the upper right and lower left quadrants of the bubbleplot (Fig. 4).

357

358 4. Discussion

359 The widespread application of surrogates in important areas of applied ecology and
360 conservation biology demands that they be subject to rigorous evaluation. In this study, we
361 used a causal framework to evaluate whether a habitat-based surrogate (hollow-bearing trees)
362 acts as a consistent and effective proxy for arboreal marsupials across a wide geographic
363 area, an array of ecosystems, and in response to a range of different disturbance types.
364 Overall, hollow-bearing trees performed consistently as a surrogate for the abundance of
365 arboreal marsupials. Additionally, we found a surprising level of concordance (in terms of
366 statistical significance and effect size) between the effect of a diverse range of treatments on
367 hollow-bearing trees and arboreal marsupials (Fig. 3). However, there were several location-
368 specific and species-specific responses that may shed light on the potential limitations of this
369 surrogacy relationship. Temporal changes in abundance of hollow-bearing trees were not able
370 to accurately predict how the abundance of arboreal marsupials will change over time,
371 especially in relation to treatment effects. As we discuss below, this has serious implications
372 for monitoring programs for biodiversity that rely on ecological surrogates to inform how the
373 target of interest responds temporally to landscape change.

374 4.1 Advantages to using a causal framework for testing surrogates

375 The framework applied in this study allowed us to test key attributes of an established habitat
376 surrogate in a stepwise process that clearly identified spatial and temporal boundaries of the
377 surrogate relationship. For example, we determined that the surrogate relationship was not
378 consistent within habitat types (i.e., open woodland) by testing the relationship between
379 hollow-bearing trees and arboreal marsupials under a variety of ecological conditions, which
380 was not expected of a habitat-based surrogate. Additionally, by explicitly testing the
381 relationship between the change over time in the surrogate and the target, we learned that the
382 surrogate relationship is limited to a fairly weak correlation averaged over one point in time.
383 Importantly, this suggests monitoring trends in the surrogate may not provide useful
384 information about trends in the target of interest. We were able to determine this important
385 limitation to an established habitat-based surrogate by using an explicit framework. This
386 approach of evaluating different spatial and temporal aspects of the surrogate relationship in a
387 structured and step-wise way (Fig. 1) can be applied to any biodiversity surrogate in any
388 ecosystem worldwide. We suggest that this new approach presents a real step forward in
389 ecological surrogate research, and provides a general and widely applicable method to
390 evaluating surrogates.

391 Recently, it has been recognized that a move toward predictive models with an
392 explicit link between the surrogate and target outcome is the next step in improving the
393 application of surrogates for conservation planning (Barton et al. in review, Collen and
394 Nicholson (2014)). Extensive review of the literature has been done of the effectiveness of
395 ecological surrogates for systematic conservation planning in both marine (Mellin et al. 2011)
396 and terrestrial environments (Lewandowski et al. 2010). In both meta-analyses, effectiveness
397 was evaluated in relation to the surrogate being better than random, while predictive ability
398 was only considered in the review of surrogates in the marine environment. Our framework
399 advocates a proactive approach to considering the predictive ability of the surrogate in
400 relation to the target under a variety of scenarios to identify boundaries prior to application.

401 4.2 Spatial limitations

402 The strength of the correlative relationship between hollow-bearing trees and arboreal
403 marsupials varied both among study locations and among species within locations. As a

404 group, arboreal marsupials had the strongest relationship with tree hollows at Nanangroe and
 405 the weakest with hollow-bearing trees at Southwest Slopes. The large disparity in effect size
 406 between these sites was somewhat surprising given these regions are both relatively close to
 407 one another (~ 100km; Fig. A1) and are both open woodland habitats.

408 Effect sizes varied substantially among different locations. Both the Victorian Central
 409 Highlands and Southwest Slopes had fairly consistent effect sizes among the species within
 410 each respective site, as well as the cumulative arboreal marsupial count. This pattern supports
 411 a consistent relationship between each individual species and hollow-bearing trees, indicating
 412 the habitat surrogate is performing fairly well at representing the suite of species at these
 413 sites. At Nanangroe and Jervis Bay, effect sizes varied greatly among individual species
 414 present at each location. This pattern suggests hollow-bearing trees perform well as a
 415 surrogate for some arboreal marsupials, but not others.

416 4.3 Species-specific responses

417 The greater glider, common ringtail possum and the common brushtail possum were present
 418 in more than one study area. The greater glider was the only species that consistently
 419 exhibited a significant relationship with hollow-bearing trees, as well as showing the largest
 420 effect size in both locations where it was detected (Fig 2).

