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1 **Bottom-up and top-down processes influence contemporary patterns of mammal species**
2 **richness in Australia's monsoonal tropics.**

3

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18

19 **Abstract**

20 In recent decades severe mammal declines have occurred in the vast and uncleared tropical savannas
21 of northern Australia. Mounting evidence suggests that feral cats (*Felis catus*), large feral herbivores
22 and increased frequency of high-severity fires, are all contributing to declines; however, the respective
23 influence of each threat remains unclear. There is an urgent need to quantify the relative impacts of
24 both 'bottom-up' (i.e. the depletion of resources and habitat simplification from contemporary
25 disturbance regimes) and 'top-down' (i.e. increased predation pressure) factors on small mammal
26 populations to inform where, and how, remedial conservation efforts should be targeted in northern
27 Australia. We conducted an extensive survey of mammals across ca. 370,000 km² of monsoonal
28 northern Australia using both camera-trapping and live-trapping methods. From multispecies
29 occupancy models, we found that feral herbivore abundance, dingo abundance and feral cat
30 occupancy were the best predictors of species richness of small (<5500 g) mammals, with species
31 richness declining as the respective pressures increased. Our results highlight that underlying
32 productivity has seemingly enhanced the capacity of native mammals to withstand pressures, as
33 species that have severely declined are now more likely to occur in areas with greater productivity.
34 We suggest that a disturbance-driven reduction in habitat complexity and productivity has
35 significantly disrupted bottom-up processes in northern Australia, subsequently increasing top-down
36 pressure from predation, causing severe declines across much of the native mammal assemblage.

37 Without maintaining, enhancing or recovering habitat condition in this region, long-term conservation
38 and recovery of mammal diversity is unlikely.

39

40 **Introduction**

41 Australia is one of the Earth's 'megadiverse' countries (Mittermeier et al. 1999). The significance of its
42 biodiversity is partly due to the continent's rich endemic mammal fauna (Woinarski et al. 2015).

43 However, since European colonisation 230 years ago, there has been an exceptional rate of extinction
44 of Australia's mammals (Woinarski et al. 2015). Extensive mammal declines were first observed in
45 the temperate and arid regions of Australia, and have been particularly severe for species within the
46 so-called 'critical weight range' (CWR, 35–5500 g; Burbidge & McKenzie, 1989). Changes in both
47 'bottom-up' (habitat modification through land clearing/production, overgrazing by livestock and
48 feral herbivores, and altered fire regimes) and 'top-down' processes (introduction of invasive
49 mesopredators: red fox [*Vulpes vulpes*] and feral cat [*Felis catus*]) have been identified as probable
50 causes of Australia's mammal declines (McKenzie et al. 2007, Woinarski et al. 2015). More recently,
51 severe mammal declines have been detected across the vast, uncleared tropical savannas of northern
52 Australia (Woinarski et al. 2010). The cause/s of these declines have been particularly difficult to
53 identify as they have mainly occurred in remote regions where environmental changes since European
54 arrival have been subtle and/or inconspicuous (Woinarski et al. 2011).

55

56 There is mounting evidence that multiple threats have contributed to northern Australia's mammal
57 declines (Legge et al. 2011, Lawes et al. 2015, Legge et al. 2019). Key threatening processes in
58 northern Australia are similar to those identified elsewhere in Australia, including predation by feral
59 cats (Southgate et al. 1996, Frank et al. 2014, Davies et al. 2017) and habitat degradation by both
60 large feral herbivores (Legge et al. 2011) and increased frequency and severity of fires (Lawes et al.
61 2015). Increased fire activity (increased frequency and severity of fires) and heavy grazing by feral
62 herbivores have likely caused long-term changes to habitat structural complexity within the tropical
63 savannas by consuming biomass and destroying critical resources (particularly food and shelter) for
64 native species (Sharp and Whittaker 2003, Vigilante and Bowman 2004, Russell-Smith et al. 2012). In
65 contrast to southern and central Australia, the red fox is absent from the tropical savannas. However,
66 feral cats are well established and predation by cats has been linked to the disproportionate decline of
67 CWR mammals (Woolley et al. 2019).

68

69 Collectively, recent studies demonstrate a complex interaction between feral cats, heavy grazing by
70 livestock and feral herbivores, and frequent high-severity fires. In northern Australia, local
71 movements of feral cats respond to simplified habitat structure, with cats moving to and likely having
72 greater predation success in recently-burnt areas and areas with an open understorey (McGregor et al.
73 2014, Leahy et al. 2016). Conversely, feral cat occurrence is low in structurally complex habitats,

74 including both topographically rugged (Hohnen et al. 2016) and productive habitats (Stobo-Wilson et
75 al. *in press*). This behaviour is likely due to the greater hunting efficiency of feral cats in open
76 habitats, compared to rugged, rocky areas or areas with dense ground cover (McGregor et al. 2015).
77 Thus, the habitat simplification that occurs under prevailing fire and grazing regimes has a
78 compounding impact on mammal populations through the initial loss of resource availability, and
79 subsequent increased predation pressure from feral cats. Disturbance-driven habitat simplification
80 may also augment impacts of other predators, such as the dingo (*Canis familiaris dingo*), through
81 greater access to prey. Dingoes prey on CWR mammals (Corbett 1995, Stokeld et al. 2018), are more
82 active in open habitats (Morrant et al. 2017a) or following fire events (Leahy et al. 2016), and are
83 scarce in topographically complex habitats (Stobo-Wilson et al. *in press*). It is therefore plausible that
84 disturbance regimes mediate the distribution of mammalian predators more generally throughout the
85 landscape, and are subsequently the primary driver of mammal declines in northern Australia.
86 Disentangling whether bottom-up (i.e. the depletion of resources and habitat simplification) or top-
87 down factors (i.e. predation by the feral cat) have a greater impact on small mammal populations, or
88 whether these have similar and complementary impacts, is critical to informing where to target
89 conservation efforts and which management actions to implement.

