

23 habitat specificity is not always a reliable proxy for sensitivity to land modification, with
24 significant implications for biodiversity conservation when used to inform agriculture and land
25 use policies.

26 *Keywords: agriculture; fragmentation; grassland; habitat specificity; habitat loss; land*
27 *modification; land sharing; land sparing; landscape; rodent*

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29 INTRODUCTION

30 Agriculture is the leading cause of biodiversity loss worldwide, requiring the conversion
31 of habitat into new land-use types for crop and livestock forage production, which reduces
32 vegetation structure and simplifies composition (Benton et al. 2003; Connor et al. 2000; Tews et
33 al. 2004; Fahrig et al. 2011). Loss of a single habitat patch results in species loss inside and
34 outside the patch itself, reverberating as widespread biodiversity loss throughout the surrounding
35 landscape (Burns & Gear 2008; Wilson et al. 2016). Over 75% of Earth's terrestrial land mass
36 shows evidence of land modification (Ellis and Ramankutty 2008), of which 39-50% is due to
37 modern agricultural and urban-industrial uses (Vitousek et al. 1997; Chapin et al. 2000; Foley et
38 al. 2005). Globally, current rates of species extinction are 100-1000x higher than expected from
39 the fossil record, indicating Earth's 6th mass extinction is underway (Tilman et al. 1994; Pimm et
40 al. 1995; Barnosky et al. 2011; Dirzo et al. 2014). A crisis has also been identified in which
41 ecological function is threatened in many biomes because of limited ecological protection
42 (Hoekstra et al. 2005). As the global human population and food demand increases, further land
43 modification will be needed, intensifying biodiversity loss and failing biome functions (Tilman
44 et al. 2001; Foley et al. 2005; Green et al. 2005; Diaz et al. 2006; Tilman et al. 2011; Cardinale et
45 al. 2012; Baudron and Giller 2013; Haddad et al. 2015).

46
47 Fragmentation effects on biodiversity are more complex, differentially influencing
48 species' habitat use, dispersal capabilities, and population persistence (Henle et al. 2004; Wilson
49 et al. 2016). Fragmentation is a process by which remaining habitat patches become smaller and
50 more isolated as land modification proceeds, changing the composition and spatial configuration
51 of habitats at the landscape level (Fahrig 2003; Ewers and Didham 2005). Observed population
52 responses to fragmentation are often inconsistent within and among taxonomic groups (Bender et
53 al. 1998; Debinski and Holt 2000; Ewers and Didham 2005; Tylianakis et al. 2008; Fahrig 2017;
54 Keinath et al. 2017). A recent meta-analysis found almost 75% of significant fragmentation
55 effects indicate positive correlations with species abundances, further identifying the variable
56 influence of habitat fragmentation (Fahrig 2017). Fragmentation is also highly correlated with
57 habitat loss (Fahrig 2003); species may not respond until enough habitat loss occurs to make the
58 change in landscape configuration relevant to the same species (Andren et al. 1994; Hanski and
59 Ovaskeinan 2002; Betts et al. 2007). Population responses to one fragmentation metric may also
60 be confounded with habitat loss or other fragmentation metrics. For example, area and edge
61 effects can be both synergistic (Ewers and Didham 2007) and independent (Banks-Leite et al.
62 2010) but are often confounded because of their high collinearity (Fletcher et al. 2005) and scale
63 dependency (Comfort et al. 2016). Population responses among species are also interdependent
64 and indirect (e.g., competitive interactions, multi-trophic relationships, pathogen infection
65 intensities, mutualisms between plants and animals; Tylianakis et al. 2008; Didham et al. 2012;
66 Wilson et al. 2016). Despite all of this, recent assessments of fragmentation effects on biome-
67 wide ecosystem function indicate the immediate need to better understand and act to reduce these
68 effects where they negatively affect biodiversity (Haddad et al. 2015).

69 Land modification may homogenize plant and animal communities by favouring habitat
70 generalists at the expense of habitat obligates. Habitat specificity is an evolutionary strategy for
71 resource acquisition within heterogeneous landscapes. Species adapt to either acquire resources
72 within one or a few habitat types and maintain resource availability through competition (i.e.,
73 habitat obligate), or use a diverse resource base across multiple habitat types and maintain access
74 through colonization (i.e., habitat generalist; Futuyma and Moreno 1988; McKinney and
75 Lockwood 1999; Marvier et al. 2004; DeVictor et al. 2008; DeVictor 2010; Clavel et al. 2011).
76 Communities maintaining populations of both obligates and generalists are resilient to
77 environmental change because species loss from some functional groups are counterbalanced by
78 gains in other groups (McNaughton 1977; Chapin et al. 2000; Diaz et al. 2006). This also
79 maintains ecosystem function by maintaining redundancy among groups experiencing loss
80 during periods of environmental change (Chapin et al. 2000; Virginia and Wall 2001; Hector and
81 Bagchi 2007). However, land modification permanently and rapidly homogenizes habitat
82 mosaics into highly productive crop monocultures that experience consistent, intra-annual
83 disturbances (Benton et al. 2003). Habitat generalists may be more capable of taking advantage
84 of this high productivity because of their ability to colonize consistently disturbed habitats
85 (Tilman et al. 1994; Wright et al. 2012). In contrast, habitat obligates are less flexible in the
86 resource base they can use, and so are more vulnerable to disturbances that eliminate habitat
87 (Tilman et al. 1994; DeVictor et al. 2008; Reino et al. 2014). The resulting generalist-dominated
88 communities may synchronize assemblage responses to environmental change, with implications
89 for ecosystem resilience (McKinney and Lockwood 1999; Chapin et al. 2000; Diaz et al. 2006;
90 Clavel et al. 2011; Cardinale et al. 2012).

91 Here, we use rodent species responses to land modification to examine whether habitat
92 specificity predicts sensitivity of rodent assemblages to habitat loss and fragmentation on the
93 Canadian Prairies. Little is known regarding how rodent assemblages respond to the
94 fragmentation of remaining habitat in agroecosystems, with implications for the ecosystem
95 processes they maintain, including predator population regulation (Korpimäki et al. 2004; White
96 et al. 2013), disease and parasite prevalence (Ostfeld and Holt 2004), plant diversity through
97 foraging habits (Sieg 1987), soil conditions, nutrient flow, and habitat availability through
98 burrowing activities (Grant and French 1980). Population abundance or density is typically
99 estimated using conventional trapping, which has logistic constraints that limit studies to patch
100 area and isolation effects (Hanser et al. 2011). Fewer studies have identified rodent species
101 responses to fragmentation at the landscape level at which fragmentation affects population
102 persistence (e.g., Pena et al. 2003; Heisler et al. 2013; Massa et al. 2013; Torre et al. 2015). The
103 Canadian Prairies experienced spatially inconsistent land modification post-European settlement
104 (Samson and Knopf 1994; Samson et al. 2004), resulting in landscapes that differ in the
105 magnitude of grassland loss and fragmentation that occurred there (Gage et al. 2016), providing
106 ideal conditions for this study.

107 We hypothesize that rodent species respond differently to fragmentation depending on
108 the degree of habitat specificity each species exhibits towards grassland habitat. We predict
109 grassland and vegetation obligates will respond negatively to increased loss and isolation of
110 remaining grassland patches, while habitat generalists will either 1) show no response because
111 individuals perceive no difference among habitat and land modified for agricultural use, or 2)
112 exhibit positive responses to the introduction of highly productive, new land-use types and edge
113 habitat providing access to additional resources.

114 METHODS

115 *Study area*

116 Samples were collected across almost 2 million km² of the mixed-grass prairie and aspen
117 parkland of the Northern Great Plains in Canada (Fig. 1). Vegetation of the mixed-grass prairie
118 consists mostly of grasses (e.g., *Agropyron* spp., *Bouteloua* spp., *Stipa* spp.), upland sedges (e.g.,
119 *Carex* spp.), forbs, club moss (e.g., *Selaginella densa*) and intermittent patches of small shrubs
120 (e.g., *Symphoricarpus* spp., *Elaiagnus* spp., *Prunus* spp., *Amelanchier* spp.) and trees (e.g.,
121 *Populus* spp., *Salix* spp.) where moisture permits (Coupland 1961). The aspen parkland
122 represents the transition zone between the southern mixed-grass prairie and northern boreal
123 forest and is characterized by aspen bluffs (e.g., *Populus* spp.) and fescue prairie (e.g., *Stipa*
124 *festuca*; Coupland 1961; Barker and Whitman 1988). Vegetation composition in the study area is
125 heavily influenced by local topography, boulder clay soil deposits of varying texture, and a
126 continental climate of extreme variation in temperature and precipitation with a short growing
127 period of 3-5 months (Coupland 1950).

128 Both ecoregions are heavily altered by land modification, through which heterogeneous
129 grasslands were converted into a few agricultural land use types, thus decreasing vegetative
130 species composition and structure and increasing bare ground (Smoliak 1988). Only 6% and 27%
131 of the aspen parkland and mixed-grass prairie remain intact, respectively (Roch and Jaeger
132 2014). Most modification occurred between the 1880's and 1940's (Smoliak 1988; Samson et al.
133 2004) but it continues today at lower rates. An average annual 2% loss has occurred since 2009
134 in some regions of the Canadian Prairies, resulting in an additional 13% loss of remaining
135 grasslands (Gage et al. 2016). Land modification was not evenly distributed across the study
136 area. Large tracts of grassland remain intact in southeast Alberta and southwest Saskatchewan,

137 while over 90% of the grasslands in other regions are heavily modified (Roch and Jaeger 2014;
138 Fig. 1). This variation in agricultural intensification provides an opportunity to examine
139 landscape-level rodent species responses to grassland loss and fragmentation, with comparisons
140 of responses among grassland obligates and habitat generalists.

141 *Rodent abundance estimates*

142 Rodent species abundances were estimated from great horned owl (*Bubo virginianus*) and
143 burrowing owl (*Athene cunicularia*) pellets collected across the study area (Heisler et al. 2016).
144 Over the last 20 years, owl nests and associated roosts were visited once to several times during
145 the breeding season and all accessible pellets were collected. Great horned owl pellets were
146 collected from 207 locations by Alberta's Environment & Sustainable Resource Development
147 Fish & Wildlife division in 2000 and 2001, and from an additional 436 locations by research
148 scientists and bird enthusiasts from 2008 until 2016. Burrowing owl pellets were collected from
149 1,179 locations by the Royal Saskatchewan Museum and the Canadian Wildlife Service from
150 1997 until 2016.

151 All pellets were processed to clean the bones and teeth in one of two ways: (1) soaked in
152 10% sodium hydroxide solution for 2 – 3 hours to dissolve the fur from the pellets; or (2) soaked
153 in water and manually separated. Prey species were then identified by the diagnostic
154 characteristics of craniomandibular elements (i.e., teeth, mandibles, skulls), using a reference
155 collection provided by the Royal Saskatchewan Museum and Royal Alberta Museum. Species
156 abundances were quantified for each collection based on the maximum number of right or left
157 mandibles, or the total number of skulls present (i.e., minimum number of individuals). The
158 resulting dataset includes 84,196 individuals of 11 grassland rodent species.

