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Dominant carnivore loss benefits native avian and invasive mammalian scavengers

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Abstract

Scavenging by large carnivores is integral for ecosystem functioning by limiting the build-up of carrion and facilitating widespread energy flows. However, top carnivores have declined across the world, triggering trophic shifts within ecosystems. In this study, we use a natural 'removal experiment' of disease-driven decline and island extirpation of native mammalian (marsupial) carnivores to investigate top-down control on utilisation of experimentally placed carcasses by two mesoscavengers – the invasive feral cat and native forest raven. Ravens were the main beneficiary of carnivore loss, scavenging for five times longer in the absence of native mammalian carnivores. Cats scavenged on almost half of all carcasses in the region without dominant native carnivores. This was eight times more than in areas where other carnivores were at high densities. In the absence of native mammalian carnivores, all carcasses persisted in the environment for 3 weeks. Our results reveal the efficiency of carrion consumption by mammalian scavengers. These services are not readily replaced by less-efficient facultative scavengers. This demonstrates the significance of global carnivore conservation and supports novel management approaches, such as rewilding in areas where the natural suite of carnivores is missing.

Keywords: scavenger, trophic cascade, carcass use, survival analysis, mesoscavenger release, carnivore extinction

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Introduction

Scavenging is ubiquitous among mammalian and avian carnivores, with most species scavenging to some degree [1-4]. Larger carnivorous mammals are highly efficient scavengers, consuming carcasses faster than most other taxa [5]. However, many larger mammalian carnivores, as well as obligate scavengers like vultures, are experiencing widespread declines due to habitat loss, disturbance, and persecution by humans [6, 7]. Fluctuations in the abundance of these species can have trophic consequences that cascade throughout the food web and impact nutrient cycling and disease transmission [8-10]. With populations of some larger mammalian carnivores now beginning to recover, this raises questions around how scavenging dynamics have shifted within modified ecosystems [11].

Larger mammalian carnivores can either provision ecosystems with a more stable supply of carrion (e.g. wolves in Yellowstone National Park [12]), or limit carrion access (e.g. bears kleptoparasiting cougar kills [13] and Tasmanian devils reducing carrion availability [14]). Carrion is a high-quality resource with low handling costs, and thus is attractive to mesoscavengers [1]. However, scavenging on carrion is also risky due to the increased likelihood of encountering dominant scavengers [15-17]. These competitive and facilitative processes can potentially make carrion "fatally attractive" for mesoscavengers [18]. For example, mesoscavengers were attracted to wolf kills yet were negatively associated with wolf density at the landscape scale [19]. Although carcasses are attractive to mesoscavengers, predator avoidance plays an important role in shaping carnivore communities [18, 20].

Across the southern-temperate continental island of Tasmania (Australia) and its large offshore islands (Fig. 1; total area: 68,401 km^2), a large-scale natural experiment is occurring due to the severe population decline of the largest extant terrestrial carnivore, the marsupial Tasmanian devil *Sarcophilus harrisii* [20]. Devils are Tasmania's dominant scavenger, being both the largest extant terrestrial mammalian carnivore and a specialist, although facultative, scavenger adapted for

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55 processing the toughest parts of carcasses [21]. Following the extinction of the thylacine *Thylacinus*
56 *cynocephalus* in the 20th century, this mesocarnivore has become the apex terrestrial carnivore [20,
57 22, 23]. Devils have experienced severe population declines due to a transmissible cancer, devil
58 facial tumour disease (DFTD) [24]. The disease has progressively spread across Tasmania over 25
59 years, causing average population declines of 83% across ~90% of Tasmania [25, 26]. The progressive
60 spread of DFTD has established a natural experiment by creating regions of Tasmania with different
61 disease histories and consequently, widely variable densities of top carnivores. Unlike most
62 threatened carnivores [6], devil population declines are not caused by humans, allowing us to study
63 the effects of a carnivore's abundance with little anthropogenic confounding. In areas where devils
64 have declined, carrion persists three-fold longer, allowing increased carrion consumption by native
65 (spotted-tailed quolls *Dasyurus maculatus*) and invasive (feral cats *Felis catus*) mammalian and avian
66 (forest ravens *Corvus tasmanicus*) mesoscavengers [14]. However, this prompts the question: what
67 would happen to carrion if all native mammalian carnivores were completely lost? Can invasive and
68 avian mesoscavengers then fully replace the ecosystem services of larger mammalian scavengers?

69 The Bass Strait Islands, between Tasmania and the Australian mainland, are ecologically similar to
70 mainland Tasmania due to intermittent land connectedness during glacial maxima [27]. However,
71 following major land-use change and human persecution, several species were driven to extinction
72 on the islands, including mammalian carnivores like spotted-tailed quolls [28, 29]. While there is no
73 evidence of the Tasmanian devil on the islands following European occupation, on Flinders Island,
74 fossil evidence suggest that devils may have persisted until at least 8000 years ago [29, 30]. This
75 mensurative experiment on the Bass Strait Islands thereby provides a unique opportunity to
76 compare scavenging between: 1) a full community (Tasmanian mainland) comprising a native
77 mammalian apex scavenger, native mammalian mesoscavenger, invasive mammalian
78 mesoscavenger and native avian mesoscavenger; 2) a community in which only the native apex
79 scavenger has declined (Tasmanian mainland in diseased areas); and 3) a community lacking all
80 native mammalian scavengers (Bass Strait Islands).

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In this study, we used experimentally deployed carcasses (n = 136) and camera traps to monitor carrion use by mammalian and avian scavengers across mainland Tasmania and the two largest Bass Strait Islands. Using this design, we investigated how the abundance and occurrence of native top scavengers (devils) and native mesoscavengers (quolls) impacts: (i) carrion use and discovery by invasive and extant native mesoscavengers, and (ii) carcass persistence within an environment. We hypothesised that avian generalist mesoscavengers (ravens) and invasive mesoscavengers (feral cats) will not match the scavenging efficiency of devils and predicted that carcasses should persist for longer in their absence. We also expected that top native mammalian scavengers (devils) would limit carrion access and total feeding time for other smaller scavengers. Furthermore, we hypothesised that devils would have a stronger impact on the scavenging community than smaller native mesoscavengers (quolls).