90
91 The scarcity of detailed historical records of mammal occurrence, coupled with spatial and temporal
92 changes in threatening processes, severely impedes our ability to link changes in mammal
93 assemblages to the onset or increased severity of threats. Instead the primary drivers of small mammal
94 decline in northern Australia can be inferred by quantifying the bottom-up and top-down factors most
95 likely influencing mammal populations and mapping the current distribution of mammals. However,
96 accurately mapping the current distribution of mammals (both native and introduced) is itself
97 challenging. Prior to the widespread availability of motion-sensor cameras, there was little capability
98 to reliably assess the distribution and/or abundance of feral cats, dingoes and feral herbivores in
99 northern Australia to evaluate the impact of these species on small mammal populations. Feral cats, in
100 particular, are extremely cryptic, making it difficult to assess their presence (let alone abundance)
101 without resource-intensive methods, such as long-term deployment of multiple motion-sensor cameras
102 (Stokeld et al. 2016). Furthermore, many studies have also been limited in their capacity to detect
103 small native mammal species and/or account for varying detectability between species. Failing to
104 distinguish between species that were present but undetected and species that were truly absent can
105 lead to erroneous conclusions, especially when modelling species richness (MacKenzie et al. 2002,
106 Guillera-Aroita et al. 2019). New technologies and analytical developments enable collection of
107 sufficient detection data for small native mammals and can account for variability in detection
108 amongst them, as well as modelling relationships with bottom-up and top-down factors.
109

110 Our objectives were to: (1) determine geographic variation in small mammal species richness in
111 monsoonal Australia following substantial declines; (2) assess environmental characteristics
112 associated with high mammal species richness to elucidate drivers of decline; and (3) identify where
113 the greatest number of mammal species that have declined are seemingly persisting. Using a
114 landscape-scale survey, with multiple sampling methods, we quantified small native mammal species
115 richness from multispecies occupancy models that explicitly account for detectability. We evaluated
116 community and species-specific relationships with environmental features (e.g. ruggedness and
117 habitat productivity) that have previously been considered to influence mammal species richness and
118 composition (Woinarski et al. 1999) and with disturbances (e.g. fire activity, feral herbivores) and key
119 predators (e.g. feral cats, dingoes). From synchronous sampling of feral cats, dingoes and feral
120 herbivores at sites where native mammals were surveyed, we were able to model the influence of
121 these factors. We hypothesised that these disturbance and stress factors have contributed to shifts in
122 patterns of mammal species richness beyond those due to environmental features. We also compared
123 patterns in the distributions of mammals that have suffered severe population declines with those for
124 which there is little evidence of decline and between different body size groups. We hypothesised that
125 mammal species that have severely declined throughout most of their geographic ranges in northern
126 Australia would have different relationships to these predictor variables compared to those of other
127 species.

128

129 **Materials and Methods**

130 *Study region*

131 This study focused on the northern portion of the Northern Territory, Australia (ca. 370,000 km²),
132 including large off-shore islands: Melville, Bathurst and Groote Eylandt (Fig. 1). The region is within
133 the world's largest remaining expanse of tropical savanna woodland, dominated by eucalypt trees
134 (*Eucalyptus* and *Corymbia* spp.) interspersed with pockets of monsoon rainforest, rugged rocky
135 plateaus and ranges, floodplain, wetland and riparian communities. The region has a wet-dry tropical
136 climate, with mean annual rainfall ranging from 700 mm in the south to 1900 mm in the northern
137 coastal areas, mostly (>90%) falling from December to April.

138

139 We conducted mammal surveys at 312 sites between August 2013 and June 2016. Sites included all
140 major vegetation types except floodplains, and a range of land tenures, including national parks
141 (Kakadu, Litchfield, Nitmiluk, Garig Gunak Barlu and Gregory/Judburra), Indigenous Protected
142 Areas (Groote Eylandt, Wardaman, Warddeken and Djelk), privately owned conservation reserves
143 (Fish River Station) and Indigenous freehold land (Melville and Bathurst Island). We did not sample
144 areas of pastoral lands in which dingoes are managed to reduce their abundance. No targeted
145 management of feral cats or dingoes has occurred in the vicinity of our survey sites. The average
146 distance between adjacent sites was 2.5 km.

147

148 *Data collection*

149 At each site we established a 50 × 50 m trapping quadrat, containing motion-sensor cameras and live-
150 traps to collect detection/non-detection records of small mammals.