421 The common ringtail possum and common brushtail possum were present at Jervis
 422 Bay, Nanangroe and Southwest Slopes. The common ringtail possum exhibited a significant
 423 relationship with hollow-bearing trees in both open woodland sites (Nanangroe and
 424 Southwest Slopes). However, the strength of the relationship was quite large in Nanangroe
 425 (effect size 32%) and very low at the Southwest Slopes (3%). This large difference may be
 426 explained by the different treatments at each site as the common ringtail possum may benefit
 427 from a pine matrix that surrounds remnant patches of eucalypt woodland (Lindenmayer et al.
 428 2001). There was no relationship between the common ringtail possum and hollow-bearing
 429 trees at Jervis Bay ($P=0.89$). The common brushtail possum had a significant relationship
 430 with hollow-bearing trees at Jervis Bay and Southwest Slopes, but not at Nanangroe.

431 The relationship between treatments, hollow-bearing trees and arboreal marsupials
 432 also showed species-specific responses. For example, in the Victorian Central Highlands, the
 433 effect of fire on arboreal marsupials appeared to be driven solely by the response of
 434 Leadbeater's possum. Conversely, at Jervis Bay, there was no significant effect of recent fire
 435 on hollow-bearing trees or on arboreal marsupials. However, there was a highly significant
 436 effect of fire on the greater glider when evaluated individually.

437 The variation in the surrogacy relationship at a given location and for individual
 438 species suggests there are some limitations to the information the surrogate is providing about
 439 the target of interest. Hollow-bearing trees indicate the presence of arboreal marsupials.
 440 However, there is not a consistent relationship between the abundance of trees and the
 441 abundance of arboreal marsupials (Fig. 2) which complicates the use of hollow-bearing trees
 442 for monitoring trends in the relative abundance of arboreal marsupials. Additionally, the
 443 surrogacy relationship is driven by different species in different locations suggesting that
 444 management actions directed at a particular species may need direct monitoring as opposed to
 445 a surrogate approach (Lindenmayer and Likens 2011).

446 4.4 Can habitat surrogates predict the response of target species over time?

447 Generally, the temporal trend we observed in hollow-bearing trees did not predict the
 448 temporal trend observed in arboreal marsupials. This is a critical temporal limitation. There
 449 are several potential reasons which may explain why the surrogacy relationship breaks down
 450 when assessing different temporal trends. The combined sampling variation from sampling
 451 both hollow-bearing trees and arboreal marsupials in our data may have been large enough to
 452 obscure a signal (if it occurred). Estimates of hollow-bearing trees may not have much
 453 sampling variation given most trees are marked and mapped, or occur on permanent
 454 transects. However, sampling variation of arboreal marsupial abundance can vary based on
 455 factors such as sampling method, weather, observer, and time of year. This means that
 456 estimates of sampling variation in both the surrogate and the target are necessary to tease
 457 apart the reason for the lack of support for the relationship between the change in the number
 458 of hollow-bearing trees and the change in the number of arboreal marsupials.

459 Natural variation in hollow-bearing trees likely varies at different time scales than for
 460 arboreal marsupials. Hollows take a long time to form in trees and therefore hollow
 461 recruitment is likely to occur at a relatively steady rate over long time frames due to natural
 462 process such as decay and insects, or in a 'pulse' due to natural process such as fire
 463 (Lindenmayer and Wood 2010). A decline in hollow-bearing trees can be dependent on many
 464 environmental factors, such as drought or fire. For example, the 2009 fire in the Victorian
 465 Central Highlands had an overwhelmingly negative effect on the abundance of hollow-
 466 bearing trees with many trees being burned or collapsing after the fire (Lindenmayer et al.
 467 2012). Natural variation in arboreal marsupials can vary annually based on variation in
 468 annual reproduction, mortality, and movement in and out of sampling areas. In the Victorian
 469 Central Highlands, we observed the relative abundance of arboreal marsupials varying among
 470 burned sites (Fig. 4) which could be linked to site specific variables such as food resources.
 471 Changes in the target variable may therefore occur over different time scales, and at different
 472 relative magnitudes as compared with the surrogate variable, potentially masking or
 473 preventing predictive relationships. This has significant implications when linking surrogates
 474 and the target entities for which they are intended to be proxies.