Methods

Study area

We measured carrion use by mammalian and avian scavengers across Tasmania and the two largest Bass Strait Islands in south-eastern Australia (Fig. 1). In Tasmania, the progressive westward spread of DFTD from its origin in the northeast, followed by rapid and severe local population decline has resulted in low devil densities across most of the state. We divided northern Tasmania and the Bass Strait islands into three regions, partitioned geographically based on the density of native mammalian scavengers: 1) a full community, where DFTD was absent or only recently invaded, and devils were abundant and quolls present although naturally at lower densities than devils; 2) a reduced community, where DFTD was prevalent and devil numbers declined by more than 80%, however, quoll densities do not appear to have increased substantially; and 3) a simple community, where devils and quolls are locally extinct (Fig. 1). In total, we experimentally deployed 136 carcasses and cameras across these regions (full community: 40; reduced community: 56; simple

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106 community: 40). Camera sites were placed in a roughly even mixture of wet eucalypt/rainforest
107 habitat and dry eucalypt/coastal scrub habitat and we selected areas where human influence was
108 minimal.

109

110 *Experimental design*

111 Carcasses were deployed during August - September 2016 for the Tasmanian mainland, and August -
112 September 2020 on the Bass Strait islands. We worked in late winter, when consumption by
113 invertebrate scavengers and microbial decomposers is at its lowest. We used Bennett's wallaby
114 (*Macropus rufogriseus*) and Tasmanian pademelon (*Thylogale billardierii*) carcasses. These are both
115 regularly culled under crop-protection permits and are a common source of carrion in the study
116 region. The carcass species used at a given site depended on local availability. To ensure
117 independence, carcasses were deployed at least 1 km apart. At each carcass, we installed one
118 camera trap (Cuddeback X-Change 1279 or Reconyx PC-800) to monitor scavengers. Cameras were
119 deployed for a minimum of 21 days, after which we expected the carcasses to be mostly consumed.

120

121 *Analysis*

122 *i) Carcass discovery & persistence*

123 We used statistical survival analysis based on a mixed-effects Cox proportional hazards model from
124 the R package `'coxme'` [31] to study carcass discovery and persistence. We ran separate analyses
125 to investigate the time it took for the carcasses to be discovered by (i) any vertebrate scavenger, (ii)
126 ravens, and (iii) feral cats. Discovery was defined as the first time an animal found and fed on the
127 carcass. Carcasses were defined as fully consumed when there was a clear final consumption event,
128 and the physical carcass was absent from subsequent images. If the final event was not clear, we

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129 used the 95th percentile foraging event, when foraging activity petered out over many days, given
130 the carcasses appeared to be more than 95% consumed.

131 We used survival analysis because the discovery and persistence data were censored [32]. Discovery
132 data were right-censored because not every carcass was discovered by ravens and feral cats before
133 the carcass was completely consumed. The persistence data were also right-censored because
134 memory cards occasionally became full before complete consumption (n = 9), several carcasses were
135 prematurely removed from the view of the camera (n = 18), one camera returned no images
136 throughout the study, and the batteries in one camera failed before the carcass was fully consumed.

137 We selected the preferred survival models using the package `'MuMIn'` [33] with combinations of
138 four predictor variables: devil activity (number of devil detections per 100 camera nights), quoll
139 activity (number quoll detections per 100 camera nights) and habitat (wet vs dry forest), with initial
140 carcass weight (kg) included as a covariate to account for variation in carcass size (see Table S1 in the
141 Supplementary Information for model combinations). To account for variation across the study sites,
142 we used site location as a random effect. All the predictors had a Pearson's cross-correlation
143 coefficient $r < 0.7$. Model selection was based on Akaike's information criterion corrected for a small
144 sample size (AIC_c). The most parsimonious models were selected using $\Delta AIC_c < 2$ (difference between
145 the AIC_c of a given model and the best model) (Grueber et al. 2011). For each supported covariate
146 (where 95% confidence limit did not overlap with zero), we calculated the model-averaged
147 exponentiated coefficients, known as hazard ratios (HR), which provide effect sizes for each variable.
148 Survival curves were visualised by separating carcass data into the three regions (Fig. 1) and
149 presenting the Kaplan-Meier estimates of the survival function using the packages `'survival'`
150 [34] and `'survminer'` [35].

151

152 *ii) Carcass use*

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153 To analyse the predictors of carcass use by forests ravens and feral cats, we tested a range of *a priori*
154 models based on ecological knowledge (Table S2, supplementary information). We again used AIC_c
155 for model selection and multi-model inference. We assessed the fit of the top models by calculating
156 the AUC (area under the receiver operator curve; suitable for classification models). We tested the
157 effects of five predictor variables: habitat, devil, and quoll activity (defined above), plus total
158 scavenging time by devils and quolls (separately, summated minutes). To account for variation in
159 carcass size, we included initial carcass weight as a covariate. We also used site location as a random
160 effect to account for variation across the study sites. We calculated the standardised regression
161 coefficient (Std. coef) based on z-values for each predictor after model averaging. For any variables
162 that were supported (95% confidence limit did not overlap with zero), we calculated the effect size
163 (ES) by comparing the model-averaged predicted probability when that categorical variable was
164 applied, against the probability of the intercept when the effect was absent. Sixteen cameras were
165 removed from the analysis in total: twelve due to premature removal of the carcass from the field of
166 view and four due to mechanical unreliability or early failure.