151

152 Camera trapping

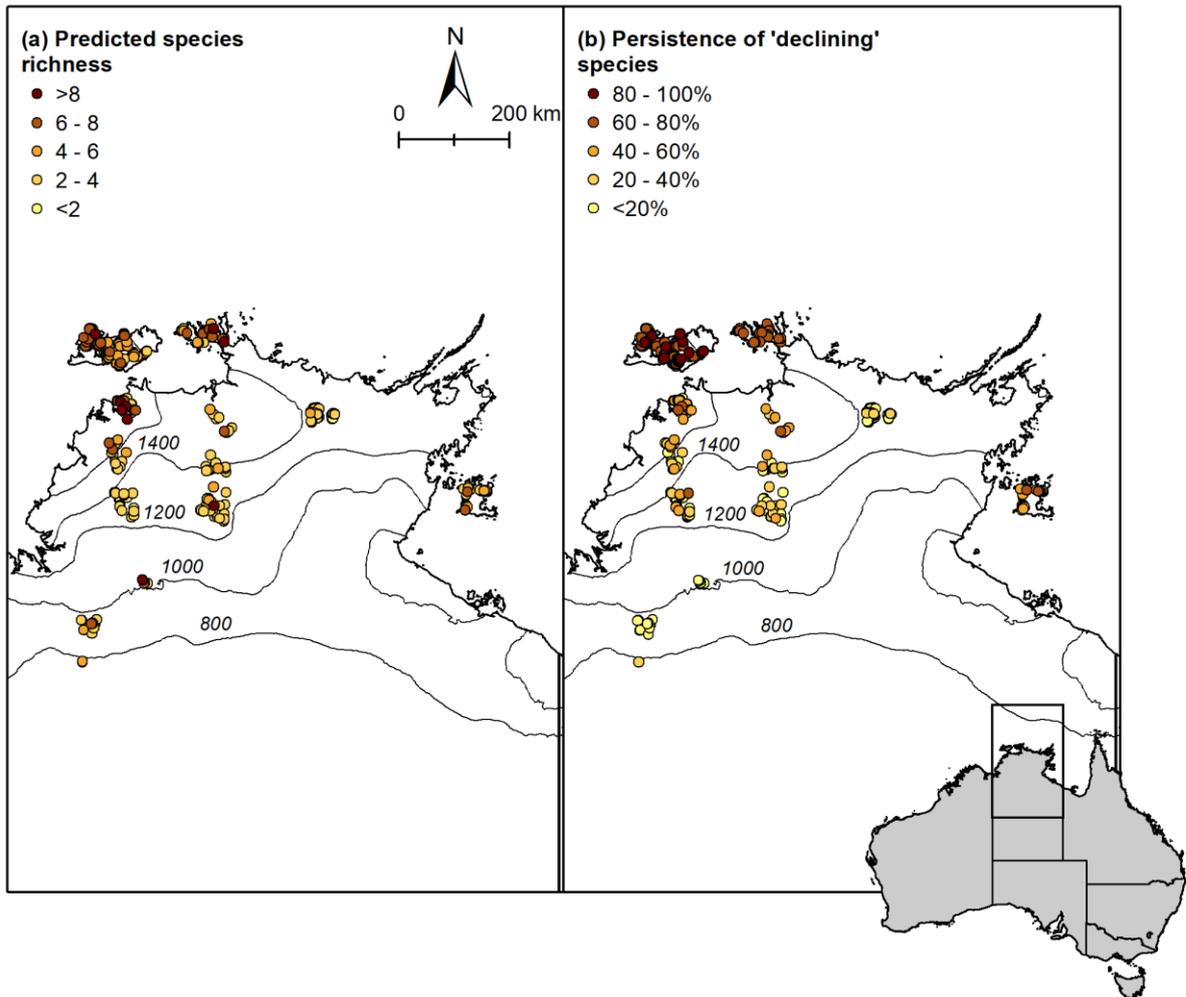
153 Five motion-sensor cameras were deployed at each site, with a central camera and four cameras
154 placed 30–50 m away (see Gillespie *et al.* 2015 for further details). Cameras were deployed for an
155 average of 50 nights (range 26–80). We deployed infrared and white-flash cameras (Reconyx HC550,
156 HC600 or PC850: Holmen, WI, USA), with a mixture of all camera models at each site. Cameras
157 were secured to a tree or other solid structure, 50–70 cm above ground. Bait stations were constructed
158 using an 80 mm length of PVC pipe, fitted with ventilated end caps. Bait stations contained a standard
159 small-mammal bait mix of peanut butter, oats and honey. Bait stations were secured to metal stakes
160 30 cm above ground, 1.5–3 m from the camera, with insecticide powder at the base. Understorey
161 vegetation directly in front of the camera was removed to maximise animal detections and minimise
162 false triggers. Cameras were programmed to take three successive photos following each trigger, with
163 a one-second interval between photos. Cameras were active day and night. To ensure independence
164 between detections at different cameras within a site, only one detection (the first) for each species
165 was used across all five cameras at the site within a 24-hr period.

166

167 Live-trapping

168 Live-trapping commenced at the same time as camera deployment. At each site, 16 Elliott (aluminium
169 box; type A) traps were placed at equal intervals around the trapping quadrat perimeter, and eight
170 medium cage traps were placed with one at each corner and mid-way along each side of the quadrat.
171 Cage and Elliott traps were baited with the same standard mammal bait mix used for camera trapping.
172 Live-traps were set at dusk, and checked and closed at dawn, corresponding to the nocturnal activity
173 rhythms of most species. We also installed three pitfall traps (20 L bucket with depth 41 cm, diameter
174 28 cm), each with a 10 m drift fence inside the trapping quadrat, at all sites except those on Melville
175 Island. Pitfall traps were not used on Melville Island as there are few mammal species that are
176 typically targeted using this method. We acknowledge the absence of pitfall traps on Melville Island
177 as a limitation of our methodology which may result in underestimation of species richness for those
178 sites. Pitfall traps were left open day and night, and were checked at dawn, midday and dusk. Elliott,
179 cage and pitfall trapping were conducted for four consecutive days/nights at each site.

180



181
 182 Figure 1. Location of the study sites (circles) across monsoonal Australia. Sites are colour-scaled
 183 according to (a) predicted small mammal species richness (darker shades indicate greater species
 184 richness) and (b) the percentage of small mammal species per site categorised as regionally declining
 185 (considered as an indicator of persistence), taken from total mammal species richness estimates at
 186 each site (darker shades indicate greater percentage of declining species), generated from hierarchical
 187 multi-species occupancy models. The black contour lines represent 200 mm mean annual rainfall
 188 isohyets. The location of the study area relative to Australia is inset.

189
 190 *Data analysis*

191 We recorded 7,824 independent detections of 27 species of small native mammals (92% from camera-
 192 trapping and 8% from live-trapping; see supplementary material, Appendix: Table S1) at 263 sites
 193 (84% of surveyed sites). There were no detections of small native mammals at 49 sites. We excluded
 194 the sugar glider (*Petaurus breviceps*) and northern brush-tailed phascogale (*Phascogale pirata*) from
 195 analyses as the ground-based survey methods used in this study were deemed inadequate for
 196 surveying these primarily arboreal species. Additionally, we collapsed records of *Sminthopsis bindi*,
 197 *S. butleri*, and *S. virginiae* into one taxon, *Sminthopsis* spp., as their geographic ranges overlap and

198 the distinguishing features of these species are too subtle to confidently identify individuals to
199 species-level using our camera-trap design (Potter et al. 2019). Thus, we included 23 unique taxa in
200 our analysis.