475

476 5. Implications for Conservation and Management

477 Our work suggests that even a habitat surrogate with a clear mechanistic link to the target of
 478 interest has limitations in providing information about species-specific and location-specific
 479 responses. If managers need detailed information on species-level responses or are interested
 480 in tracking trends over time, then direct monitoring of the target of interest (i.e., directly
 481 measuring the biodiversity metric of interest such as abundance of arboreal marsupials) may
 482 be more appropriate than using a surrogate approach (Lindenmayer and Likens 2011).
 483 However, if managers are interested in the status of general diversity of a suite of species,
 484 then a habitat-based surrogate approach may have merit.

485 We recommend the use of our framework to evaluate surrogacy relationships across a
 486 range of scenarios prior to their application. Ecologists and managers can apply this
 487 framework to established surrogates to determine if a surrogacy relationship persists in
 488 distinct environments, and therefore if it can be used in areas other than where the surrogate
 489 is established. For example, this framework could be used to identify the spatial and temporal
 490 boundaries of an established habitat surrogate such as percent tree cover as a surrogate for
 491 avian richness. Similarly, the framework provides a good way to determine if a surrogate is
 492 robust to disturbances and if the surrogate can provide useful information about the target

493 over time. Such an approach can greatly enhance understanding of the broader applicability
494 of the surrogate, which is essential for their improvement.

495

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668 **Tables**669 **Table 1. Summary of study site data used**

Study	Treatment	Number of sites with temporal samples	Hollows sampling method	Hollows Year1	Hollows Year2	Arboreal marsupials sampling method	Arboreal marsupials Year1	Arboreal marsupials Year2
Jervis Bay	Recent fire (2000+)	107 (recent fire = 79; no recent fire = 28)	Number of trees w/ hollow	2004	2012	spot lighting + trapping	2004	2013
Victorian Central Highlands	Recent fire (2009)	124 (recent fire = 68; no recent fire = 56)	Number of trees w/ hollow	1997	2009	Stag watching	1997	2010-2012
Nanangroe	landscape matrix	105 (pine matrix = 55; agricultural matrix = 50)	Number of hollows	1999	2010	spotlighting	1999	2011
Southwest Slopes	restoration method	157 (remnants = 121; plantings = 36)	Number of trees w/ hollows/ha	2002	2013	spotlighting	2002	2013

670

671 **Table 2. Results from GLM with arboreal marsupials as the response variable and the number of hollows**
 672 **or hollow-bearing trees as the explanatory variable (as in Figure 2).** A Poisson distribution with log-link
 673 was used; estimates have not been back-transformed.

Response variable	coeff	SE	dispersion 'c'	P
Jervis Bay				
all arboreal marsupials	0.1273	0.0428	1.31	0.003
greater glider	0.2208	0.0530	0.55	<0.001
common ringtail possum	0.0116	0.0701	0.69	0.869
common brushtail possum	0.1346	0.0538	0.86	0.013
Victorian Central Highlands				
all arboreal marsupials	0.0635	0.0109	2.54	<0.001
greater glider	0.0764	0.0135	1.42	<0.001
mountain brushtail possum	0.0579	0.0152	1.31	<0.001
leadbeaters possum	0.0416	0.0208	1.77	0.047
sugar glider	0.0761	0.0200	1.04	<0.001
Nanangroe				
all arboreal marsupials	0.1951	0.0541	1.50	<0.001
common ringtail possum	0.2762	0.0548	0.98	<0.001
common brushtail possum	0.0869	0.0811	1.08	0.285
Southwest Slopes				
all arboreal marsupials	0.02214	0.00271	2.31	<0.001
common ringtail possum	0.02552	0.00308	1.71	<0.001
common brushtail possum	0.01794	0.00337	1.39	<0.001

674

675

676 **Table 3. Results from GLM with arboreal marsupials or number of hollows or hollow-bearing trees as**
 677 **the response variable and treatment as the explanatory variable.** A Poisson distribution with log-link was
 678 used for the Jervis Bay, Nanangroe and Southwest Slopes studies; estimates have not been back-transformed. In
 679 Victorian Central Highlands, the change in the number of arboreal marsupials and hollow-bearing trees was
 680 used as a response variable since the treatment occurred between sampling periods, using a Gaussian
 681 distribution with an identity link.