167 To analyse carcass use by forest ravens, we used hurdle models, because the scavenging data were
168 zero-inflated and followed a gamma distribution. We first modelled whether ravens fed at a carcass
169 (GLMs with binomial link function) and then modelled the total scavenging time by ravens for the
170 carcasses at which they fed (GLMs with a Gamma distribution and a log link function). Total
171 scavenging time for each camera was calculated by summing the number of minutes any raven
172 spent scavenging on the carcass. GLMs with a binomial link function were used to assess carcass use
173 by feral cats, but we were unable to model the predictors of total scavenging time by feral cats due
174 to insufficient data, particularly in the full community region. Carcass use was defined as whether a
175 feral cat found and scavenged upon a carcass during the study period.

176

177 **Results**

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178 *i) Carcass discovery & persistence*

179 The absence of native mammalian carnivores had a significant effect on extending the persistence
180 time of carcasses. Carcasses within the simple community region lasted 1.8 times longer than
181 reduced community regions and 4.6 times longer than full community region (Fig. 2). 'Devil activity'
182 had a negative effect on carcass persistence (Hazard Ratio, HR = 1.09) while 'carcass weight' had a
183 positive effect, with larger carcasses persisting for longer (HR = 0.96).

184 There was no difference in the discovery rates between the various scavenger communities when all
185 species were aggregated (Fig. 3a), although carcasses in wet forests took longer to be discovered (HR
186 = 0.54). Ravens discovered carcasses in significantly less time at both reduced and simple scavenger
187 community (Fig. 3b) with 'devil activity' (HR = 0.92) and wet forest 'habitat' (HR = 0.47) suppressing
188 carcass discovery by ravens. Cats showed a similar but weaker response to those observed in ravens
189 (Fig. 3c), however, there were no supported variables.

190

191 *ii) Carcass use*

192 Forest ravens were the main beneficiary of the absence of native mammalian carnivores (Table 1; Fig.
193 4a). As a proportion of total foraging time for all species, we found that ravens fed almost twice as
194 long in the simple scavenger community (88.2% of total foraging time by all species) compared to
195 ravens in the reduced scavenger community (47.9%) and five times as long as in the full scavenger
196 community (17.3%; Fig. 4d). Both devil scavenging time (Std. coef = 0.53; ES: -0.99; Fig. 4b) and devil
197 activity (Std. coef = 0.47; ES: -0.98; Fig. 4c) had a strong negative effect on the likelihood of a raven
198 feeding at a carcass. However, only devil scavenging time impacted total duration of raven
199 scavenging (Std. coef = 0.81), having an overall negative effect (ES: -0.99; Fig. 4e).

200 Feral cats scavenged on a higher proportion of carcasses in the absence of native mammalian
201 carnivores. Cats in the simple scavenger community fed on 44% of carcasses, which was 2.4 times

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more than in the reduced community region (19%), and eight-fold more than in the full community region (6%; Fig. 5a). The probability of cats scavenging was best predicted by devil activity (Std. coef = 0.65) and the relationship was negative (ES: -0.91; Fig. 5b).

Discussion

We used a naturally occurring experiment, of reduction or extirpation of native mammalian scavengers, to examine the effects on scavenging by avian and invasive-mammalian scavengers. The apex mammalian scavenger, the Tasmanian devil, had an overwhelmingly dominant effect on scavenger dynamics, with carcasses persisting 4.6 times longer in areas with a simple scavenger community structure. Smaller scavengers, most notably forest ravens, were the main beneficiary of native mammalian carnivore loss. Further, invasive cats scavenged almost 50% of all carcasses in areas with simplified carnivore communities, highlighting that—contrary to general wisdom [36, 37]—scavenging can contribute an important source of food for cats. This also suggests potential avenues for reducing the cat's devastating effects on native wildlife. Overall, this research highlights the crucial role of scavenging by larger mammals and shows that their effects are not easily replaced once lost. Rewilding of larger carnivores could restore their function within an ecosystem and provide top-down control on mesoscavenger populations (Fielding et al. 2020).

We found that smaller mesoscavengers were unable to replicate the scavenging efficiency of the larger, specialist scavenger, the Tasmanian devil [21]. In the absence of native mammalian carnivores, carcasses persisted for almost five times longer than in areas with higher mammalian carnivore diversity (Fig. 2). While a higher proportion of carcasses in the simple community region were of the larger Bennett's wallaby, the several Tasmanian pademelon carcasses we used also persisted until the end of the study. Previous research has found that mesoscavengers, including corvids, were unable to functionally replace raptors in urban areas, with 70% of fish carcasses remaining [38]. Additionally, the experimental exclusion of carcasses from vultures resulted in 10

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227 times as many carcasses not fully consumed by the remaining scavengers [39]. While all carcasses
228 within the simple community region in our study persisted until the study's end, only 5% of
229 carcasses were not discovered and scavenged upon by the remaining mesoscavengers (Fig. 3a).
230 Clearly, the absence of native mammalian carnivores had little impact on the remaining scavengers
231 locating and feeding upon the carcasses, thereby indicating little facilitation of carrion resources by
232 top scavengers through advertising or increased accessibility.

233 We found evidence that top carnivores limit carrion access for smaller scavengers. Ravens were the
234 main beneficiary of native mammalian carnivore loss, with ravens in the simple community region
235 finding 88% of the carcasses (Fig. 3b) and foraging for seven times longer than in the full scavenger
236 community regions (Fig. 4d). Devils suppressed raven carcass utilisation (Fig. 4e), probably because
237 nocturnal devils consumed the resources before diurnal ravens discovered them. This finding
238 supports previous findings that under low levels of competition raven populations on the Bass Strait
239 islands prioritise scavenging on roadkill across the entire year even when other resources (e.g.,
240 invertebrates, fruit, seeds) are available [40].