159 Owl pellets accumulated over differing amounts of time at each pellet collection location,
160 requiring standardizing to account for differential sampling effort. Great horned owl pellet
161 collection locations were visited once and likely represent owl foraging efforts for that year. In
162 contrast, burrowing owl pellet collection locations were visited once to several times during the
163 breeding season, and some locations were visited over multiple years. To account for these
164 differences, rodent abundances were summed when more than 1 visit was made each year to the
165 same pellet collection location. Each pellet sample therefore represents all pellets collected from
166 a single location within a single year, hereafter referred to as a sample. To accurately reflect
167 rodent community composition and be included in subsequent statistical analyses, each pellet
168 sample also met a threshold of the minimum number of individuals identified necessary to reach
169 the average prey species richness represented in pellet collections for both owl species (great
170 horned owl, $\bar{X} = 4$ species; burrowing owl, $\bar{X} = 3$ species). We therefore used great horned owl
171 pellet samples with 30 or more individuals, and burrowing owl pellet samples with 10 or more
172 individuals, respectively. A total 323 great horned owl and 1,061 burrowing owl samples were
173 used in subsequent statistical analyses (Table 1).

174 Each rodent species was categorized as a grassland obligate or a habitat generalist
175 according to its habitat description in Eder and Kennedy (2011; Table 1). Grassland habitats are
176 dominated by herbaceous and shrub vegetation maintained by fire, grazing, drought, and freezing
177 temperatures (Axelrod 1985; White et al. 2000). Vegetation composition and structure is largely
178 determined locally by topography, precipitation, and soil texture (Epstein et al. 1997; Lane et al.
179 1998; Hooke and Burke 2000). Here, we use species natural history accounts from Eder and
180 Kennedy (2011) to characterize grassland obligates as those species selecting for habitat
181 vegetated with a combination of native grasses, forbs, and short woody plants, and habitat

182 generalists as those species that occupy a variety of habitat types and are not limited by
183 vegetation cover (McKinney and Lockwood 1999; Marvier et al. 2004; DeVictor et al. 2008;
184 DeVictor et al. 2010; Clavel et al. 2011).

185 *Metrics of habitat loss, fragmentation, habitat composition, soil texture, and climate*

186 We used several metrics to characterize habitat composition, grassland loss and
187 fragmentation, and abiotic conditions surrounding pellet collection locations. Habitat
188 composition (i.e., relative proportions of habitat types within landscapes), percent habitat loss,
189 and several metrics of grassland fragmentation were quantified across the Canadian Prairies from
190 raster thematic data generated from Landsat5-TM and Landsat 7-ETM+ multi-spectral imagery
191 of 30 m resolution, representative of circa-2000 conditions (Agriculture & Agri-Food Canada
192 2012), which was reclassified to 6 broad land use (i.e., crop, tame forage, urban) and habitat
193 categories (i.e., grass, woody, riparian).

194 Habitat composition was estimated using the proportion of each habitat type (i.e.,
195 grassland (GRASS), forest and shrub (WOOD), riparian (RIPARIAN)) and agricultural land-use
196 type (i.e., cropland (CROP), tame forage (TAME), urban (URBAN)) within the foraging range
197 surrounding each owl pellet collection location (Table 2). The influence of habitat loss was
198 estimated using the cumulative percentage of the landscape comprised of crop, tame forage, and
199 urban developments (LOSS; Table 2). Habitat fragmentation was characterized using measures
200 of grassland edge density (m/ha; ED), average grassland patch perimeter-area ratio (i.e., shape
201 complexity; PARA), average grassland patch size (ha; AREA), grassland patch density (number
202 of patches per 100 ha; PD), and grassland patch cohesion (i.e., monotonic index of patch
203 connectivity; COH; Table 2).

204 We used other abiotic variables known to influence small mammal assemblage
205 composition across the study area to produce more complete statistical representations of
206 landscape-level habitat associations for each rodent species. We compiled soil texture variables
207 from existing soil survey maps by Agriculture and Agri-Food Canada (Soil Landscapes of
208 Canada Working Group 2010; Heisler et al. 2013). Soil texture was characterized from existing
209 digitized soil survey maps using the mean proportion of sand (SAND) in the soils of each owl
210 foraging range surrounding owl pellet collection locations (Centre for Land and Biological
211 Resources Research 1996; Table 2).

212 We generated three climate variables from monthly precipitation and temperatures
213 averaged over a 30-year period (i.e., 1971-2000; Agriculture and Agri-Food Canada 2013;
214 Heisler et al. 2013; Heisler et al. 2014). Growing degree days were generated as the cumulative
215 temperature above 5 °C from May to September averaged from 1971 to 2000 (GDD5), while the
216 total annual precipitation from May to September and from October to April averaged from 1971
217 to 2000 characterized summer rainfall (RAIN) and winter snowfall (SNOW), respectively (Table
218 2). Lastly, we included habitat composition as the proportions of each land-use and habitat type
219 (Heisler et al. 2013).

220 Metrics were calculated within radii varying in distance (i.e., 1 - 4 km at 0.5 km intervals)
221 from pellet collection locations to estimate the appropriate scale of effect reflecting the foraging
222 distances of burrowing owls and great horned owls from nests and associated roosts (Heisler et
223 al. 2013). We used generalized additive models (GAMs) with a negative binomial distribution
224 including the most abundant species (i.e., deer mouse) as the response and all fragmentation
225 metrics as splines for each radius (see below for model structure). We chose a scale of effect
226 with the least amount of information loss, or low Akaike Information Criterion (AIC), in both the

227 burrowing owl and great horned owl GAMs so that all further statistical analysis could be done
228 in a single GAM for each rodent species. Each metric was therefore estimated within a 2.5-km
229 radius of each owl pellet collection location (Burnham and Anderson 2002).

230 All reclassifying, data preparation, and metric calculation was done using R version 3.5.3
231 (R Development Core Team 2019). The package raster (Hijmans 2019) was used to read and
232 mosaic tiles, reclassify land cover, and prepare soil and climate data. Packages rgdal (Bivand et
233 al. 2019) and raster were used to read and prepare owl pellet, soil, and climate data. Package
234 landscapemetrics (Hesselbarth et al. 2019) was used to calculate landscape metrics.

235 *Statistical analyses*

236 Non-linear responses of rodent species to fragmentation were identified using generalized
237 additive models (GAMs). Land modification for agricultural use is a highly correlated, spatially
238 explicit, sometimes non-linear process (Fahrig 2002) that may be reflected in rodent species
239 responses to fragmentation. GAMs examine both linear and non-linear relationships using
240 generalized regression of multiple predictors (Hasti and Tibshirani 1990; Wood 2006; Zuur et al.
241 2009; Zuur 2012). We fit GAMs for each species starting with a Poisson distribution and log link
242 to account for positive integers:

$$\begin{aligned} 243 \quad R_i \sim \text{Poisson}(\mu_i), \text{ where } \log(\mu_i) = & \alpha + f_1(\text{LOSS}_i) + f_2(\text{ED}_i) + f_3(\log \text{AREA}_i) + \\ 244 \quad & f_4(\text{PARA}_i) + f_5(\text{PD}_i) + f_6(\text{COH}_i) + f_7(\text{ED}_i, \text{LOSS}_i) + f_8(\text{AREA}_i, \text{LOSS}_i) + \\ 245 \quad & f_9(\text{PARA}_i, \text{LOSS}_i) + f_{10}(\text{PD}_i, \text{LOSS}_i) + f_{11}(\text{COH}_i, \text{LOSS}_i) + f_{12}(\text{WET}_i) + \\ 246 \quad & f_{13}(\text{WOOD}_i) + f_{14}(\text{SAND}_i) + f_{15}(\text{GDD5}_i) + f_{16}(\text{RAIN}_i) + f_{17}(\text{SNOW}_i) + \\ 247 \quad & f_{18}(\text{YEAR}_i) + \log(\text{IDED}_i) \end{aligned}$$

248 where R_i is rodent abundance in the i^{th} observation (pellet sample). The terms $f_1 - f_{18}$ are smooth
249 functions of habitat loss (LOSS), grassland edge density (ED), average grassland patch size
250 (AREA), average grassland patch shape complexity (PARA), grassland patch density (PD),
251

252 grassland patch cohesion (COH), percent riparian (WET), percent woodland (WOOD), percent
253 sand in soils (SAND), average annual growing degree days >5 °C (GDD5), average summer
254 rainfall (RAIN), average winter snowfall (SNOW), and the year samples were collected
255 (YEAR). The natural log-transformed sample size (IDED) was also included as an offset
256 variable. The restricted maximum likelihood (REML) was used to avoid overfitting while
257 estimating smoothing parameters. Parameters were penalized to zero and removed from the
258 model during smoothing parameter estimation when they had little to no effect on rodent
259 abundance. Overdispersion was accounted for by changing distributions to a negative binomial
260 distribution when necessary (Zuur et al. 2009; Zuur 2012). Species abundance was included as
261 the response. Species absences were included only when they were located within the species'
262 geographic range. To account for high concurrency between LOSS and fragmentation metrics (i.e.,
263 ED, AREA, PARA, PD, and COH), each fragmentation metric was included as a tensor product
264 (i.e., synergistic effect) and tensor product interaction with LOSS (i.e., independent effect; Wood
265 2006). Habitat composition, and soil and annual climate conditions were included to improve
266 model fit (Heisler et al. 2013; Heisler et al. 2014). Year was included to account for variable
267 environmental conditions among years samples were collected. Total rodent individuals per
268 sample was included as a log-transformed offset to account for differing sampling effort.
269 Concurrency among all predictors was then assessed, those showing high concurrency with LOSS or
270 fragmentation metrics were removed from the model (Ramsay et al. 2003).

271 Null models for each species included smooth functions of soil texture, annual climate
272 conditions, habitat composition, year, and the offset term. Comparisons of the fitted and null
273 models using AIC tested for statistical influence of habitat loss and fragmentation (Burnham and
274 Anderson 2002). Only models >10 delta AIC units (i.e., competing models) from the null model

275 were considered. The variance explained by fragmentation of each fitted model was estimated by
276 subtracting the deviance explained of the null model from that of the fitted model. Inferences
277 were made only from statistically significant predictors using $p < 0.001$ to account for variability
278 in estimated p values (Zuur et al. 2009; Zuur 2012).

279 All statistical analyses were done using R version 3.6.3 (R Development Core Team).
280 GAMs were estimated using the `mgcv` (Wood et al. 2016) and `gamlss` (Rigby and Stasinopoulos
281 2005) packages.