201

202 Predictor variables and preliminary analysis

203 To model spatial patterns of small mammal species richness, we used predictor variables arising from
204 hypotheses for mammal decline and/or mammal species richness in northern Australia. As outlined in
205 the introduction, these hypotheses related to environmental features (i.e. habitat productivity and
206 ruggedness), the distribution and/or abundance of key predators (i.e. feral cat occupancy and dingo
207 abundance), and disturbances driving changes in habitat structural complexity (i.e. anthropogenic
208 disturbance, fire activity, large feral herbivore abundance and feral pig presence). See supplementary
209 material, Appendix: Table S2 for a detailed justification of each hypothesis. We generated indices for
210 feral herbivores, feral pigs, feral cats and dingoes from occurrence records across the five cameras at
211 each study site. We predicted feral cat occupancy from single-species occupancy models to account
212 for imperfect detection and calculated relative abundance indices for dingoes and feral herbivores as
213 these species could be readily detected using our five-camera survey methods (Stobo-Wilson et al. *in*
214 *press*). All other predictor variables were generated using various remotely-sensed and land use
215 mapping GIS layers; indices of fire activity and habitat productivity were generated using LANDSAT
216 imagery, topographic ruggedness was calculated from a digital elevation model and anthropogenic
217 disturbance was determined from multiple GIS layers that depict land use, locations of towns and
218 population size, and roads. Where possible, these predictor variables (indices of fire activity,
219 ruggedness, habitat productivity and anthropogenic disturbance) were extracted at multiple spatial
220 scales (i.e. calculated over various neighbourhood radii from the centre of the quadrat), as the scale at
221 which these variables may influence small mammals is not well understood. See supplementary
222 material, Appendix: Table S3 for a detailed explanation about generating each variable.

223

224 To reduce the number of modelled predictor variables and avoid overfitting models, we included only
225 a subset of the generated predictor variables in our models. One variable for each corresponding
226 hypothesis was selected. To determine the strongest predictor variable for each hypothesis, we first
227 modelled each predictor variable against the raw (observed) species richness using univariate,
228 generalised linear models with a Poisson error family. We used Akaike's Information Criterion (AIC)
229 to rank the suite of predictor variables that corresponded to a given hypothesis (Burnham and
230 Anderson 2002) so as to determine the strongest predictor variable for each hypothesis. The predictor
231 variables that had the lowest AIC by ≥ 2 were later used in more advanced models (hierarchical multi-
232 species occupancy models) of small mammal species richness. The final predictor variables were:
233 predicted feral cat occurrence, feral herbivore relative abundance index, dingo relative abundance
234 index, feral pig presence, average proportion of area burnt over a 10-year time period within a 3.2 km

235 radius (as an index of fire activity), average terrain ruggedness index within a 3.2 km radius,
236 anthropogenic disturbance index averaged over a 2.5 km radius, and average green vegetation density
237 within a 1.6 km radius (as an index of habitat productivity). Prior to analyses, we checked for
238 collinearity between predictor variables selected for including in our models (no predictor variables
239 were strongly correlated with another $r \leq 0.7$).

240

241 Multispecies occupancy model

242 We used hierarchical multispecies occupancy models to investigate relationships between species
243 richness and our predictor variables. Occupancy models explicitly account for imperfect detection by
244 estimating the detectability (p ; probability a species was detected at a site on a given night, if present)
245 and occupancy (Ψ ; probability a species was present at a site) of a species at a site (MacKenzie et al.
246 2002). Multi-species occupancy models also provide an approach to model species-specific, group-
247 and community-level occupancy and habitat use (Kéry and Schaub 2011, Rich et al. 2016).

248

249 Distinguishing the true absence of a species from the non-detection of a species (i.e. species present
250 but not detected) requires spatially or temporally replicated detection data. We combined the camera-
251 trapping and live-trapping data at each site to calculate the number of detections for each species at
252 each site. There was substantial variability in the number of camera-trap detections between species.
253 To reduce heterogeneity of detections between species and to improve model fit (Tobler et al. 2015),
254 we collapsed the camera trapping period at each site (average 50 days) into six-day intervals. For the
255 five cameras at each site we pooled species detections into six-day intervals, so there could only be
256 one capture record for each species at a site within a six-day interval. For the live-trapping data, we
257 collapsed detections at each site so that there could only be one capture record per night for each
258 species. We then calculated the number of captures for each species at each site by combining the
259 final number of detections from the camera- and live-trapping surveys over the entire survey period.
260 We calculated camera-trapping survey effort for each site to account for variation in effort across all
261 sites because of the different survey periods and camera failures; average camera survey effort was
262 243 camera nights per site (range 78–968). Live-trapping was standardised across all sites so was not
263 included as a survey effort variable.