241 Until recently, cats were believed to rarely scavenge [36, 37]. However, there is now a growing body
242 of evidence that they actively scavenge, especially when they perceive little risk [41]. Our data show
243 that in the simple scavenger community, feral cats scavenged at eight times the rate of cats living in
244 a full scavenger community (Fig. 5a). Furthermore, the presence of devils in the landscape
245 suppressed cat scavenging behaviour, potentially through interference competition (cats also being
246 mostly nocturnal foragers). Past research has demonstrated that the presence of devils within an
247 environment can trigger avoidance strategies in cats to evade interspecific conflict [14, 42, 43].
248 Reduced interference competition caused by top-carnivore loss can have cascading effects
249 throughout an ecosystem, potentially leading to population increases of, and expanded functional
250 roles for, smaller carnivores [44]. However, fear effects imposed by larger carnivores on
251 mesocarnivores are not fully understood, and further studies are required to disentangle these

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252 dynamics between carnivores [18]. Combining several lines of investigation (e.g., GPS data on
253 multiple predators combined with cameras on carcasses) would help quantify the risk-reward trade-
254 off of carcasses, and could help reveal under what circumstances carcasses are "fatally attractive" to
255 mesopredators [19].

256 Following the disease-driven decline of devils across Tasmania, quolls also increased their use of
257 carrion in areas of low devil density [14]. Indeed, in areas of greater devil decline, such as north-
258 Eastern Tasmania, quoll scats contained many large-mammal remains, suggesting that the loss of
259 top scavengers improved scavenging opportunities for quolls [45]. Despite quolls being
260 mesoscavengers, they have, like devils, also been documented chasing cats from carcasses,
261 providing evidence of interference competition [14]. However, we only found a weak effect of quoll
262 abundance on carcass use by ravens and cats. As quolls are non-specialised and smaller scavengers,
263 they are much less efficient than devils and it is therefore difficult for them to monopolise a carcass
264 in the same way [46]. Additionally, the effects of devils—as a dominant and specialised scavenger—
265 on other opportunistic scavengers might simply be too strong, acting to mask any potential impacts
266 the quoll may have on cats and ravens [21].

267 As highly efficient scavengers, the loss of apex scavengers can lead to increased food availability for
268 mesoscavengers which could result in increases in abundance [1]. For example, the absence of
269 vultures (*Gyps* spp.) in south-eastern Spain led to a higher abundance of red foxes (*Vulpes vulpes)*
270 due to greater availability of carrion [47]. Similarly, feral dogs (*Canis lupus*) and rodents have
271 increased in abundance in areas of India due to a rise in carrion availability following widespread
272 vulture declines [48]. In the Bass Strait region, anecdotal evidence suggests that forest-raven and
273 feral-cat populations are growing on King Island [28, 49]. Enhanced opportunities to feed to on
274 roadkill [40] and other carrion, as demonstrated in this study, may provide explanations for this
275 apparent increase in abundance. Further research is needed to confirm whether these species are
276 truly increasing in abundance. Elevated numbers of forest ravens could have destructive effects for

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277 the local birds on the islands through heightened levels of depredation, and impact local farmers
278 through increased attacks on livestock, as shown in other corvid studies [41, 50], as well as on King
279 Island specifically [51]. While past research in Tasmania found no impact of forest raven abundance
280 on the abundance of other bird species [52], these impacts may differ on the Bass Strait islands if the
281 raven population size is greater. Meanwhile, the impacts of the invasive feral cat on small mammals
282 or birds are well-documented, with many species now threatened with extinction or already lost due
283 to heightened predation risk [53, 54]. Despite these apparent increases in abundance, feral cats and
284 forests ravens are less efficient scavengers than devils [46], meaning carcasses may persist in an
285 environment for longer. This could have adverse effects on both animal and human health due to
286 the increased spread of carrion-borne diseases [1, 17, 55].

287 Large carnivore populations have fluctuated due to human persecution and habitat loss, causing
288 trophic cascades throughout food webs across the globe [6]. In our study, we found that top
289 scavengers, like Tasmanian devils, limit carrion use and discovery by smaller scavengers, such as
290 ravens and cats. However, it remains unclear how this may impact mesoscavenger population
291 abundance and whether there are cascading effects on small prey species. In the absence of top
292 mammalian scavengers, we found that carcasses persisted beyond the study length (~ 3 weeks).
293 Further research is required to see how this may impact the transmission of carrion-borne diseases
294 and scavenging by invertebrates. In this mensurative experiment, we demonstrate that the absence
295 of top mammalian scavengers results in the loss of essential ecosystem functions, providing support
296 for novel management approaches, such as trophic rewilding [56-58]. Overall, our findings further
297 highlight and clarify the integral role native mammalian scavengers perform within an ecosystem,
298 demonstrating the ecological significance of global mammalian carnivore conservation.

299

300 **Acknowledgements**

301 The authors would like to acknowledge the palawa peoples of lutruwita, the traditional custodians of

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the lands on which this work was completed. We extend our gratitude to the many fieldwork volunteers. We would also like to thank the Flinders Island Aboriginal Association Inc. (FIAAI) and various landowners across Tasmania who allowed us to complete fieldwork on their properties. This work was funded by the Holsworth Wildlife Research Endowment and Australian Research Council (ARC) grants FL160100101, CE170100015 to B.W.B. and DP110103069 to M.E.J.

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459 Table 1. Total foraging times and proportion of total foraging time for the top four scavengers in

460 each scavenger community.

Scavenger community	Species	Time foraging (hours)	Proportion total foraging time (overall)
Full	Tasmanian devil (*Sarcophilus harrisii*)	108.6	70.7%
	Forest raven (*Corvus tasmanicus*)	26.5	17.3%
	Spotted-tailed quoll (*Dasyurus maculatus*)	8.3	5.4%
	Feral cat *(Felis catus)*	4.8	3.1%
Reduced	Forest raven (*Corvus tasmanicus*)	238.7	47.9%
	Spotted-tailed quoll (*Dasyurus maculatus*)	118.9	23.9%
	Tasmanian devil (*Sarcophilus harrisii*)	81.2	16.3%
	Feral cat *(Felis catus)*	23.3	4.6%
Simple	Forest raven (*Corvus tasmanicus*)	448.3	88.2%
	Feral cat *(Felis catus)*	33.9	7.0%
	Black rat (*Rattus rattus*)	8.7	1.7%
	Black currawong (*Strepera fuliginosa*)	5.3	1.0%