282 RESULTS

283 Six of the eleven rodent species considered here responded to metrics of habitat loss and
284 fragmentation on the Canadian Prairies. Fitted models for four grassland obligates (i.e., meadow
285 vole, prairie vole, Ord's kangaroo rat, and Richardson's ground squirrel) and one habitat
286 generalist (i.e., long-tailed vole) were competitive with their corresponding null models,
287 suggesting these models did no better at explaining variance in abundance than random chance
288 (Table 3). Null models were not competitive for the remaining six species (Table 3), of which
289 three were grassland obligates (i.e., sagebrush voles, olive-backed pocket mice, and thirteen-
290 lined ground squirrels) and three habitat generalists (i.e., deer mice, northern grasshopper mice,
291 and northern pocket gophers). Three species responded to the main effect of habitat loss (i.e.,
292 deer mice, olive-backed pocket mice, and northern pocket gophers; Table 4). All six species
293 responded to at least one metric of fragmentation. Fitted models explained 35-82% of variance in
294 abundance for each rodent species, of which fragmentation effects accounted for <11% for all
295 species (Table 3).

296 All three species that responded to habitat loss (LOSS), estimated here as the summed
297 proportions of annual cropland, perennial livestock forage, and urban development, did so up to

298 a threshold of ~40% LOSS, above which the trajectory of their response changed. Olive-backed
299 pocket mice, considered an arid-adapted grassland obligate, responded negatively to increasing
300 habitat loss to up to 70% LOSS, above which their response reversed to positive (Fig. 2a). The
301 other two grassland obligates (i.e., sagebrush voles and thirteen-lined ground squirrels) showed
302 no response to habitat loss. Predictably for a habitat generalist, deer mice responded positively to
303 <50% LOSS and >90% LOSS but reversed its response to negative where 50-90% LOSS
304 occurred (Fig. 2b). Northern pocket gophers, another habitat generalist, responded positively to
305 <10% LOSS, negatively between 10-80% LOSS, and positively to >90% LOSS (Fig. 2c).

306 Half of the rodent species considered here responded consistently with predictions based
307 on their specificity for grassland habitat. Thirteen-lined ground squirrels were the only obligate
308 species to respond predictably to grassland fragmentation, increasing linearly with increasing
309 cohesion, or connectivity among patches (Fig. 3a). Thirteen-lined ground squirrels also
310 responded predictably to grassland edge density, declining in abundance to up to 50 m/ha (Fig.
311 3b). In contrast, two habitat generalists responded as predicted to at least one metric of grassland
312 fragmentation. Northern grasshopper mice responded positively to decreasing average grassland
313 patch size, showing elevated abundances where patches were <1 ha in landscapes with <40% or
314 >90% LOSS (Fig. 4a). And northern pocket gophers responded positively to landscapes with 2-4
315 grassland patches/100 ha in landscapes with 20-60% LOSS (Fig. 4b).

316 Responses to fragmentation that were inconsistent with our predictions were also
317 observed among grassland obligates. Sagebrush voles declined in abundance with increasing
318 grassland patch cohesion (Fig. 5a), and in 30-80% LOSS shifted from a positive response where
319 average grassland patch size was <2 ha to a negative response where patches were >5 ha in size
320 (Fig. 6a). Thirteen-lined ground squirrels responded positively to landscapes containing >5

321 patches/100 ha and 20-80% LOSS (Fig. 6b). Olive-backed pocket mice responded positively to
322 landscapes with grassland edge densities >50 m/ha and 30-80% LOSS (Fig. 6c). Responses from
323 habitat generalists were also inconsistent with our predictions. Deer mice responded positively to
324 grassland patch cohesion (Fig. 5b), negatively to >50 m/ha of grassland edge (Fig. 5c), and
325 negatively to simple grassland patch shapes (i.e., <0.06 PARA; Fig. 5d). Northern grasshopper
326 mice responded negatively to increasing grassland patch density (Fig. 5e). Northern pocket
327 gophers responded negatively to landscapes containing >4 patches/100 ha and 20-80% LOSS
328 (Fig. 6d).

329 Responses were also observed where fragmentation metrics characterized habitat
330 heterogeneity instead of fragmentation per se. These responses were observed among species
331 that responded to fragmentation effects independent of habitat loss where little to no habitat loss
332 had occurred (i.e., $<20\%$ LOSS). In these landscapes, sagebrush voles responded positively to
333 grassland patches that were >4 ha in size (Fig. 7a). Olive-backed pocket mice responded
334 negatively to increasing grassland patch density (Fig. 7b). Thirteen-lined ground squirrels
335 showed decreased abundance with increasing grassland patch density (Fig. 7c). Deer mice
336 responded positively to landscapes containing 4-12 grassland patches/100 ha (Fig. 7d).

337 DISCUSSION

338 We found rodent populations showed stronger responses to changes in habitat
339 composition than habitat configuration on the Canadian Prairies. Our results found the combined
340 effects of habitat loss and fragmentation explained an average 9x less variation in rodent
341 abundances relative to habitat composition, soil texture, and climate variation within the
342 landscape. Additionally, only three species responded to habitat loss (i.e., olive-backed pocket
343 mice, deer mice, and northern pocket gophers) while all species responded to at least one metric

344 of habitat fragmentation. The only two studies comparable to this one found lower rodent
345 diversity in fragmented landscapes (Massa et al. 2013) and shifts in assemblage composition
346 with increasing habitat fragmentation (Pena et al. 2003). Studies not including fragmentation
347 effects per se also found strong associations between rodent dynamics and habitat composition at
348 the landscape-level (e.g., Heisler et al. 2013; Rodriguez and Peris 2007; Torre et al. 2015).
349 However, too few fragmentation studies on rodent assemblages have been conducted at the
350 landscape level to draw definitive conclusions. But on the Canadian Prairies, habitat loss and the
351 corresponding change in habitat configuration appear to play minor roles in delineating rodent
352 population responses to landscape-level habitat modification for agriculture.

353 This is the first study to distinguish fragmentation effects from those of habitat loss on
354 rodent assemblages at a landscape level. We found habitat specificity does predict population
355 responses to habitat loss and fragmentation among grassland obligates and generalists alike,
356 providing further evidence that modifying natural habitats for agricultural production has
357 potential to threaten these obligate species with regional extirpation as landscapes are simplified
358 in habitat composition, shifting rodent assemblages towards generalist-dominated communities
359 (Heisler et al. 2013). In fact, we also found half of the species considered here (i.e., olive-backed
360 pocket mice, deer mice, and northern pocket gophers) reversed the trajectory of their responses
361 to land modification in landscapes where ~50% of the natural habitat was converted, suggesting
362 a threshold above which land modification begins homogenizing habitat heterogeneity with
363 similar consequences for biodiversity. This threat persists on the Canadian Prairies as remaining
364 habitat is converted to up to an average 3.5% per year (Gage et al. 2016). Reduced rodent
365 diversity in heavily modified landscapes has implications for the ecosystem functions they
366 facilitate among higher trophic levels. For example, meadow vole irruptions in this study area are

367 now dampened and less consistent (Poulin et al. 2001; Heisler et al. 2014), with potential to
368 influence the persistence of some prairie predators, including the endangered burrowing owl
369 (Todd et al. 2001) and the short-eared owl, a species of special concern (Colvin and Spaulding
370 1983). Habitat generalists such as deer mice and northern grasshopper mice appear to benefit
371 from land modification, potentially increasing the prevalence of zoonotic diseases in populated
372 rural areas (Mills and Childs 1998; Ostfeld and Holt 2004; Mills 2005; Hjelle and Torres 2010;
373 Jonsson et al. 2010). Further research on how landscape-level population responses inform the
374 spatial distributions of these rodent species and affect their functional roles in highly modified
375 landscapes is needed in this study area and elsewhere.

376 Several species responded to fragmentation metrics characterizing habitat heterogeneity
377 in landscapes where grasslands remain intact (i.e., 0-20% LOSS). In these landscapes,
378 fragmentation metrics estimate heterogeneity in grassland patch configuration amongst a mosaic
379 of other natural habitats (i.e., wetlands, shrubland, aspen bluffs, forest patches; Li and Reynolds
380 1995) instead of fragmentation per se (Andren et al. 1994; Hanski and Ovaskeinan 2002; Fahrig
381 2003; Betts et al. 2007). For example, both deer mice and thirteen-lined ground squirrels
382 responded positively to increasing heterogeneity in intact landscapes (deer mouse: >4
383 patches/100 ha; thirteen-lined ground squirrels: patches 2-4 ha in size in low densities). These
384 and other species also responded positively to increasing grassland fragmentation where
385 considerable habitat loss occurred (i.e., >80% LOSS), identifying similar responses among
386 rodent species between heterogeneous and fragmented landscapes, which has been observed in
387 other studies (e.g., Jonsen and Fahrig 1997; Holland et al. 2004; Thies et al. 2003; Holzschuh et
388 al. 2010). This may be because the structural complexity of habitat composition in heterogeneous
389 landscapes provides a greater diversity of habitat niches through which a higher diversity of

390 rodent species can exploit environmental resources (Bazzaz 1975; Tews et al. 2004; Stein et al.
391 2014). Several studies of local-level fragmentation effects on biodiversity also observed higher
392 biodiversity in agroecosystems (e.g., Lack 1969; Bazzaz 1975; Allouche et al. 2011).
393 Additionally, Fahrig (2017) found over half of all significant fragmentation effects were positive,
394 suggesting these effects may not be uniformly negative on biodiversity.

395 Habitat specificity may not be a definitive indicator of sensitivity to habitat loss and
396 fragmentation among rodent species in this study area. None of the rodent species considered
397 here responded consistently to all fragmentation metrics as predicted by their respective
398 specificity towards grassland habitat. All grassland obligates except olive-backed pocket mice
399 failed to decline in abundance with increasing percent habitat loss, and all three grassland
400 obligates responded positively to at least one metric of increasing grassland fragmentation. These
401 anomalies may be due to assuming all habitat obligates are dependent on the availability of a
402 single habitat type. Habitat specificity is a proxy for the trade-off between a species' ability to
403 exploit a range of resources relative to its capacity to use each resource (i.e., ecological
404 specialization, or the 'jack of all trades is a master of none' hypothesis; MacArthur 1972; Clavel
405 et al. 2010). Use of this proxy requires the assumption that the habitat(s) occupied by obligates
406 encompass all their required biotic and abiotic conditions, while unoccupied habitats are missing
407 key conditions for population persistence (DeVictor et al. 2010). Some taxonomic groups exhibit
408 highly ordered responses to habitat loss according to each species' position along habitat
409 specificity gradients (Patterson and Atmar 1986; Wright et al. 1988; Nupp and Swihart 2000;
410 Presley et al. 2010), identifying habitat specificity as an effective proxy for ecological
411 specialization in some cases. Depending on which aspect of fragmentation is under scrutiny,

412 using habitat specificity as a proxy for susceptibility to deleterious effects of habitat loss and
413 fragmentation may not be informative.