264

265 There was biogeographic variability in species distributions across our study area, as some species are
266 known to be historically absent from the offshore islands (see supplementary material, Appendix:
267 Table S1 ‘Biogeographic distribution’). To accommodate the biogeographic distribution of each
268 species detected during fauna surveys, we defined a regional presence matrix P_{ij} , with elements P_{ij}
269 equal to one where the i^{th} species could at least potentially occur at the j^{th} site, based on each species’
270 known biogeographic distribution, and zero if it is historically absent. Following Rich et al. (2016),
271 we further defined a partially-observed (latent) matrix of occupancy states \mathbf{z} , with elements z_{ij} equal to

272 one if the i^{th} species was present at the j^{th} site, and zero if it was absent. We treated the elements of z
273 as Bernoulli random variables with $z_{ij} \sim \text{Bern}(\Psi_{ij} * P_{ij})$ where Ψ_{ij} is the probability that the i^{th} species
274 was present at the j^{th} site. This formulation of the model ensures that the occupancy states (z_{ij}) of
275 regionally-absent species are always zero. We modelled the probability of observing species i at site j
276 from survey effort k as $y_{ijk} \sim \text{Bern}(p_{ijk} * z_{ij})$ where p_{ijk} are the probabilities of detection of species i , at
277 site j during survey k . Inclusion of the latent occupancy state z_{ij} ensures that detection is conditional
278 on the species being present at the site (i.e. $z_{ij}=1$; MacKenzie et al., 2002). Model fitting involved
279 direct estimation of the latent occupancy state matrix \mathbf{Z} using a state-space approach equivalent to the
280 single species version devised by Royle and Kéry (2007); for further model details see Appendix 1.

281

282 Population status and body mass groups

283 Using a multispecies hierarchical framework, species can be classified into groups to examine the
284 relative impact of predictor variables at both species- and group-levels (Rich et al. 2016). To
285 investigate whether severely declined species have a similar relationship to the respective predictor
286 variables, relative to other species, we modelled a group response for population status. We
287 distinguished between species for which there is evidence of severe regional decline in both
288 abundance and distribution within the last 30 years (hereafter referred to as declining) against species
289 for which there is less evidence of decline (hereafter referred to as stable). Eight species were classed
290 as declining and 15 species as stable (see supplementary material, Appendix: Table S1). Our
291 categorisation was informed by documented declines in the abundance and distribution of each
292 species, as reported in Woinarski et al. (2014), Woinarski et al. (2010) and Northern Territory
293 Government (unpublished). We additionally hypothesised that body mass may influence how a
294 species responds to the predictor variables. We divided species into three body mass categories: <50 g
295 (ten species), 50–500 g (five species) and 501–5500 g (eight species) (see supplementary material,
296 Appendix: Table S1). There was a low incidence of declining species that are also <50 g (only one
297 species, the fawn antechinus [*Antechinus bellus*]). Our approach to modelling this dataset was to first
298 assess community-level hyper-parameters by a model that pooled all species together in a
299 “community” and then run the two group models (population status and body mass).

300

301 All analyses were conducted in R (R Core Team, 2017). We fitted the hierarchical multispecies
302 occupancy models using a Bayesian approach in JAGS, version 3.4.0 (Plummer 2003), with R
303 package ‘jagsUI’. We made inference from 5,400 samples of the posterior distribution obtained from
304 three chains each of 90,000 iterations after a burn-in of 10,000, and retaining every 50th iteration. As
305 recommended by Guillera-Arroita et al. (2019), we used relatively narrow normal priors for the
306 remaining covariates effects ($X1_{ir}, \dots, X9_{ir}$, and $M1_{ir}, \dots, M4_{ir}$), specifying a normal distribution with
307 mean 0 and standard deviation 2.5. We assessed model convergence by visually inspecting the chains
308 and by ensuring the Gelman-Rubin statistic for each parameter was close to 1. We assessed the

309 adequacy of the model using a posterior predictive check with the Bayesian p -value based on
310 Pearson's χ^2 discrepancy for binomial data. The discrepancy measure was calculated between the
311 observed data, and for simulated data generated at each iteration of the MCMC algorithm. The
312 Bayesian p -value is defined as: $\Pr(\chi^2_{\text{obs}} > \chi^2_{\text{sim}})$. Values larger than 0.95 or smaller than 0.05 indicate
313 a lack of fit. We also calculated a 'lack-of-fit' statistic $\chi^2_{\text{obs}} / \chi^2_{\text{sim}}$ which is expected to be equal to 1 if
314 the model fits the data perfectly (Kéry and Schaub 2011).