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Figure Legends

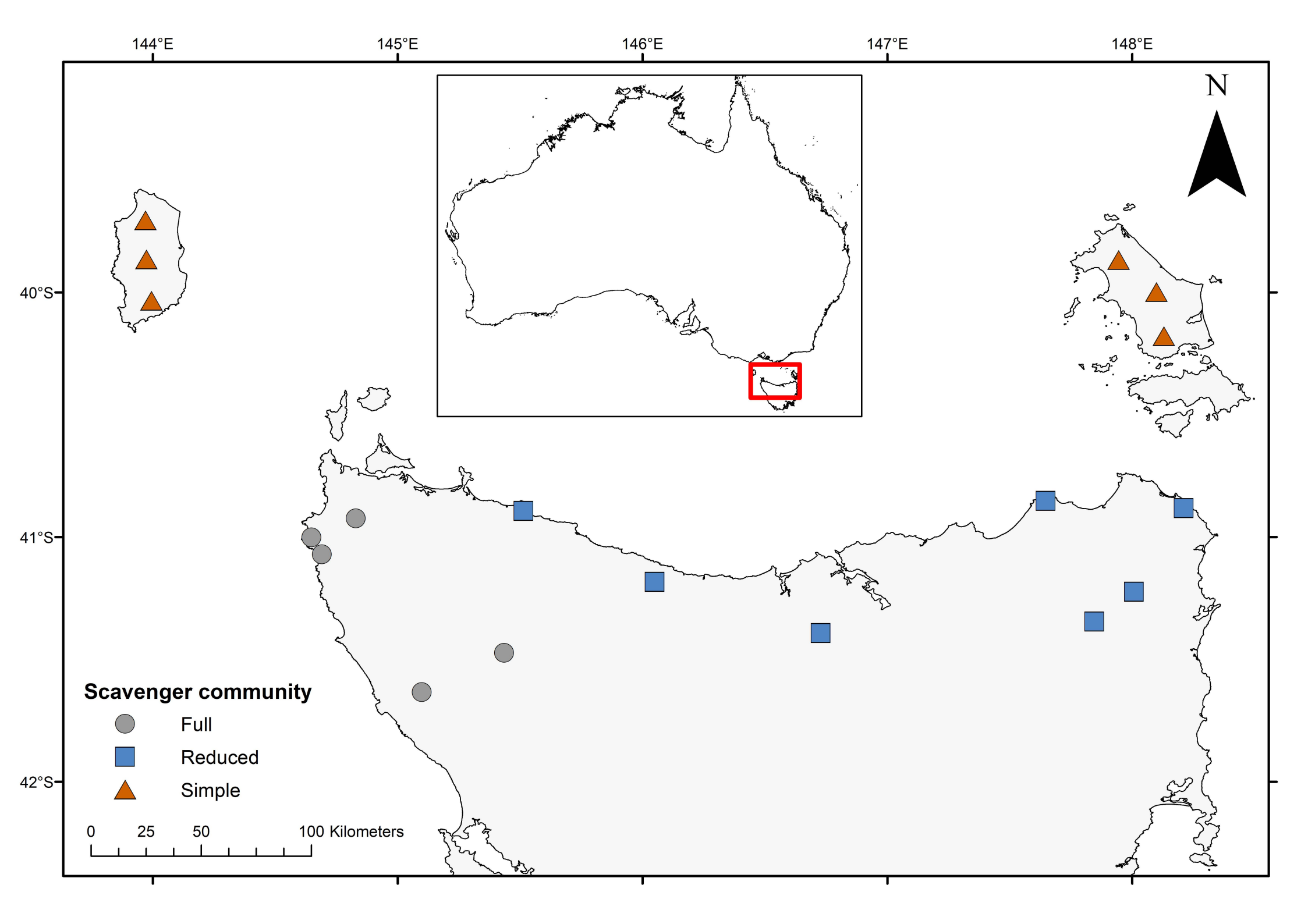
Figure 1. Geographic location of study sites across Northern Tasmania and the Bass Strait Islands. Each shape indicates a site that contains between 6 to 8 camera traps.

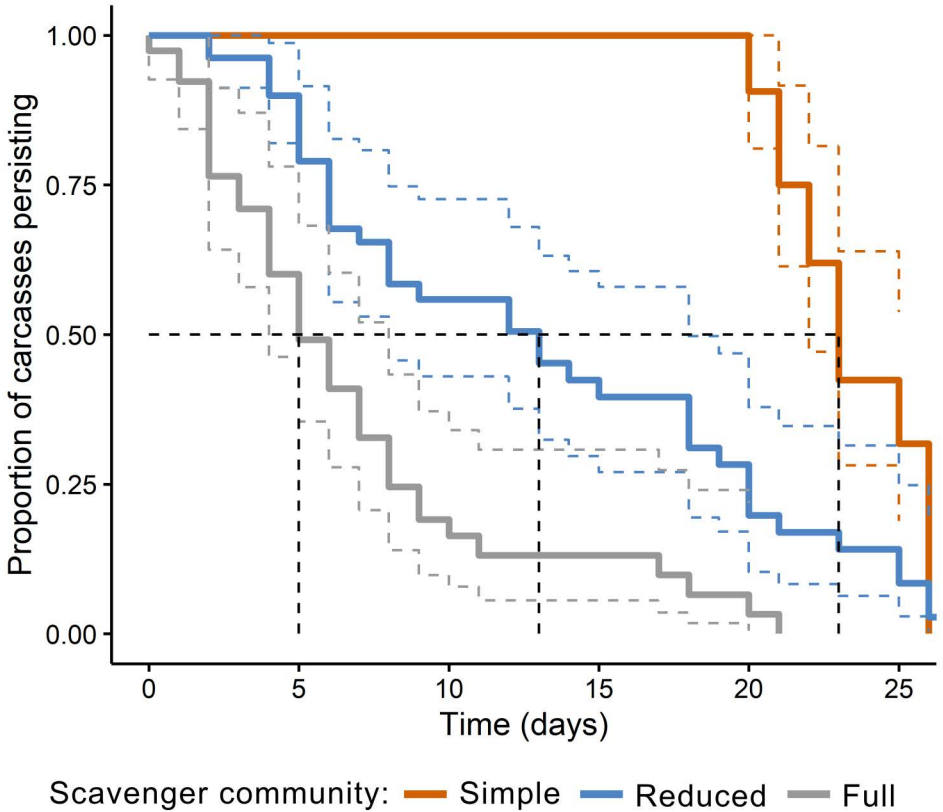
Figure 2. The proportion of carcasses persisting in the environment for each level of scavenger diversity and abundance. Colour dashed lines indicate the 95% confidence interval. Black dotted line shows the median carcass persistence times for each of the three categories.