414 Fragmentation effects inconsistent with predictions of habitat specificity gradients may
415 indicate a mismatch between what constitutes habitat for each species and how habitat is defined
416 in studies. Habitat is one of the most ambiguous terms used in ecology (Hall et al. 1997; Kearney
417 2006; Bamford and Calver 2014), referring to all biotic and abiotic conditions influencing
418 population persistence of a species (Morris 2003). Comparisons of habitat use among species is
419 facilitated by Hutchinson's concept of the ecological niche, defined as the n-dimensional
420 hypervolume of resources used, each of which is represented by an axis (i.e., food, water
421 sources, shelter, parturition sites, etc.; Hutchinson 1957). Along each axis, each species displays
422 a wide or narrow tolerance or pattern of use relative to other species. A species can therefore be
423 generalist in the use of some resources but specialist in others (Futuyma and Moreno 1988;
424 Clavel et al. 2010). Within this context, the use of habitat specificity as a proxy for ecological
425 specialization is problematic for some species. Habitat is often used synonymously with natural
426 vegetation cover in fragmentation studies (Almeida-Gomez et al. 2015), which may not
427 encompass the gradients of resource uses most limiting to the species of interest in highly
428 fragmented agroecosystems (Fischer and Lindenmeyer 2007; Presley et al. 2010; Betts et al.
429 2014). For example, olive-backed pocket mice are thought to be restricted to unmodified
430 grassland habitat throughout their geographic range (Hayward and Killpack 1956; Banfield
431 1974; Lampe et al. 1974; Wilhelm et al. 1981) but elevated abundances were observed in
432 modified landscapes with high grassland edge densities. Large populations of this species may
433 therefore be limited to grassland vegetation in less modified landscapes but released from that
434 limitation in modified landscapes where individuals may take advantage of increased seed

435 production along grassland-cropland edges. Similarly, northern pocket gophers responded
436 negatively to up to 40% habitat loss despite being characterized as a habitat generalist. This
437 fossorial species may not select for vegetative habitat(s) per se but are limited to those that do
438 not experience intra-annual soil disturbances like annual cropland (Salt 2000). This hypothesis
439 does not explain the increase in abundance of this species to up to 100% habitat loss. Future
440 studies should carefully consider which dimension of the ecological niche defines habitat
441 specificity for all species under study prior to assuming the natural vegetation of the study area
442 appropriately characterizes resource limitation among all species (Franklin et al. 2005; Fischer
443 and Lindenmeyer 2007; Flynn et al. 2009; Betts et al. 2014).

444 The use of habitat specificity as a proxy for ecological specialization may have
445 significant implications for biodiversity conservation when used to inform land modification
446 policies at a national or international scale. The amount of land modified for global agricultural
447 production is expected to increase 10–50% by 2050 (Tilman et al. 2001; Tilman et al. 2011),
448 most likely in developing countries where the world’s biodiversity hotspots remain (Myers et al.
449 2000; Green et al. 2005). Two strategies, or a combination of both, have been proposed to
450 conserve these remaining hotspots: 1) promoting agricultural intensification in existing
451 agroecosystems considered low priority for biodiversity conservation to save remaining
452 biodiversity hotspots from land modification (i.e., land sparing approach; Green et al. 2005;
453 Phalan et al. 2011; Tilman et al. 2011), or 2) preventing agricultural intensification by improving
454 crop yields instead of continued land modification, maintaining mosaics of natural habitats
455 interspersed among agricultural land-use types where biodiversity conservation is a priority (i.e.,
456 land sharing approach; Foley et al. 2011; Wright et al. 2012; Mendenhall et al. 2014). Habitat
457 specificity is now being used to predict biodiversity responses to different conservation

458 strategies, with little to no empirical research to assess its reliability for use to inform global
459 biodiversity conservation (Green et al. 2005; Cardinale et al. 2012; Baudron and Giller 2013).
460 For example, Phalan et al. (2011) found more bird and tree species showed lower densities in 1
461 km² plots of modified habitat and advocate for land sparing to conserve large expanses of intact
462 natural habitat elsewhere. In contrast, Wright et al. (2012) found not all species maintain high
463 population densities in natural habitats, but some species are now reliant on agricultural land-use
464 types showing high densities in heavily modified agricultural areas. Both studies fail to recognize
465 those species whose population persistence is limited by biotic or abiotic conditions not defined
466 by vegetation, including grassland habitats and agricultural land-use types. Our study finds
467 species exhibit complex, sometimes contradictory responses to habitat fragmentation dependent
468 on the magnitude of habitat loss that has occurred that may not be predicted by habitat
469 specificity. Use of habitat specificity to predict anthropogenic impacts on biodiversity should be
470 done with caution considering the finality of land modification, or at the very least explicitly
471 define the specialization gradient of interest.

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479 LITERATURE CITED

- 480 Agriculture and Agri-Food Canada. 2012. Land cover for agricultural regions of Canada, circa
481 2000. Toronto, Ontario, Canada.
- 482 Agriculture and Agri-Food Canada. 2013. Monthly long-term average precipitation accumulation
483 for the year. Toronto, Ontario, Canada.
- 484 Almeida-Gomez M, J Augusto Prevedello, and R Crouzeilles. 2015. The use of native vegetation
485 as a proxy for habitat may overestimate habitat availability in fragmented landscapes.
486 *Landscape ecology* 31: 711-719.
- 487 Allouche O, M Kalyuzhny, G Moreno-Rueda, and R Kadmon. 2012. Area-heterogeneity tradeoff
488 and the diversity of ecological communities. *PNAS* 109: 17495-17500.
- 489 Andren H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with
490 different proportions of suitable habitat: a review. *Oikos* 71: 355-366.
- 491 Axelrod DI. 1985. Rise of the grassland biome, central North America. *Botanical Review* 51:
492 163-201.
- 493 Bamford MJ, and MC Calver. 2014. A precise definition of habitat is needed for effective
494 conservation and communication. *Australian Zoologist* 37: 245-247.
- 495 Banfield AWF. 1974. *The mammals of Canada*. University of Toronto Press.
- 496 Banks-Leite C, RM Ewers, and JP Metzger. 2010. Edge effects as the principal cause of area
497 effects on birds in fragmented secondary forest. *Oikos* 119: 918-926.
- 498 Barker WT, and WC Whitman. 1988. Vegetation of the northern Great Plains. *Rangelands* 10:
499 266-272.
- 500 Barnosky AD, N Matzke, S Tomlya, GOU Wogan, B Swartz, TB Quental, C Marshall, JL
501 McGuire, EI Lindsey, KC Maguire, B Mersey, and EA Ferrer. 2011. Has the Earth's
502 sixth mass extinction already arrived? *Nature* 471: 51-57.

- 503 Baudron F and KE Giller. 2014. Agriculture and nature: trouble and strife? *Biological*
504 *Conservation* 170: 232-245.
- 505 Bazzaz FA. 1975. Plant species diversity in old-field successional ecosystems in southern
506 Illinois. *Ecology* 56: 485-488.
- 507 Bender DJ, TA Contreras, and L Fahrig. 1998. Habitat loss and population decline: a meta-
508 analysis of the patch size effect. *Ecology* 79: 517-533.
- 509 Benton TG, JA Vickery, and JD Wilson. 2003. Farmland biodiversity: in habitat heterogeneity
510 the key? *Trends in Ecology and Evolution* 18: 182-188.
- 511 Betts MG, GJ Forbes, and AW Diamond. 2007. Thresholds in songbird occurrence in relation to
512 landscape structure. *Conservation Biology* 21: 1046-1058.
- 513 Betts MG, L Fahrig, AS Hadley, KE Halstead, J Bowman, WD Robinson, JA Wiens, and DB
514 Lindenmayer. 2014. A species-centered approach for uncovering generalities in organism
515 responses to habitat loss and fragmentation. *Ecography* 37: 517-527.
- 516 Bivand R, T Keitt, and B Rowlingson. 2019. Rgdal: bindings for the geospatial data abstraction
517 library. R package version 1.4-3. <https://CRAN.R-project.org/package=rgdal>.
- 518 Burnham KP, and DR Anderson. 2002. Model selection and multimodel inference: a practical
519 information-theoretic approach. Springer, New York.
- 520 Burns CE, and JS Grear. 2008. Effects of habitat loss on populations of white-footed mice:
521 testing matrix model predictions with landscape-scale perturbation experiments.
522 *Landscape Ecology* 23: 817-831.
- 523 Cardinale BJ, JE Duffy, A Gonzalez, DU Hooper, C Perrings, P Venail, A Narwani, GM Mace,
524 D Tilman, DA Wardle, AP Kinzig, GC Daily, M Loreau, JB Grace, A Larigauderie, DS

- 525 Srivastava, and S Naeem. 2012. Biodiversity loss and its impact on humanity. *Nature*
526 486: 59-68.
- 527 Centre for Land and Biological Resources Research. 1996. *Soil landscapes of Canada*, version
528 2.2, Research Branch, Agriculture and Agri-Food Canada. Ottawa, Ontario, Canada.
- 529 Chapin FS III, ES Zavaleta, VT Eviners, RL Naylor, PM Vitousek, HL Reynolds, DU Hooper, S
530 Lavorel, OE Sala, SE Hobbie, MC Mack, and S Diaz. 2000. Consequences of changing
531 biodiversity. *Nature* 405: 234-242.
- 532 Clavel J, R Julliard, and V Devictor. 2011. Worldwide decline of specialist species: toward a
533 global functional homogenization? *Frontiers in Ecology and the Environment* 9: 222-228.
- 534 Colvin BA, and SR Spaulding. 1983. Winter foraging behavior of short-eared owls (*Asio*
535 *flammeus*) in Ohio. *American Midland Naturalist* 110: 124-128.
- 536 Comfort EJ, DA Clark, RG Anthony, J Bailey, MG Betts. 2016. Quantifying edges as gradients
537 at multiple scales improves habitat selection models for northern spotted owl. *Landscape*
538 *Ecology* 31: 1227-1240.
- 539 Connor EF, AC Courtney, and JM Yoder. 2000. Individuals-area relationships: the relationship
540 between animal population density and area. *Ecology* 81: 734-748.
- 541 Coupland RT. 1950. Ecology of mixed prairie in Canada. *Ecological Monographs* 20: 271-315.
- 542 Coupland RT. 1961. A reconsideration of grassland classification in the northern Great Plains of
543 North America. *Journal of Ecology* 49: 135-167.
- 544 Debinski DM, and RD Holt. 2000. A survey and overview of habitat fragmentation experiments.
545 *Conservation Biology* 14: 342-355.
- 546 DeVictor V, R Julliard, and F Jiguet. 2008. Distribution of specialist and generalist species along
547 spatial gradients of habitat disturbance and fragmentation. *Oikos* 117: 507-514.