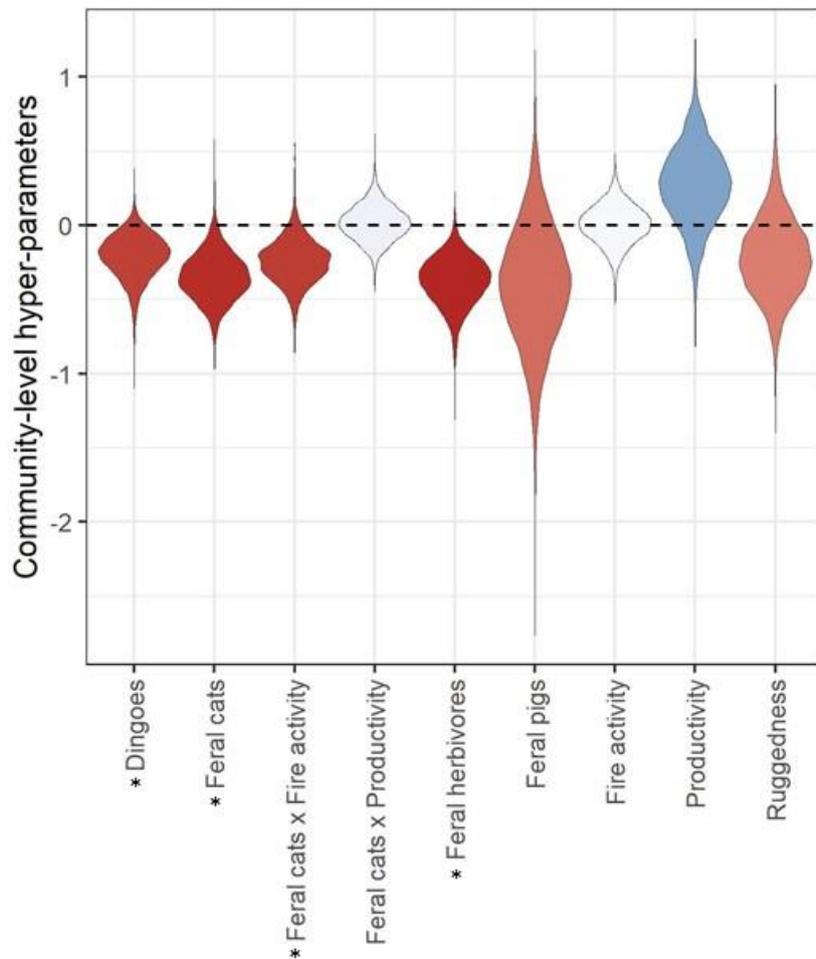
315

316 **Results**

317 *Species richness*

318 Estimates of small mammal species richness varied between 1 and 10 species per site (Fig. 1a). There
319 was a greater proportion of regionally declining species on offshore islands (Fig. 1b), suggesting
320 greater persistence of declining species at these sites. Feral herbivore abundance, dingo abundance
321 and feral cat occupancy were the best predictors of site-based richness (Fig. 2). As feral herbivore
322 abundance, dingo abundance and feral cat occupancy increased, species richness of small mammals
323 decreased. Feral herbivore abundance and feral cat occupancy had the strongest influence on site-
324 based species richness (see supplementary material, Appendix: Fig. S1); all species declined with
325 increasing feral cat occupancy (community response: -0.35, 95% Bayesian credible interval [BCI]: -
326 0.66, -0.02) and all but two species (common brushtail possum and *Sminthopsis* spp.) declined with
327 increasing herbivore abundance (community response: -0.38, 95% BCI: -0.75, -0.09). We found
328 slightly less support for the effect of dingo abundance, as the credible intervals for this variable
329 slightly overlapped zero (community response: -0.21, 95% BCI: -0.55, 0.04). Dingo abundance was
330 negatively correlated with all but two mammal species (grassland melomys [*Melomys burtoni*] and
331 common rock-rat [*Zyzyomys argurus*]; Appendix: Fig. S1). Julian day was the only important
332 predictor of small mammal detectability from the four covariates that were considered (see
333 supplementary material, Appendix: Table S4), with detectability peaking in the winter dry season,
334 between May and October.

335



336

337 Figure 2. Posterior distributions of the overall (across all species) effects of covariates on occupancy
 338 of mammal species at our study sites. Shading reflects the certainty of the results – dark blue implies
 339 an unambiguously positive effect, dark red negative. More neutral tones imply effects not
 340 distinguishable from zero. Statistically important covariates are indicated by an asterisk.

341 *Population status and body mass groups*

342 We found substantial variation within the population status and body mass groups, in response to the
 343 predictor variables (Appendix: Table S5, Fig. S2). Relative to stable species, declining species were
 344 more likely to occur in areas of greater productivity (intercept: -0.24, mean effect: 1.29, 95% BCI:
 345 0.66, 1.95) than rugged areas (intercept: 0.13, mean effect: -1.03, 95% BCI: -1.90, -0.19).

346 Specifically, the occurrence of all eight declining species increased with productivity (green
 347 vegetation density) and the occurrence of six of those species decreased with ruggedness. Thus,
 348 declining species were more prevalent in, and had seemingly greater persistence in, productive
 349 environments than rugged environments. There was evidence that the occurrence of declining species
 350 increased with fire activity (proportion of area burnt), relative to stable species (six of eight declining

351 species increased with proportion of area burnt); however, credible intervals slightly overlapped zero
352 (intercept: -0.21, mean effect: 0.40, 95% BCI: -0.03, 0.80).

353

354 The occurrence of species <50 g decreased with productivity (intercept= 0.66, main effect= -1.24,
355 95% BCI: -2.32, -0.19), relative to other body mass groups. Of the 10 species <50 g, five decreased
356 with increasing productivity, but only one species from the 50–500 g (of five species) and >500 g (of
357 eight species) body mass groups declined with increasing productivity. There was a low incidence of
358 declining species that also had a body mass <50 g. This relationship may somewhat explain why the
359 <50 g body mass group has an inverse relationship to productivity relative to other body mass groups
360 (i.e. a greater proportion of species >50 g were also classified as declining species and the occupancy
361 of declining species generally increased with productivity).

362

363 **Discussion**

364 Ours is the first study of northern Australia's native mammals – a group of high conservation concern
365 given ongoing declines – to quantify both community and species-specific relationships with
366 environmental features and contemporary disturbances, while accounting for variation in species'
367 detectability. The novelty of our study lies in our consistent sampling of feral cats, dingoes and feral
368 herbivores at the site level and thence modelling of the influence of these putative pressures on
369 species richness of small mammals. We found the occurrence of both declining and stable mammal
370 species was negatively associated with feral herbivore and dingo abundance, as well as feral cat
371 occupancy. However, high productivity seems to enhance the capacity of mammals to withstand these
372 pressures, as declining species that were historically widely distributed, now predominantly occur in
373 areas with greater productivity (green vegetation density). Collectively, our findings suggest that
374 changes in both bottom-up and top-down processes across northern Australia are reducing small
375 mammal species richness, with areas of relatively high productivity acting as important refugia for
376 species that have suffered severe population declines in less productive areas (McKenzie et al. 2007).

377

378 One of our most important findings is the significant negative influence of feral herbivores on the
379 species richness of small mammals. Previous research from the Kimberley region of northwestern
380 Australia has demonstrated the negative impacts of feral herbivores on mammal diversity (Legge et al.
381 2011, Radford et al. 2015, Legge et al. 2019). In those studies, the low mammal diversity associated
382 with high cattle density was attributed to low grass biomass under heavy grazing and the associated
383 high predation pressure from feral cats (McGregor et al. 2014). Our study highlights the extent to
384 which a broad suite of large feral herbivores (including swamp buffalo [*Bubalus bubalis*], banteng
385 [*Bos javanicus*], horse [*Equus caballus*], cattle [*Bos indicus*], donkey [*Equus asinus*] and rusa deer
386 [*Cervus timorensis*], ordered from most- to least-frequently detected), at a landscape-scale, are
387 negatively affecting populations of small native mammals in monsoonal northern Australia, with such

388 impacts more substantial than previously recognised. The impact of feral herbivores is particularly
389 important considering the uncontrolled, and relatively high abundance of these species in a number of
390 regions, including conservation reserves.