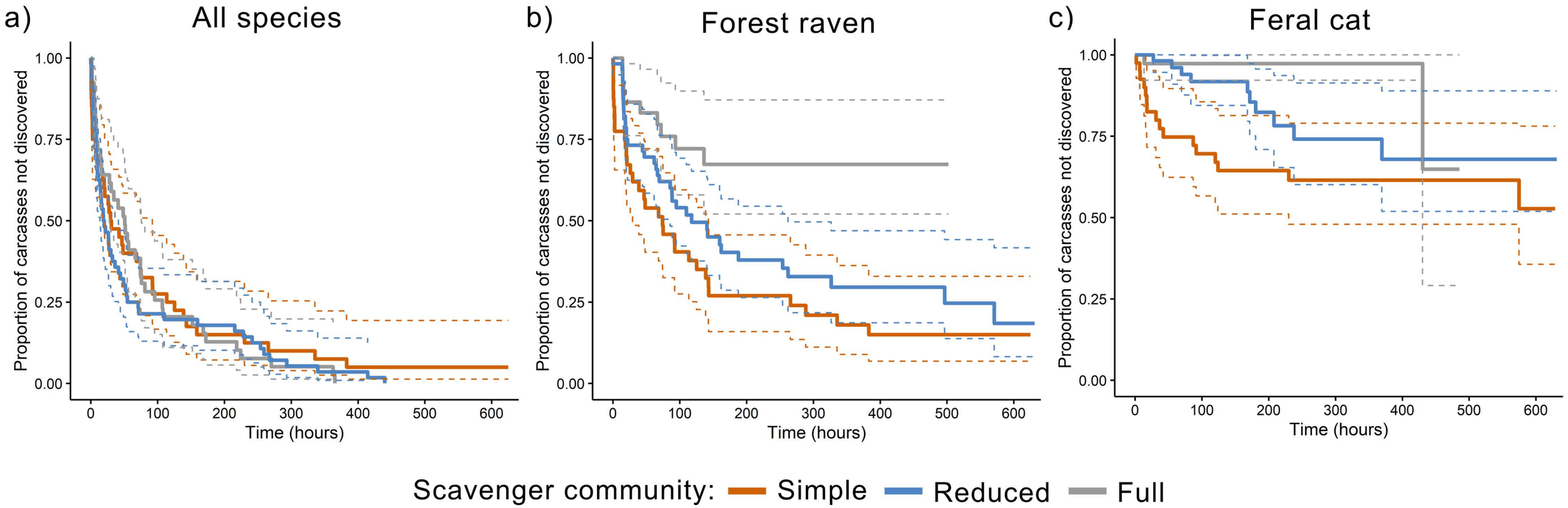
Figure 3. The proportion of carcasses not discovered by (a) all species, (b) forest ravens and (c) feral cats for each level of scavenger diversity and abundance. Colour dashed lines indicate the 95% confidence interval.

Figure 4. Carcass consumption by forest ravens. Top row: (a) the proportion of total carcasses foraged, with the response curves of the best predictors, being (b) devil scavenging time and (c) devil activity. Bottom row: (d) the average proportion of total foraging time with the response curve of the best predictor, (e) devil scavenging time. In (a) and (d) each dot corresponds to the mean value for the study sites and error bars are bootstrapped 95% confidence intervals.

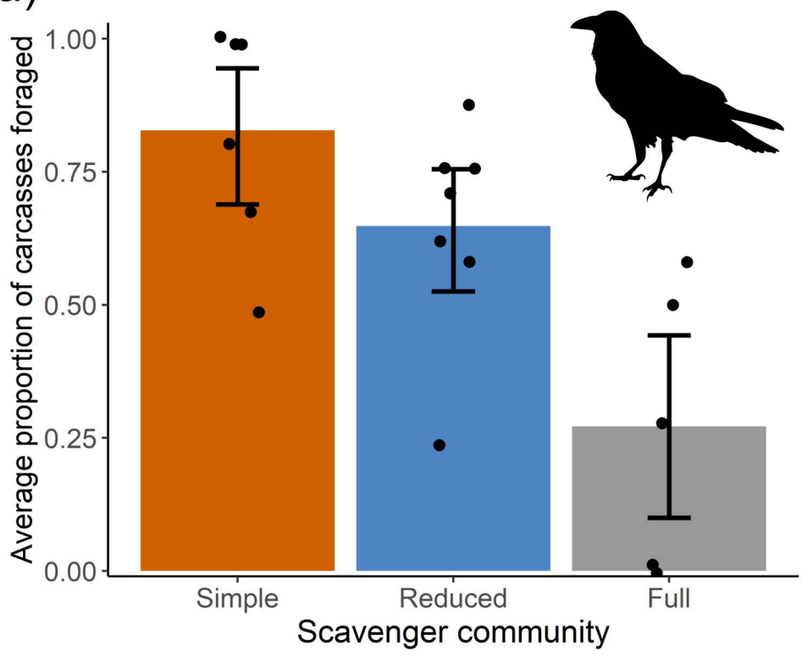
Figure 5. Carcass consumption by feral cats: (a) the proportion of total carcasses foraged, and (b) the response curves of the best predictor, devil activity. In (a) each dot corresponds to the mean value for the study sites and error bars are bootstrapped 95% confidence intervals.