- 548 DeVicor V, J Clavel, R Julliard, S Lavergne, D Moullet, W Thuiller, P Venail, S Villéger, and N
549 Mouquet. 2010. Defining and measuring ecological specialization. *Journal of Applied*
550 *Ecology* 47: 15-25.
- 551 Diaz S, J Fargione, FS Chapin III, and D Tilman. 2006. Biodiversity loss threatens human well-
552 being. *PLoS Biology* 4: 1300-1305.
- 553 Didham RK, V Kapos, and RM Ewers. 2012. Rethinking the conceptual foundations of habitat
554 fragmentation research. *Oikos* 121: 161-170.
- 555 Dirzo, HS Young, M Galetti, G Ceballos, NJB Isaac, and B Collen. 2014. Defaunation in the
556 Anthropocene. *Science* 345: 401-406.
- 557 Eder T, and G Kennedy. 2011. *Mammals of Canada*. Lone Pine Publishing, Edmonton, Alberta.
- 558 Ellis, EC, and N Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the
559 world. *Frontiers in Ecology and Evolution* 6: 439-447.
- 560 Epstein HE, WK Lauenroth, and IC Burke. 2007. Effects of temperature and soil texture on
561 ANPP in the US Great Plains. *Ecology* 78: 2628-2631.
- 562 Ewers RM, and RK Didham. 2005. Confounding factors in the detection of species responses to
563 habitat fragmentation. *Biological Reviews* 81: 117-142.
- 564 Ewers RM, and RK Didham. 2007. Synergistic interactions between edge and area effects in a
565 heavily fragmented landscape. *Ecology* 88: 96-106.
- 566 Fahrig L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis.
567 *Ecological Applications* 12: 346-353.
- 568 Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Reviews in Ecology and*
569 *Evolutionary Systems* 34: 487-515.
- 570 Fahrig, L, J Baudry, L Brotons, FG Burel, TO Crist, RJ Fuller, C Sirami, GM Siriwardena, JL

- 571 Martin. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural
572 landscapes. *Ecology Letters* 14: 101-112.
- 573 Fahrig L. 2017. Ecological responses to habitat fragmentation per se. *Annual Reviews of*
574 *Ecology, Evolution and Systematics* 48: 1-23.
- 575 Fischer J, and DB Lindenmeyer. 2007. Landscape modification and habitat fragmentation: a
576 synthesis. *Global Ecology and Biogeography* 16: 265-280.
- 577 Fletcher RJ Jr. 2005. Multiple edge effects and their implications in fragmented landscapes.
578 *Journal of Animal Ecology* 74: 342-352.
- 579 Flynn DFB, M Gogol-Prokurat, T Nogeire, N Molinari, B Trautman Richers, BB Lin, N
580 Simpson, MM Mayfield, and F DeClerck. 2009. Loss of functional diversity under land
581 use intensification across multiple taxa. *Ecology Letters* 2009: 22-33.
- 582 Foley AJ, R DeFries, GP Asner, C Barford, G Bonan, SP Carpenter, FS Chapin, MT Coe, GC
583 Daily, HK Gibbs, JH Helkowski, T Holloway, EA Howard, CJ Kucharik, C Monfreda,
584 JA Patz, IC Prentice, N Ramankutty, and PK Snyder. 2005. Global consequences of land
585 use. *Science* 309: 570-574.
- 586 Foley JA, N Ramankutty, KA Brauman, ES Cassidy, JS Gerber, M Johnston, ND Mueller, C
587 O'Connell, DK Ray, PC West, C Balzer, EM Bennett, SR Carpenter, J Hill, C Monfreda,
588 S Polasky, J Rockstrom, J Sheeham, S Siebert, D Tilman, and DPM Zaks. 2011.
589 Solutions for a cultivated planet. *Science* 478: 337-342.
- 590 Franklin AB, BR Noon, and TL George. 2005. What is habitat fragmentation? *Studies in Avian*
591 *Biology* 25: 20-29.
- 592 Futuyma DJ, and G Moreno. 1988. The evolution of ecological speciation. *Annual review of*
593 *ecology and systematics* 19: 207-233.

- 594 Gage AM, SK Olimb, and J Nelson. 2016. Plowprint: tracking cumulative cropland expansion to
595 target grassland conservation. *Great Plains Research* 26: 107-116.
- 596 Grant WE and NR French. 1980. Evaluation of the role of small mammals in grassland
597 ecosystems: a modeling approach. *Ecological Modeling* 8: 15-37.
- 598 Green RE, SJ Cornell, JPW Scharlemann, and A Balmford. 2005. Farming and the fate of nature.
599 *Science* 307: 550-555.
- 600 Haddad NM, LA Brudvig, J Clobert, KF Davies, A Gonzalez, RD Holt, TE Lovejoy, JO Sexton,
601 MP Austin, CD Collins, WM Cook, EI Damschen, RM Ewers, BL Foster, CN Jenkins,
602 AJ King, WF Laurence, DJ Levey, CR Margules, BA Melbourne, AO Nicholls, JL
603 Orrock, DX Song, and JR Townsend. 2015. Habitat fragmentation and its lasting impact
604 on Earth's ecosystems. *Science Advances* 1: 1-9.
- 605 Hall LS, PR Krausman, and ML Morrison. 1997. The habitat concept and a plea for standard
606 terminology. *Wildlife Society Bulletin* 25: 173-182.
- 607 Hanser SE et al. 2011. Occurrence of small mammals: deer mice and the challenge of trapping
608 across large spatial extents. Pp. 337-356 in *Sagebrush ecosystems conservation and*
609 *management: ecoregional assessment tools and models for the Wyoming basins* (SE
610 Hanser, M Leu, ST Knick, and CL Aldridge, eds.). Allen Press, Lawrence, Kansas.
- 611 Hanski I., and O Ovaskainen. 2002. Extinction debt at extinction threshold. *Conservation*
612 *Biology* 16: 666-673.
- 613 Hesselbarth MHK, M Sciaini, J Nowosad, and S Hanss. 2019. landscapemetrics: landscape
614 metrics for categorical map patterns. R package version 1.0. [https://CRAN.R-](https://CRAN.R-project.org/package=landscapemetrics)
615 [project.org/package=landscapemetrics](https://CRAN.R-project.org/package=landscapemetrics)
- 616 Hasti T, and R Tibshirani. 1990. *Generalized additive models*. Chapman and Hall, New York.

- 617 Hayward CL, and ML Killpack. 1956. Occurrence of *Perognathus fasciatus* in Utah. Journal of
618 Mammalogy 37: 451-452.
- 619 Hector A, and R Bagchi. 2007. Biodiversity and ecosystem multifunctionality. Nature 448: 188-
620 191.
- 621 Heisler LM, CM Somers, TI Wellicome, and RG Poulin. 2013. Landscape-scale features
622 affecting small mammal assemblages on the northern Great Plains of North America.
623 Journal of Mammalogy 94: 1059-1067.
- 624 Heisler LM, CM Somers, and RG Poulin. 2014. Rodent populations on the northern Great Plains
625 respond to weather variation at a landscape scale. Journal of Mammalogy 95: 82-90.
- 626 Heisler LM, CM Somers, and RG Poulin. 2016. Owl pellets: a more effective alternative to
627 conventional trapping for broad-scale studies of small mammal communities. Methods in
628 Ecology and Evolution 7: 96-103.
- 629 Henle K, KF Davies, M Kleyer, C Margules, and J Settele. 2004. Predictors of species sensitivity
630 to fragmentation. Biodiversity and Conservation 13: 207-251.
- 631 Hijmans RJ, J Etten, J Cheng, M Mattiuzzi, M Sumner, JA Greenberg, OP Lamigueiro, A Bevan,
632 EB Racine, A Shortridge, and A Ghosh. 2019. Geographic data analysis and modeling. R
633 package version 2.8-19. <https://CRAN.R-project.org/package=raster>.
- 634 Hjelle B, and F Torres-Perez. 2010. Hantaviruses in the Americas and their role as emerging
635 pathogens. Viruses 2: 2559-5286.
- 636 Hoekstra JM, TM Boucher, TH Ricketts, and C Roberts. 2005. Confronting a biome crisis:
637 global disparities of habitat loss. Ecology Letters 8: 23-29.
- 638 Holland JD, DG Bert, and L Fahrig. 2004. Determining the spatial scale of species' response to
639 habitat. BioScience 54: 227-233.

- 640 Holzschuh A, I Steffan-Dewenter, and T Tscharntke. 2010. How do landscape composition and
641 configuration, organic farming and fallow strips affect the diversity of bees, wasps and
642 their parasitoids? *Journal of Animal Ecology* 79: 491-500.
- 643 Hook PB, and IC Burke. 2000. Biogeochemistry in a shortgrass landscape: control by
644 topography, soil texture, and microclimate. *Ecology* 81: 2686-2703.
- 645 Hutchinson GE. 1957. The multivariate niche. *Cold Springs Harbour Symposium on*
646 *Quantitative Biology* 22: 415-421.
- 647 Jonsen ID, and L Fahrig. 1997. Response of generalist and specialist insect herbivores to
648 landscape spatial structure. *Landscape Ecology* 12: 185-197.
- 649 Jonsson CB, LT Moraes Figueiredo, and O Vapalahti. 2010. A global perspective on hantavirus
650 ecology, epidemiology, and disease. *Clinical Microbiology Reviews* 23: 412-441.
- 651 Kearney M. 2006. Habitat, environment, and niche: what are we modelling? *Oikos* 115: 186-191.
- 652 Keinath DA, DF Doak, KE Hodges, LR Prugh, W Fagan, CH Sekercioglu, SHM Buchart, and M
653 Kauffman. 2017. A global analysis of traits predicting species sensitivity to habitat
654 fragmentation. *Global Ecology and Biogeography* 26: 115-127.
- 655 Korpimäki E, PR Brown, J Jacob, and RP Pech. 2004. The puzzles of population cycles and
656 outbreaks of small mammals solved? *BioScience* 54: 1071-1079.
- 657 Lack D. 1969. The numbers of bird species on islands. *Bird Study* 16: 193-209.
- 658 Lampe RP, JK Jones Jr, RS Hoffman, and EC Birney. 1974. The mammals of Carter County,
659 southeastern Montana. *Occasional Papers of Museum Natural History, University of*
660 *Kansas* 25: 1-39.

- 661 Lane DR, DP Coffin, and WK Lauenroth. 1998. Effects of soil texture and precipitation on
662 above-ground productivity and vegetation structure across the central grassland region of
663 the United States. *Journal of Vegetation Science* 9: 239-250.
- 664 Li H and JF Reynolds. 1995. On definition and quantification of heterogeneity. *Oikos* 73: 280-
665 284.
- 666 MacArthur RH. 1972. *Geographical ecology*. Harper & Row, New York, NY.
- 667 Marvier M, P Kareiva, and MG Neubert. 2004. Habitat destruction, fragmentation, and
668 disturbance promote invasion by habitat generalists in a multispecies metapopulation.
669 *Risk Analysis* 24: 869-878.
- 670 Massa C, P Teta, and G Ruben Cueto. 2013. Effects of regional context and landscape
671 composition on diversity and composition of small rodent assemblages in Argentinian
672 temperate grasslands and wetlands. *Mammalia* 78: 371-382.
- 673 McKinney ML, and JL Lockwood. 1999. Biotic homogenization: a few winners replacing many
674 losers in the next mass extinction. *Trends in Ecology and Evolution* 14: 450-453.
- 675 McNaughton SJ. 1977. Diversity and stability of ecological communities: a comment on the role
676 of empiricism in ecology. *The American Naturalist* 111: 515-525.
- 677 Mendenhall CD, DS Karp, CFJ Meyer, EA Hadly, and GC Daily. 2014. Predicting biodiversity
678 change and averting collapse in agricultural landscapes. *Nature* 509: 213-217.
- 679 Mills JN. 2005. Regulation of rodent-borne viruses in the natural host: implications for human
680 disease. *Archives of Virology* 19: 45-57.
- 681 Mills JN, and JE Childs. 1998. Ecologic studies of rodent reservoirs: their relevance for human
682 health. *Emerging Infectious Diseases* 4: 529-537.