391

392 In addition to the effects of feral herbivores, we found that mammal species richness was lower at
393 sites where feral cats were more likely to occur and where dingoes were more abundant. In the last
394 decade, feral cats have been strongly implicated as a key driver of mammal declines in northern
395 Australia (Frank et al. 2014, Davies et al. 2017) and Australia more broadly (Woinarski et al. 2014,
396 Woinarski et al. 2019). Our results provide further evidence that feral cats are a key threat to small
397 mammals in northern Australia. In contrast to the threat posed by feral cats, there has been little
398 exploration of any potentially negative impact of dingoes on northern Australia's small mammal
399 populations, despite dingoes preying extensively on small mammals (Corbett 1995, Stokeld et al.
400 2018). A lack of emphasis on the potentially negative impact of dingoes is most likely for two
401 reasons: firstly, dingoes have been present in Australia for ca. 4000 years (Balme et al. 2018)
402 demonstrating that native mammals can, and have, persisted in this landscape with dingoes; and
403 secondly, it is often argued dingoes (as a top predator) may suppress feral cat populations in turn
404 providing a net benefit for small mammals (Letnic et al. 2009, Brook et al. 2012, Leo et al. 2019).
405 Indeed, a long history of dingo presence in northern Australia means that dingo predation *per se*
406 cannot explain the relatively recent pattern of mammal decline in northern Australia. However, in a
407 previous study from the same region (Stobo-Wilson et al. *in press*) there was no evidence of spatial
408 avoidance of dingoes by feral cats, providing no evidence that dingoes benefit small mammals by
409 suppressing cats in northern Australia. Furthermore, Stobo-Wilson et al. (*in press*) found that both
410 predators had a higher probability of occurrence in areas with reduced habitat structural complexity.
411 Considering the above lines of evidence, we suggest that there have been pervasive changes to
412 bottom-up processes (driven by the combined influence of high fire activity and heavy grazing by
413 feral herbivores; Sharp and Whittaker 2003, Vigilante and Bowman 2004, Russell-Smith et al. 2012)
414 in northern Australia's tropical savannas such that mammal populations are less resilient to predation
415 (by both feral cats and dingoes) than they were in the past. Similar to feral cats, dingoes tend to be
416 more active in recently burnt areas (Leahy et al. 2016) and in open habitats in general (Morrant et al.
417 2017a), most likely due to greater hunting efficiency as dingoes typically chase, rather than ambush,
418 their prey (Corbett 1995, Morrants et al. 2017b). Consequently, high fire activity (frequent, high
419 severity fires) and heavy grazing by feral herbivores, may have triggered a 'trophic squeeze', where
420 bottom-up and top-down processes squeeze populations of small mammals into local extinction. High
421 fire activity and heavy grazing by feral herbivores reduce the availability of critical food and shelter
422 resources (altering bottom-up processes) and hence reduce the resilience of mammal populations.
423 However, these factors also increase predation pressure (top-down processes), not just by feral cats,
424 but also native predators.

425

426 Historically, most of the mammals we categorised as regionally declining, occupied extensive areas of
427 lowland woodland, occurring across a wide productivity gradient in monsoonal Australia (Woinarski
428 et al. 2014). However, we found these species are now largely restricted to more productive habitats at
429 the mesic ends of their former distributions. This pattern of contraction is consistent with previous
430 studies from northern Australia (McKenzie et al. 2007, Stobo-Wilson et al. 2019). For lowland
431 mammals, productive areas provide the greatest refuge from current threatening processes as these
432 habitats are likely to be somewhat more resilient to the deleterious effects of heavy grazing by feral
433 herbivores and high fire activity. This is because there is both a greater baseline of habitat structural
434 complexity within these habitats and greater capacity for vegetation to recover from such disturbances
435 (Cook et al. 2015). Additionally, previous studies have found that key predators (e.g. feral cats and
436 dingoes) have relatively low abundance in productive and/or structurally complex environments
437 (Hohnen et al. 2016, Stobo-Wilson et al. *in press*). Consequently, in northern Australia productive
438 habitats provide greater refuge and food availability for resident mammals, and relatively low
439 abundance and/or activity of mammalian predators (feral cats and dingoes).

440

441 Surprisingly, we found a greater occurrence of declining mammals in areas of high fire activity, which
442 is inconsistent with previous studies (Lawes et al. 2015, Radford et al. 2015). However, we suggest
443 this relationship reflects greater overlap in the distribution of declining lowland species with areas of
444 high fire activity (as these habitats are prone to higher fire activity, Murphy et al. 2019), as opposed to
445 a specific preference for high fire activity. Furthermore, unlike other studies (e.g. Leahy et al. 2016)
446 our findings most likely do not reflect the short-term response of mammals to fire, but rather the long-
447 term impacts of frequent fire. Generally, we found weak and varied responses of individual mammal
448 species to varying fire activity. Differences in our findings to those of other studies likely reflect the
449 complex relationships, and feedbacks, between fire activity, feral herbivores (Legge et al. 2019),
450 predators (Leahy et al. 2016) and underlying productivity (Cook et al. 2015). Regardless, our findings
451 provide no additional support that severe fire regimes (without the underlying influence of
452 productivity, and the additive influence of predators and introduced herbivores) directly explain the
453 pattern of mammal decline in northern Australia (Lawes et al. 2015).