144°E
145°E
146°E
147°E
148°E
40°S
41°S
42°S
N
Scavenger community
Full
Reduced
Simple
0
25
50
100 Kilometers

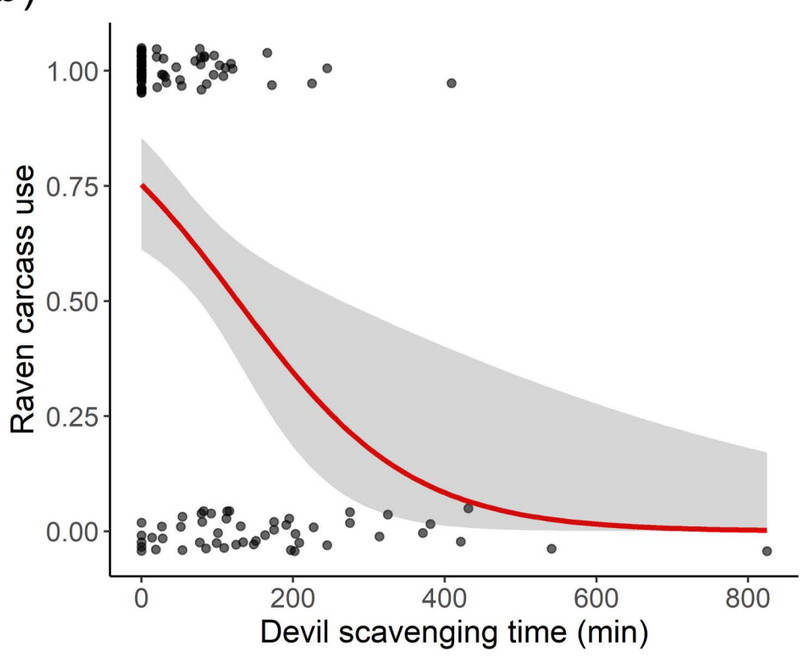

1.00
0.75
0.50
0.25
0.00
Proportion of carcasses persisting
0
5
10
15
20
25
Time (days)
Scavenger community:
Simple
Reduced
Full


a)
All species
b)
Forest raven
c)
Feral cat
Proportion of carcasses not discovered
1.00
0.75
0.50
0.25
0.00
0
100
200
300
400
500
600
Time (hours)
Scavenger community:
Simple
Reduced
Full

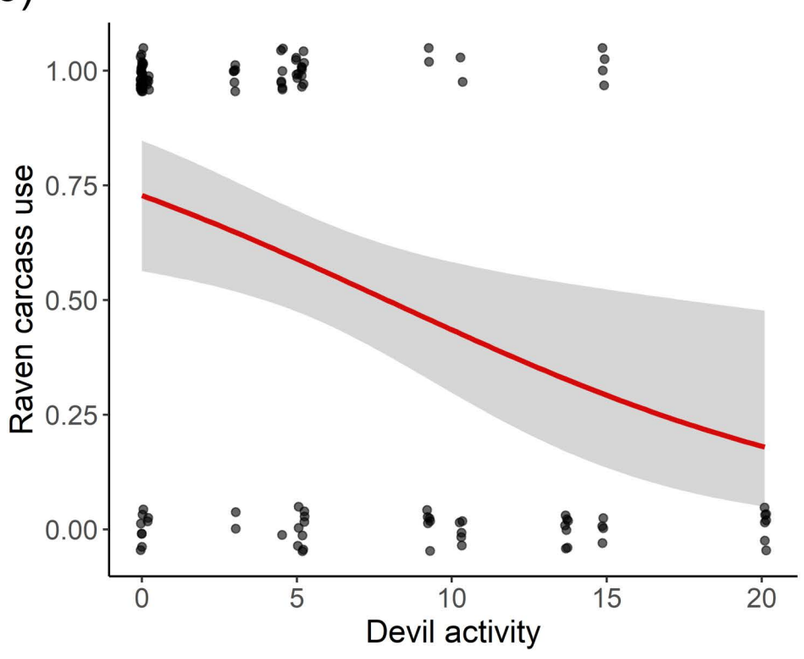
a)


Average proportion of carcasses foraged
1.00
0.75
0.50
0.25
0.00
Simple
Reduced
Full
Scavenger community

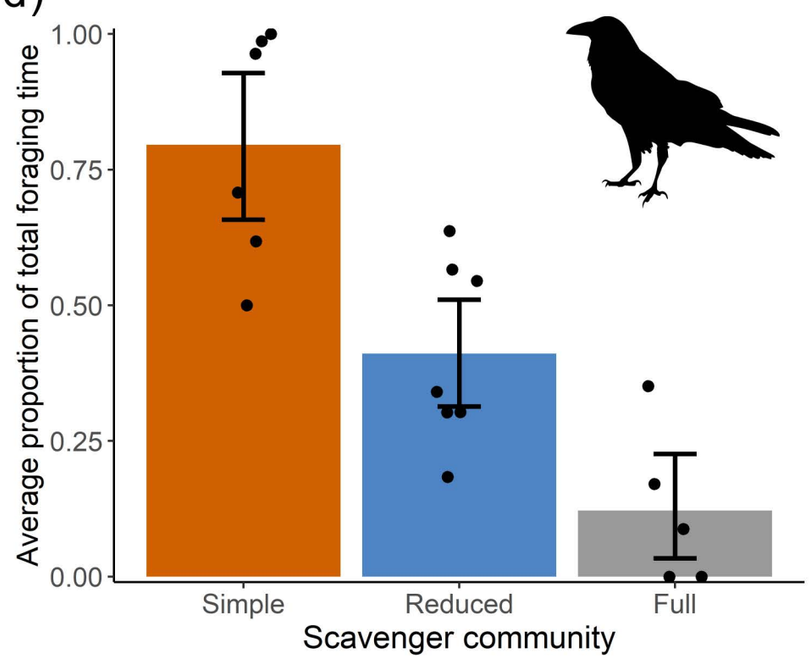
b)