- 683 Morris DW. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136:
684 1-13.
- 685 Myers N, RA Mittermeier, CG Mittermeier, GAB da Fonseca, and J Kent. 2000. Biodiversity
686 hotspots for conservation priorities. *Nature* 403: 853-858.
- 687 Nupp TE, and RK Swihart. 2000. Landscape-level correlates of small-mammal assemblages in
688 forest fragments of farmland. *Journal of Mammalogy* 81: 512-526.
- 689 Ostfeld RS and RD Holt. 2004. Are predators good for your health? Evaluating evidence for top-
690 down regulation of zoonotic disease reservoirs. *Frontiers in Ecology and the Environment*
691 2: 13-20.
- 692 Patterson BD, and W Atmar. 1986. Nested subsets and the structure of insular mammalian
693 faunas and archipelagos. *Biological Journal of the Linnean Society* 28: 65-82.
- 694 Pena NM, A Butet, Y Delettre, G Paillat, P Morant, L Le Du, and F Burel. 2003. Response of the
695 small mammal community to changes in western French agricultural landscape.
696 *Landscape Ecology* 18: 265-278.
- 697 Phalan B, M Onial, A Balmford, RE Green. 2011. Reconciling food production and biodiversity
698 conservation: land sharing and land sparing compared. *Science* 333: 1289-1291.
- 699 Pimm SL, GJ Russel, JL Gittelman, and TM Brooks. 1995. The future of biodiversity. *Science*
700 269: 347-350.
- 701 Poulin RG, TI Wellicome, and LD Todd. 2001. Synchronous and delayed numerical responses of
702 a predatory bird community to a vole outbreak on the Canadian Prairies. *Journal of*
703 *Raptor Research* 35: 288-295.
- 704 Presley SJ, CL Higgins, and MR Willig. 2010. A comprehensive framework for the evaluation of
705 metacommunity structure. *Oikos* 119: 908-917.

- 706 R Development Core Team. 2017. R: a language and environment for statistical computing. R
707 Foundation for Statistical Computing, Vienna, Austria.
- 708 Ramsay TO, RT Burnett, and D Krewski. 2003. The effect of concurvity in generalized additive
709 models linking mortality to ambient particulate matter. *Epidemiology* 14: 18-23.
- 710 Reino L, P Beja, MB Araújo, S Dray, and P Segurado. 2014. Does local habitat fragmentation
711 affect large-scale distributions? The case of a specialist grassland bird. *Biodiversity*
712 *Research* 19: 423-432.
- 713 Rigby RA, and DM Stasinopoulos. 2005. Generalized additive models for location, scale and
714 shape, (with discussion). *Applied Statistics* 54: 507-554.
- 715 Roch L, and JAG Jaeger. 2014. Monitoring an ecosystem at risk: what is the degree of grassland
716 fragmentation in the Canadian Prairies? *Environmental Monitoring and Assessment* 186:
717 2505-2534.
- 718 Rodríguez C, and SJ Peris. 2007. Habitat associations of small mammals in farmed landscapes:
719 implications for agri-environmental schemes. *Animal Biology* 57: 301-314.
- 720 Salt JR. 2000. Pocket gopher/mouse associations on the Milk river grasslands. *Blue Jay* 58: 139-
721 143.
- 722 Samson FB and FL Knopf. 1994. Prairie conservation in North America. *BioScience* 44: 418-
723 421.
- 724 Samson FB, FL Knopf, and WR Ostlie. 2004. Great Plains ecosystems: past, present, and future.
725 *Wildlife Society Bulletin* 32: 6-15.
- 726 Sieg CH. 1987. Small mammals: pests or vital components of the ecosystem. Paper presented at
727 the 8th wildlife damage control workshop, April 26-30, 1987. Rapid City, South Dakota.
- 728 Smoliak S. 1988. The northern Great Plains – Canadian connection. *Rangelands* 10: 210-212.

- 729 Soil Landscapes of Canada Working Group. 2010. Soil landscapes of Canada version 3.2.
730 Agricultural and Agri-Food Canada (digital map and database at 1:1 million scale).
- 731 Tews, J, U Brose, V Grimm, K Tielbörger, MC Wichmann, M Schwager, and F Jeltsch. 2004.
732 Animal species diversity driven by habitat heterogeneity/diversity: the importance of
733 keystone structures. *Journal of Biogeography* 31: 79-92.
- 734 Thies C, I Steffan-Dewenter, and T Tschardt. 2003. Effects of landscape context on herbivory
735 and parasitism at different spatial scales. *Oikos* 101: 18-25.
- 736 Tilman D, RM May, CL Lehman, MA Nowak. 1994. Habitat destruction and the extinction debt.
737 *Nature* 371: 65-66.
- 738 Tilman D, J Fargione, B Wolff, C D'Antonio, A Dobson, R Howarth, D Schindler, WH
739 Schlesinger, D Simberloff, and D Swackhamer. 2001. Forecasting agriculturally driven
740 global environmental change. *Science* 292: 281-284.
- 741 Tilman D, C Balzer, J Hill, and BL Befort. 2011. Global food demand and the sustainable
742 intensification of agriculture. *Proceedings of the National Academy of Sciences* 108:
743 20260-20264.
- 744 Todd LD, RG Poulin, TI Wellicome, and RM Brigham. 2001. Post-fledging survival of
745 burrowing owls in Saskatchewan. *Journal of Wildlife Management* 67: 512-519.
- 746 Torre I, L Gracia-Quintas, A Arrizabalaga, J Baucells, and M Diaz. 2015. Are recent changes in
747 the terrestrial small mammal communities related to land use change? A test using pellet
748 analyses. *Ecological Research* 30: 813-819.
- 749 Tylianakis JM, RK Didham, J Bascompte, and DA Wardle. 2008. Global change species
750 interaction in terrestrial ecosystems. *Ecology Letters* 11: 1351-1363.

- 751 VanDerWal J, L Falconi, S Januchowski, and C Storlie. 2015. SDMTools: species distribution
752 modelling tools: tools for processing data associated with species distribution modelling
753 exercises. R package version 1.1-13. 2012. [http://CRAN.R-](http://CRAN.R-project.org/package=SDMTools)
754 [project.org/package=SDMTools](http://CRAN.R-project.org/package=SDMTools).
- 755 Virginia RA, and DH Wall. 2001. Principles of ecosystem function. Encyclopedia of
756 Biodiversity 2: 345-352.
- 757 Vitousek, PM, HA, Mooney, J. Lubchenco, and J.M. Melillo. 1997. Human domination of
758 Earth's ecosystems. *Science* 277: 494-499.
- 759 White R, S Murray, and M Rohweder. 2000. Pilot analysis of global ecosystems: grassland
760 ecosystems. World Resources Institute.
- 761 White TCR. 2013. Experimental and observational evidence reveals that predators in natural
762 environments do not regulate their prey: they are passengers, not drivers. *Acta*
763 *Oecologica* 53: 73-87.
- 764 Wilhelm RB, JR Choate, and JK Jones. 1981. Mammals of Lacreek national wildlife refuge,
765 South Dakota. Special Publications Museum of Texas Tech University 17: 1-39.
- 766 Wilson MC, XY Chen, RT Corlett, RK Didham, P Ding, RD Holt, M Holyoak, G Hu, AC
767 Hughes, L Jiang, WF Laurance, J Liu, SL Pimm, SK Robinson, SE Russo, X Si, DS
768 Wilcove, J Wu, and M Yu. 2016. Habitat fragmentation and biodiversity conservation:
769 key findings and future challenges. *Landscape Ecology* 31: 219-227.
- 770 Wood SN, N Pya, and B Säfken. 2016. Smoothing parameter and model selection for general
771 smooth models. *Journal of the American Statistical Association* 111: 1548-1563.
- 772 Wright HL, IR Lake, and PM Dolman. 2012. Agriculture – a key element for conservation in the
773 developing world. *Conservation Letters* 5: 11-19.

774 Zuur AF, EN Ieno, NJ Walker, AA Saveliev, and GM Smith. 2009. Mixed effects models and
775 extensions in ecology with R. Springer, New York.
776 Zuur AF. 2012. A beginner's guide to generalized additive models with R. Highland Statistics
777 Ltd., Newburgh, United Kingdom.
778

779 FIG. 1 Distribution of owl pellet collection locations (black dots) in grasslands modified for
780 agricultural use (cropland = shaded light grey; grassland = dark grey) in Alberta (left),
781 Saskatchewan (middle), and Manitoba (right; lines = provincial boundaries) of Canada. Major
782 cities in Alberta (i.e., Calgary and Edmonton) and Saskatchewan (i.e., Regina and Saskatoon) are
783 given for reference. White areas represent waterbodies and regions outside the study area.

784 FIG. 2 Estimated effect of habitat loss (%; including cropland, perennial livestock forage, and
785 urban and industrial land use types) on **(a)** olive-backed pocket mouse, **(b)** deer mouse, and **(c)**
786 northern pocket gopher abundances across the Canadian Prairies. Trends were modeled on the
787 scale of the linear predictor (solid black line; dotted black line indicates no effect) with 95%
788 confidence intervals (grey shade).

789 FIG. 3 Responses to fragmentation effects that were consistent with predictions based on habitat
790 specificity, including the estimated effect of **(a)** grassland patch cohesion (%) and **(b)** grassland
791 edge density (m/ha) on thirteen-lined ground squirrel abundances across the Canadian Prairies.
792 Trends were modeled on the scale of the linear predictor (solid black line; dotted black line
793 indicates no effect) with 95% confidence intervals (grey shade).

794 FIG. 4 Responses to fragmentation effects independent of habitat loss that were consistent with
795 predictions based on habitat specificity, including the estimated effect of **(a)** average grassland
796 patch area (ha) on northern grasshopper mouse abundance and **(b)** grassland patch density (#
797 patches/100 ha) on northern pocket gopher abundance across the Canadian Prairies. Trends
798 were modeled on the scale of the linear predictor (white contour lines; positive effects shaded
799 light, negative effects shaded dark).

800 FIG. 5 Responses to fragmentation effects that were inconsistent with predictions based on
801 habitat specificity, including the estimated effect of **(a)** grassland patch cohesion (%) on

802 sagebrush vole abundance, the effects of **(b)** grassland patch cohesion, **(c)** grassland edge
803 density (m/ha), and **(d)** grassland patch shape complexity on deer mouse abundance, and the
804 effects of **(e)** grassland patch density (# patches/100 ha) on northern grasshopper mouse
805 abundance. Trends were modeled on the scale of the linear predictor (white contour lines;
806 positive effects shaded light, negative effects shaded dark).