454

455 We found a low occurrence of declining species in rugged areas. This result is contrary to studies
456 from other regions in Australia where rugged environments have provided important refugia for
457 declining mammal species (Start et al. 2007, McDonald et al. 2017). Most of the regionally declining
458 species in our dataset are historically associated with topographically simple, lowland habitats
459 (Woinarski et al. 2014). In contrast, the distinctive mammal assemblages of rugged areas have been
460 more resilient to decline (McKenzie 1981, Freeland et al. 1988), with only a few notable exceptions
461 (e.g. the golden-back tree-rat [*Mesembriomys macrurus*] has been extirpated from its rugged habitat in

462 the Northern Territory; Woinarski et al. 2014). Our findings likely reflect greater exposure and
463 vulnerability of lowland species to current threatening processes, relative to species that utilise rugged
464 habitats. For example, the severity of disturbance by feral herbivores, including removal of grass
465 cover and creation of large tracks, or 'game paths', may be less pronounced in rugged areas due to
466 fewer palatable grasses. Additionally, relative to lowland habitats, fires are typically patchier in
467 rugged habitats where the greater proportion of bare rock acts as a natural firebreak (Price et al. 2003).
468 Native mammals may also be less susceptible to mammalian predators in rugged areas because they
469 can more readily find permanent shelter sites, such as crevices, and because feral cats and dingoes are
470 less likely to occur in rugged areas (Hohnen et al. 2016, Stobo-Wilson et al. *in press*). Thus, although
471 rugged environments are subjected to the same disturbance regimes, the overall impact is less
472 detrimental to resident mammal species (and hence rugged areas have fewer declining species) than is
473 the case in lowland habitats because there is little to no subsequent change in bottom-up processes.
474 Nevertheless, at least some declines of small mammals have been documented within rugged areas
475 (Ibbett et al. 2018), indicating resident species are not safe from declines; rather, population declines
476 have been slower and less marked, relative to lowland species.

477

478 By examining patterns of contemporary mammal species richness, we offer new insights into the
479 drivers of mammal decline in northern Australia. Whereas previous studies have identified an
480 influence of habitat productivity and ruggedness on mammal species richness (Woinarski et al. 1999),
481 this study demonstrates that disturbance factors have an even more pronounced influence.
482 Additionally, disturbance factors mediate the relationship between these underlying environmental
483 factors and mammal species richness, but are also mediated by environmental factors. We conclude
484 that ongoing disturbance regimes – heavy grazing by livestock and feral herbivores and frequent high-
485 severity fires – in the tropical savannas of northern Australia underpin the observed pattern of
486 mammal persistence and loss. We argue that disturbance-driven reduction in habitat complexity and
487 productivity has significantly disrupted bottom-up processes in northern Australia (Sharp and
488 Whittaker 2003, Vigilante and Bowman 2004, Russell-Smith et al. 2012), subsequently increasing
489 top-down pressure, together causing severe mammal decline. However, our findings suggest that high
490 productivity and ruggedness are likely to increase the capacity of mammals to withstand current
491 pressures. Collectively, our findings indicate areas that are exposed to intense disturbance from
492 grazing and high fire activity are unlikely to support the same suite of mammal species they did
493 historically. Indeed, the distribution of mammal species in northern Australia has shifted so markedly
494 that large offshore islands that historically supported fewer native mammal species relative to the
495 mainland, now have greater site-level mammal species richness, with a high proportion of species that
496 have elsewhere suffered severe population declines. Our study highlights that the tropical savannas of
497 northern Australia, putatively the Earth's largest intact savanna landscape, are in a state of ecological

498 dysfunction, with significant implications for at least the mammal component of the biodiversity of
499 this region.

500

501 *Management implications*

502 Our findings provide guidance for policy makers and managers seeking to halt and potentially reverse
503 mammal declines in northern Australia. Without maintaining, enhancing or recovering habitat
504 condition in this region, long-term conservation and recovery of mammal diversity will be
505 unachievable. Targeting the disturbances driving the loss of habitat structural complexity and
506 productivity – heavy grazing by livestock and feral herbivores and high fire activity (Sharp and
507 Whittaker 2003, Vigilante and Bowman 2004, Russell-Smith et al. 2012) – should be the highest
508 management priority. These disturbances should be managed simultaneously to be effective in
509 recovering mammal populations (Legge et al. 2019).

510

511 Our results demonstrate that areas with relatively high productivity and/or habitat complexity, for
512 example large offshore islands (e.g. Tiwi Islands, Groote Eylandt), provide critical refugia for
513 northern Australia’s biodiversity. Both high productivity, and a slightly lower incidence of
514 mammalian predators (relatively low occurrence of feral cats and low abundance of dingoes; see
515 Appendix: Fig. S2) on these islands, has presumably facilitated the persistence of regionally declining
516 mammals (Davies et al. 2018, Heiniger et al. *in press*). However, reducing feral herbivore populations
517 and improving fire regimes on these islands should be a priority, especially considering recent
518 evidence of local mammal decline (Davies et al. 2018). Although large offshore islands may currently
519 provide refuge for a number of declining mammals, they do not support populations of declining
520 species that occur only on the mainland. Thus, to ensure the protection of the full complement of
521 northern Australia’s unique mammal assemblage, targeted conservation efforts directed at reducing
522 the impacts of grazing and predators also need to be applied to mainland areas. Specifically, we
523 advocate for the protection and enhancement of habitat structural complexity to reduce the decline of
524 small mammals. This approach is likely to be a more successful management option than lethal
525 predator control, especially as dingoes have a long history in this region and may provide other
526 ecological benefits not accounted for in this study (e.g. control of large macropods; Letnic et al.
527 2018). Relatively productive areas identified in our study as supporting high residual species richness
528 should be used as starting points for conservation efforts, as they signify environments in which
529 recovery may be most feasible.

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