Raven carcass use
1.00
0.75
0.50
0.25
0.00
0
200
400
600
800
Devil scavenging time (min)

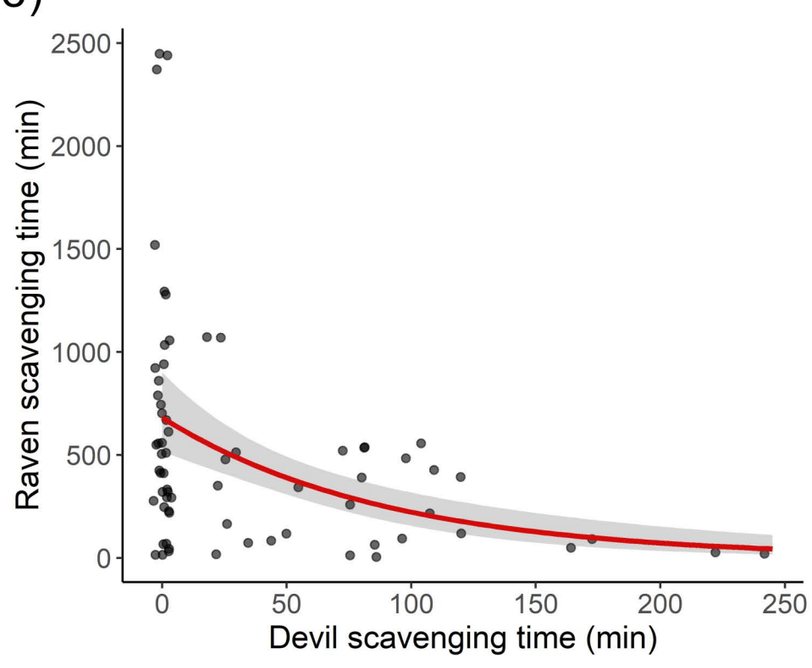
c)

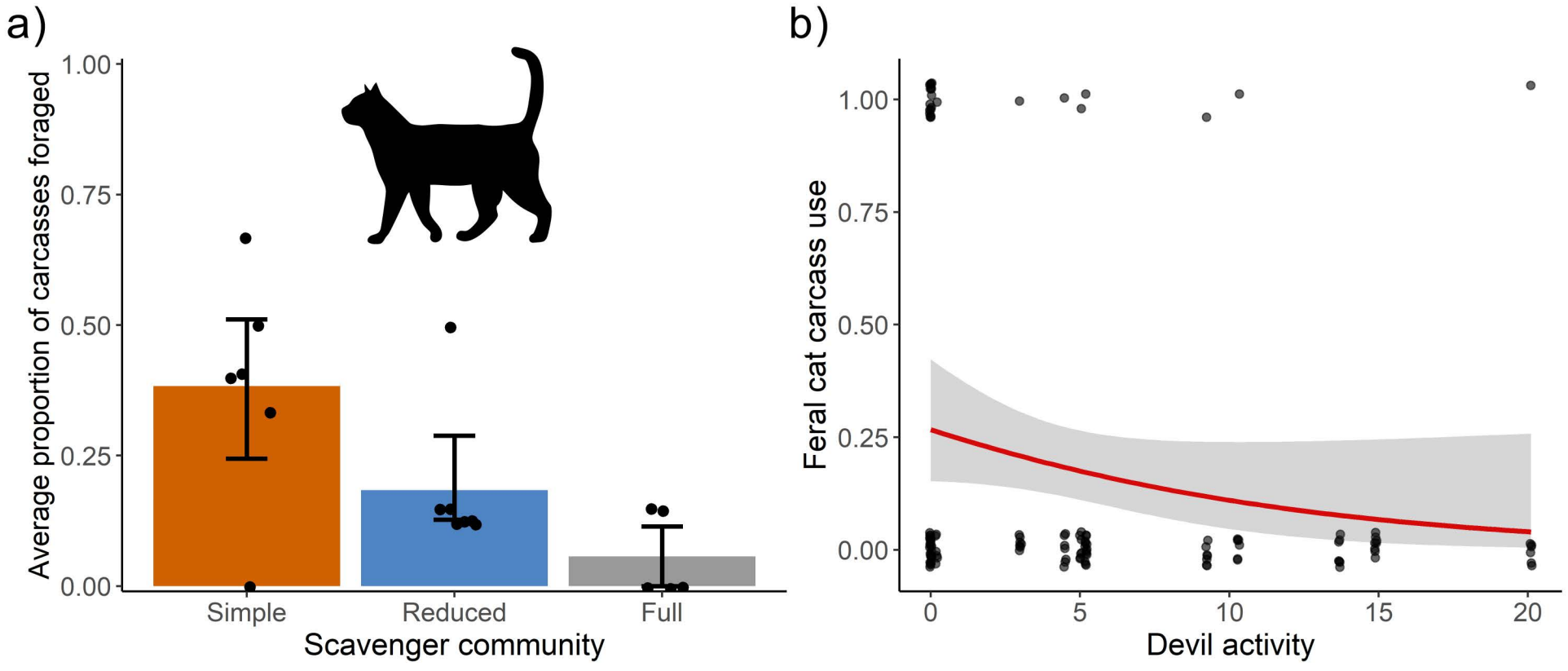

Raven carcass use
1.00
0.75
0.50
0.25
0.00
0
5
10
15
20
Devil activity

d)


Average proportion of total foraging time
1.00
0.75
0.50
0.25
0.00
Simple
Reduced
Full
Scavenger community

e)


Raven scavenging time (min)
2500
2000
1500
1000
500
0
0
50
100
150
200
250
Devil scavenging time (min)


a)
Average proportion of carcasses foraged
1.00
0.75
0.50
0.25
0.00
Simple
Reduced
Full
Scavenger community
b)
Feral cat carcass use
1.00
0.75
0.50
0.25
0.00
0
5
10
15
20
Devil activity