807 FIG. 6 Responses to fragmentation effects independent of habitat loss that were inconsistent with
808 predictions based on habitat specificity, including the estimated effect of **(a)** average grassland
809 patch area (ha) on sagebrush vole abundance, **(b)** grassland patch density (# patches/100 ha) on
810 thirteen-lined ground squirrel abundance, **(c)** grassland edge density (m/ha) on olive-backed
811 pocket mouse abundance, and **(d)** grassland patch density (# patches/100 ha) on northern pocket
812 gopher abundance. Trends were modeled on the scale of the linear predictor (white contour
813 lines; positive effects shaded light, negative effects shaded dark).

814 FIG. 7 Responses to habitat heterogeneity in landscapes where <20% habitat loss has occurred,
815 including the estimated effect of **(a)** average grassland patch area (ha) on sagebrush vole
816 abundance and grassland patch density (# patches/100 ha) on **(b)** olive-backed pocket mouse
817 abundance, **(c)** thirteen-lined ground squirrel abundance, and **(d)** deer mouse abundance. Trends
818 were modeled on the scale of the linear predictor (white contour lines; positive effects shaded
819 light, negative effects shaded dark).

820

821 TABLE 1 Frequency among samples (N) and abundance (Total) of rodent species estimated from
 822 great horned (GHOW) and burrowing owl (BUOW) pellet samples. Characterization as
 823 grassland obligates (Grass) or habitat generalists (General) based on habitat descriptions in Eder
 824 and Kennedy (2011).

Common Name	Habitat Specialization	N	Total	BUOW	GHOW
Deer mouse <i>(Peromyscus maniculatus)</i>	General	1,363	48,348	24,205	24,143
Meadow vole <i>(Microtus pennsylvanicus)</i>	Grass	1,182	15,270	8,695	6,575
Sagebrush vole <i>(Lemmyscus curtatus)</i>	Grass	729	7,790	5,198	2,592
Northern grasshopper mouse <i>(Onychomys leucogaster)</i>	General	488	2,738	525	2,213
Olive-backed pocket mouse <i>(Perognathus fasciatus)</i>	Grass	377	1,926	829	1,097
Richardson's ground squirrel <i>(Urocitellus richardsonii)</i>	Grass	242	471	230	241
Northern pocket gopher <i>(Thomomys talpoides)</i>	General	126	648	179	469
Thirteen-lined ground squirrel <i>(Ictidomys tridecemlineatus)</i>	Grass	70	302	26	276
Prairie vole	Grass	29	170	2	168

(Microtus ochragaster)

Ord's kangaroo rat	Grass	9	27	7	20
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(Dipodomys ordii)

Long-tailed vole	General	6	7	0	7
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(Microtus longicaudatus)

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826

827 TABLE 2 Average (+/- standard deviation) percent habitat loss (LOSS), habitat fragmentation
 828 (i.e., average grassland patch area (AREA), grassland edge density (ED), average grassland
 829 patch shape edge to area ratio (PARA), grassland patch density (PD), and grassland patch
 830 cohesion (COH)), habitat composition (cropland (CROP), grassland (GRASS), perennial
 831 livestock forage (TAME), urban development (URBAN), riparian areas (WET), and woody
 832 vegetation (WOOD), climate (total growing degrees >5 °C (GDD5), summer rainfall (RAIN),
 833 and winter snowfall (SNOW)), and soil texture (sand (SAND)) within a 2.5 km radius from
 834 each burrowing owl and great horned owl pellet collection location. Fragmentation metrics were
 835 taken from VanDerWal 2015.

Environmental Conditions		Burrowing Owl	Great Horned	All
		Foraging Range	Owl Foraging Range	Pellet Samples
Habitat composition	GRASS (%)	31.9 (34.0)	15.2 (20.8)	28.0 (32.2)
	CROP (%)	48.5 (33.6)	62.2 (27.4)	51.7 (32.8)
	TAME (%)	11.2 (14.6)	13.6 (15.5)	11.8 (14.8)
	URBAN (%)	3.3 (10.1)	2.7 (2.5)	3.2 (8.9)
	WET (%)	2.7 (4.7)	2.7 (4.6)	2.7 (4.7)
	WOOD (%)	1.4 (2.1)	2.5 (2.7)	1.7 (2.5)
Habitat configuration	LOSS (%)	63.0 (36.2)	78.5 (23.4)	66.6 (34.3)
	AREA (ha)	2.9 (2.2)	1.9 (1.5)	2.7 (2.1)
	ED (m/ha)	12.4 (11.7)	14.1 (12.2)	12.8 (11.9)
	PARA	0.05 (0.04)	0.06 (0.03)	0.05 (0.04)
	PD (#/100 ha)	0.9 (1.2)	1.4 (1.5)	1.0 (1.3)

	COH (%)	78.8 (34.0)	77.9 (29.6)	78.6 (33.1)
	SAND (%)	30.8 (23.3)	36.7 (19.5)	32.2 (22.6)
Abiotic	GDD5 (°C)	1529.9 (46.6)	1448.4 (106.8)	1510.9 (74.2)
	RAIN (mm)	235.5 (23.8)	242.3 (30.6)	237.1 (25.7)
	SNOW (mm)	116.8 (13.0)	117.8 (17.4)	117.1 (14.2)

836

837

838 TABLE 3 Model performance of fitted generalized additive models estimating change in
 839 abundance of each rodent species to habitat loss and fragmentation on the Canadian Prairies.
 840 The number of samples used to model each species' response (N) differed among species
 841 because only samples within each species' geographic range were used. All species models
 842 were fit using mgcv, except the deer mouse and sagebrush vole models, which were fit using
 843 gamlss. Statistical influence of each model was estimated by subtracting the Akaike Information
 844 Criterion (AIC) of each fitted model from the AIC of each corresponding null model (Δ AIC).
 845 Only models >10 Δ AIC units from the null model were considered. The strength of each fitted
 846 model was estimated by deviance explained (DE). The strength of habitat loss and
 847 fragmentation effects alone in each model was estimated by subtracting the DE of each null
 848 model from that of each corresponding fitted model (Δ DE).

Species	Habitat		Δ AIC	Δ DE	DE
	specialization	N		(%)	(%)
Sagebrush vole	Grass	1,327	188	10.0	44.3
Deer mouse	General	1,384	134	6.7	57.0
Thirteen-lined ground squirrel	Grass	1,384	110	7.8	81.8
Olive-backed pocket mouse	Grass	1,094	77	10.2	35.3
Northern pocket gopher	General	1,384	35	7.0	62.9
Northern grasshopper mouse	General	1,372	22	2.4	40.3
Richardson's ground squirrel	Grass	1,384	10	n/a	n/a
Long-tailed vole	General	265	1	n/a	n/a
Ord's kangaroo rat	Grass	263	-1	n/a	n/a
Prairie vole	Grass	654	-1	n/a	n/a

Meadow vole	Grass	1,384	-256	n/a	n/a
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TABLE 4 Summary statistics for generalized additive models of the influence of habitat loss and fragmentation on rodent species abundances across the Canadian Prairies. Predictors include habitat loss (LOSS), grassland edge density (ED), average grassland patch size (AREA), average grassland patch shape complexity (PARA), grassland patch density (PD), and grassland patch cohesion (COH). ED, AREA, PARA, PD, and COH were included in models as interactions with LOSS to account for the dependence of fragmentation effects on the presence of habitat loss. Bolded predictors are significant at $p < 0.001$ as identified by the F-statistic (F) and estimated degrees of freedom (EDF). These models form the analytical basis for Figures 2-9.

Species	Predictor	Main Effects			Effect Mediated by LOSS		
		edf	F	p value	edf	F	p value
Deer mouse	LOSS	2.4	2.5	0.0005	n/a	n/a	n/a
	ED	3.7	6.5	3.4×10^{-7}	5.7	0.8	0.01
	AREA	2.5	1.4	0.03	5.5×10^{-7}	0.0	0.6
	PARA	2.2	3.5	0.0001	5.4	1.1	0.0002
	PD	1.9	1.1	0.04	7.5	2.1	4.0×10^{-5}
	COH	1.6	3.9	6.8×10^{-6}	3.0	1.2	9.3×10^{-5}
Sagebrush vole	LOSS	1.2×10^{-6}	0.0	0.4	n/a	n/a	n/a
	ED	8.1×10^{-7}	0.0	0.6	0.005	0.0	0.3

	AREA	1.8x10 ⁻⁷	0.0	0.8	2.0	2.4	6.9x10⁻¹⁰
	PARA	1.5x10 ⁻⁷	0.0	1.0	1.0	0.2	0.06
	PD	8.1x10 ⁻⁷	0.0	1.0	1.6	0.4	0.02
	COH	2.0	30.0	2.0x10⁻¹⁶	3.0	0.5	0.05
Northern grasshopper mouse	LOSS	0.0003	0.0	0.6	n/a	n/a	n/a
	ED	0.0002	0.0	0.9	0.0002	0.0	0.6
	AREA	0.0001	0.0	0.5	1.0	19.2	3.3x10⁻⁷
	PARA	0.7	1.9	0.06	0.001	0.001	0.4
	PD	1.5	8.4	0.0008	0.9	1.7	0.1
	COH	0.0001	0.0	1.0	2.1	4.5	0.07
Olive-backed pocket mouse	LOSS	2.9	43.2	1.0x10¹²	n/a	n/a	n/a
	ED	0.2	0.3	0.2	1.5	19.2	1.9x10⁻⁷
	AREA	0.0002	0.0	0.8	0.0004	0.0	0.6
	PARA	0.0002	0.0	0.8	0.6	1.3	0.09
	PD	0.0002	0.0	0.7	4.3	18.9	0.0001
	COH	0.0003	0.0	0.7	2.2	10.0	0.001

Northern pocket gopher	LOSS	1.7	13.2	5.8x10⁻⁵	n/a	n/a	n/a
	ED	6.9x10 ⁻⁵	0.0	0.7	0.7	1.6	0.08
	AREA	8.0x10 ⁻⁵	0.0	0.5	0.0001	0.0	0.5
	PARA	7.3x10 ⁻⁵	0.0	0.9	0.0001	0.0	0.9
	PD	5.4x10 ⁻⁵	0.0	0.8	4.2	14.4	0.0008
	COH	0.9	8.1	0.001	0.0001	0.0	0.8
Thirteen-lined ground squirrel	LOSS	0.09	0.1	0.1	n/a	n/a	n/a
	ED	2.4	34.1	1.9x10⁻¹²	6.8x10 ⁻⁵	0.0	0.8
	AREA	5.4x10 ⁻⁵	0.0	1.0	2.8	12.3	1.4x10⁻⁵
	PARA	2.9	16.5	2.5x10⁻⁵	1.8	5.4	0.01
	PD	1.6x10 ⁻⁵	0.0	0.6	9.6	55.5	1.2x10⁻¹³
	COH	0.9	9.8	3.0x10⁻⁵	2.5	4.7	0.02