Response variable	coeff	SE	dispersion 'c'	P
Jervis Bay				
hollow-bearing trees	-0.339	0.197	2.59	0.086
all arboreal marsupials	-0.102	0.246	1.35	0.679
greater glider	-1.037	0.317	0.56	0.001
common ringtail possum	-0.056	0.324	0.69	0.862
common brushtail possum	0.654	0.383	0.87	0.089
Victorian Central Highlands				
hollow-bearing trees	1.811	0.408	na	<0.001
all arboreal marsupials	1.519	0.479	na	0.002
greater glider	0.085	0.208	na	0.684
mountain brushtail possum	0.106	0.212	na	0.618
leadbeaters possum	0.675	0.287	na	0.020
Nanangroe				
hollows	-0.341	0.178	1.28	0.057
all arboreal marsupials	-0.067	0.202	1.57	0.742
common ringtail possum	-0.302	0.253	1.06	0.234
common brushtail possum	0.141	0.233	1.08	0.546
Southwest Slopes				
hollow-bearing trees	3.118	0.427	16.60	<0.001
all arboreal marsupials	2.178	0.388	2.26	<0.001
common ringtail possum	2.284	0.508	1.75	<0.001
common brushtail possum	1.991	0.417	1.32	<0.001

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683

684 **Table 4. Results from GLM with the change in the number of arboreal marsupials between time-points as**
 685 **the response variable and the change in the number of hollows or hollow-bearing trees as the explanatory**
 686 **variable.** A Gaussian distribution with an identity link was used in all models.

Response variable	coeff	SE	<i>P</i>
Jervis Bay			
all arboreal marsupials	-0.0214	0.0602	0.723
greater glider	0.0032	0.0353	0.929
common ringtail possum	-0.0329	0.0331	0.323
common brushtail possum	-0.0705	0.0438	0.11
Victorian Central Highlands			
all arboreal marsupials	0.174	0.101	0.087
greater glider	0.0645	0.0425	0.132
mountain brushtail possum	0.013	0.0437	0.766
leadbeaters possum	0.0408	0.0603	0.5
Nanangroe			
all arboreal marsupials	-0.0755	0.0865	0.385
common ringtail possum	-0.0232	0.0443	0.602
common brushtail possum	-0.0477	0.0651	0.466
Southwest Slopes			
all arboreal marsupials	0.01502	0.00956	0.118
common ringtail possum	0.00451	0.00581	0.438
common brushtail possum	0.01115	0.0062	0.074

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688

689 **Figure Legends**

690 **Figure A1. A map of Australia with the four study locations**

691 **Figure 1. A conceptual diagram describing the framework for evaluating the efficacy of**
692 **an ecological surrogate in monitoring a target of interest.**

693

694 **Figure 2. Responses of the relative abundance of arboreal marsupials to the abundance**
695 **of hollow-bearing trees (or hollows in Nanangroo) across the four study locations.** All
696 responses, except the common ringtail possum in Jervis Bay and the common brushtail
697 possum in Nanangroo, were significant ($P < 0.05$). Effect sizes are back-transformed from the
698 log scale, and expressed as percentages on the y-axis, which has a log-scale. Error bars
699 represent standard errors. Species abbreviations are as follows; ALL: all arboreal marsupials
700 recorded in the study; GG: greater glider; MBP: mountain brushtail possum; LP: leadbeater's
701 possum; CRP: common ringtail possum; CBP: common brushtail possum.

702

703 **Figure 3. Responses of the abundance of hollow-bearing trees (or hollows in Nanangroo)**
704 **and the relative abundance of arboreal marsupials to various treatments in each of the**
705 **four study locations.** Treatment type is indicated beneath each study. The x-axis represents
706 hollow-bearing trees or number of hollows (HBT) and all arboreal marsupials recorded in
707 each study (AM). Effect sizes are expressed as percentages on the y-axis, which has a log-
708 scale, except for in the Victorian Central Highlands. In the Victorian Central Highlands, the
709 change in the number of arboreal marsupials and hollow-bearing trees was used as a response
710 variable since the treatment occurred between sampling periods; therefore we used a
711 Gaussian distribution with an identity link. Error bars represent standard errors.

712

713 **Figure 4. The change in the number of hollows or hollow-bearing trees ($\Delta_{\text{hollow-bearing trees}}$)**
714 **plotted against the change in the number of arboreal marsupials ($\Delta_{\text{arboreal marsupials}}$) in all**
715 **four study areas.** The area of the bubble reflects the number of observation at each point.
716 For each study area, points are stratified by treatment. The plots show a scatter of both
717 positive and negative responses supporting the lack of a correlative relationship between the
718 change in the number of hollow-bearing trees and the change in the number of arboreal
719 marsupials over time.

720