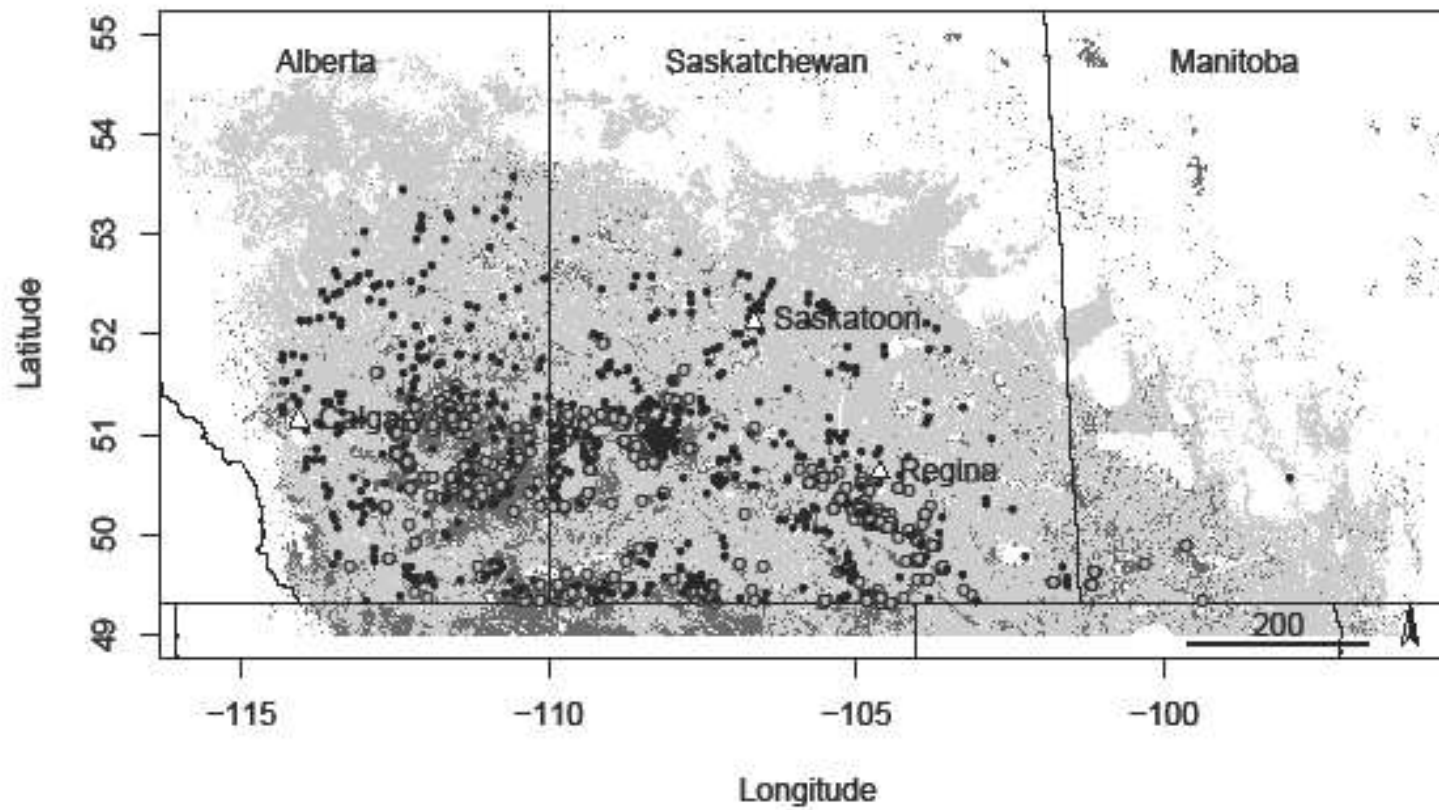


Figure 1.

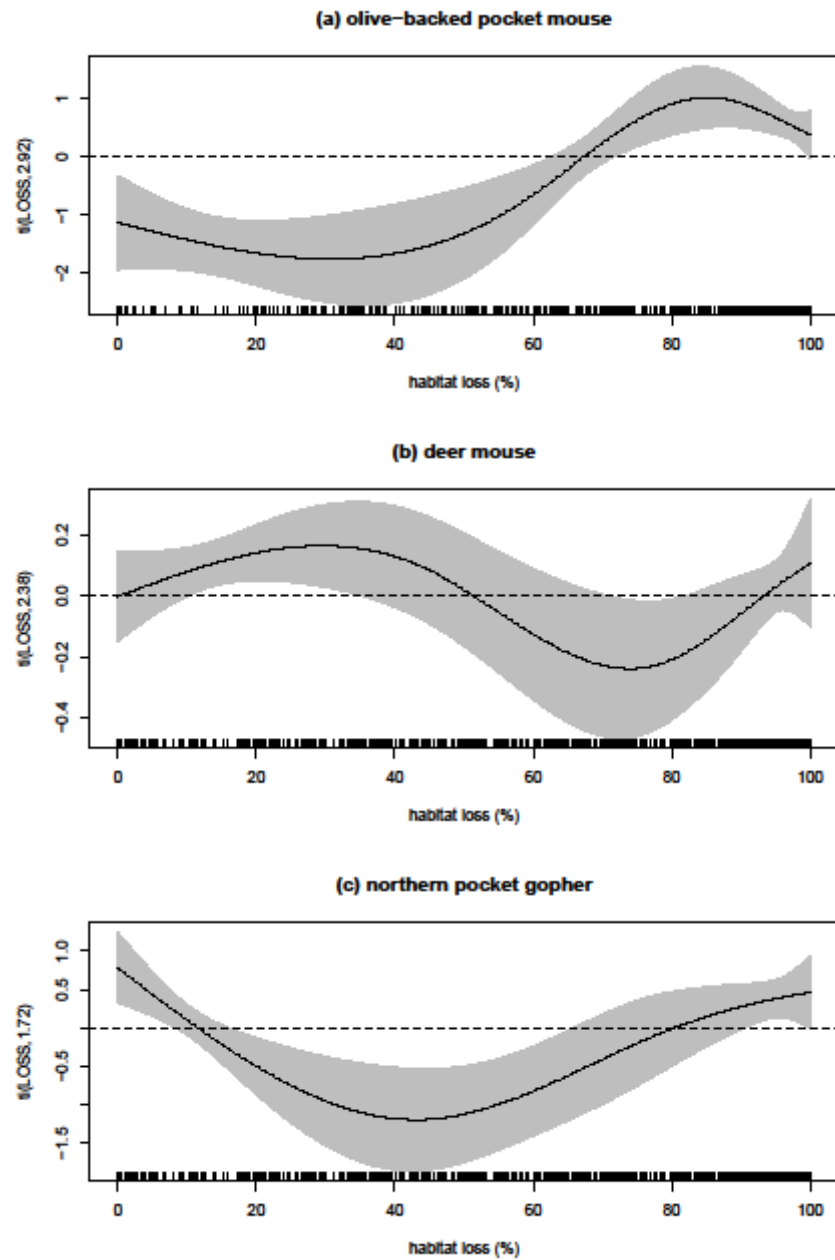


Figure 2.

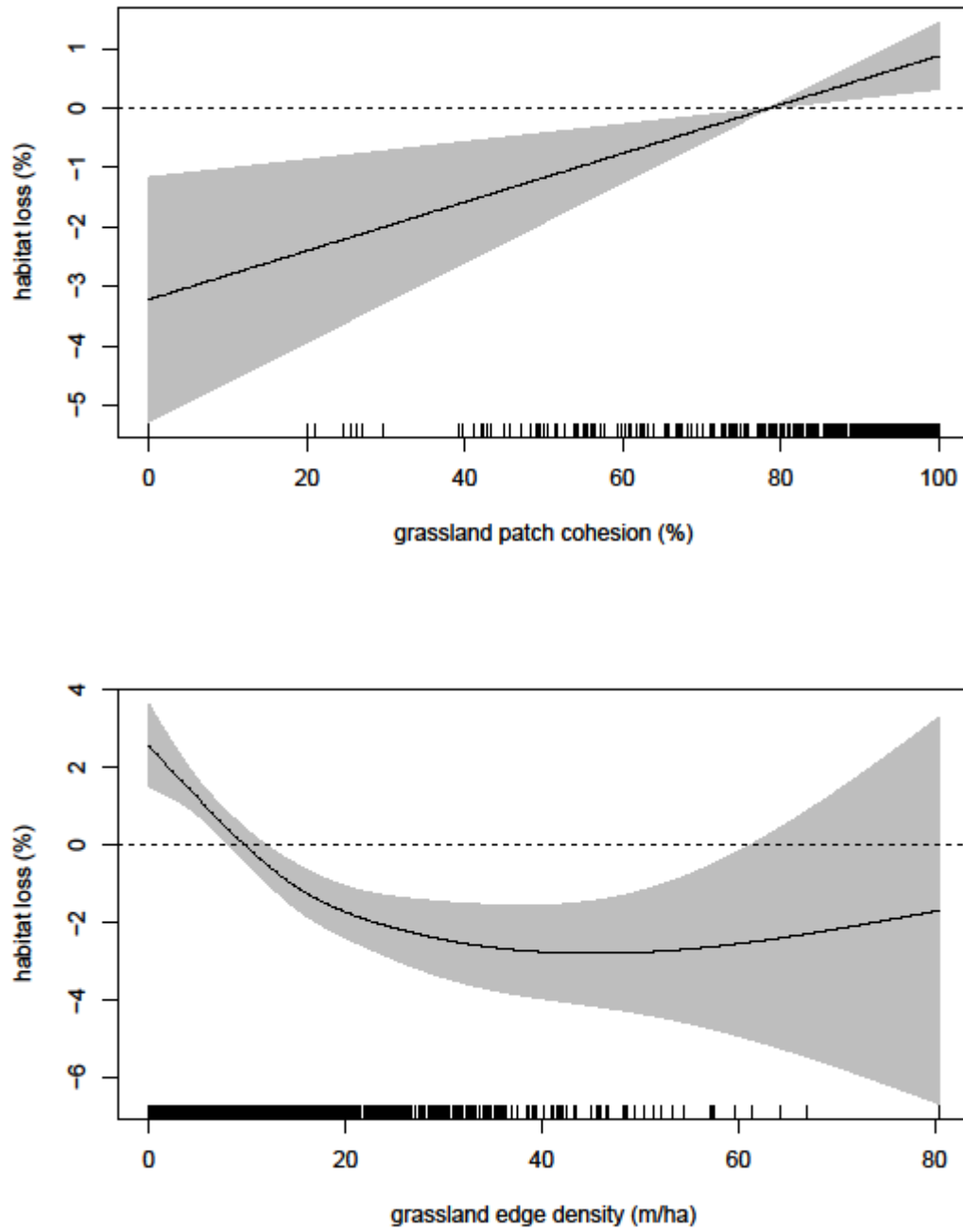


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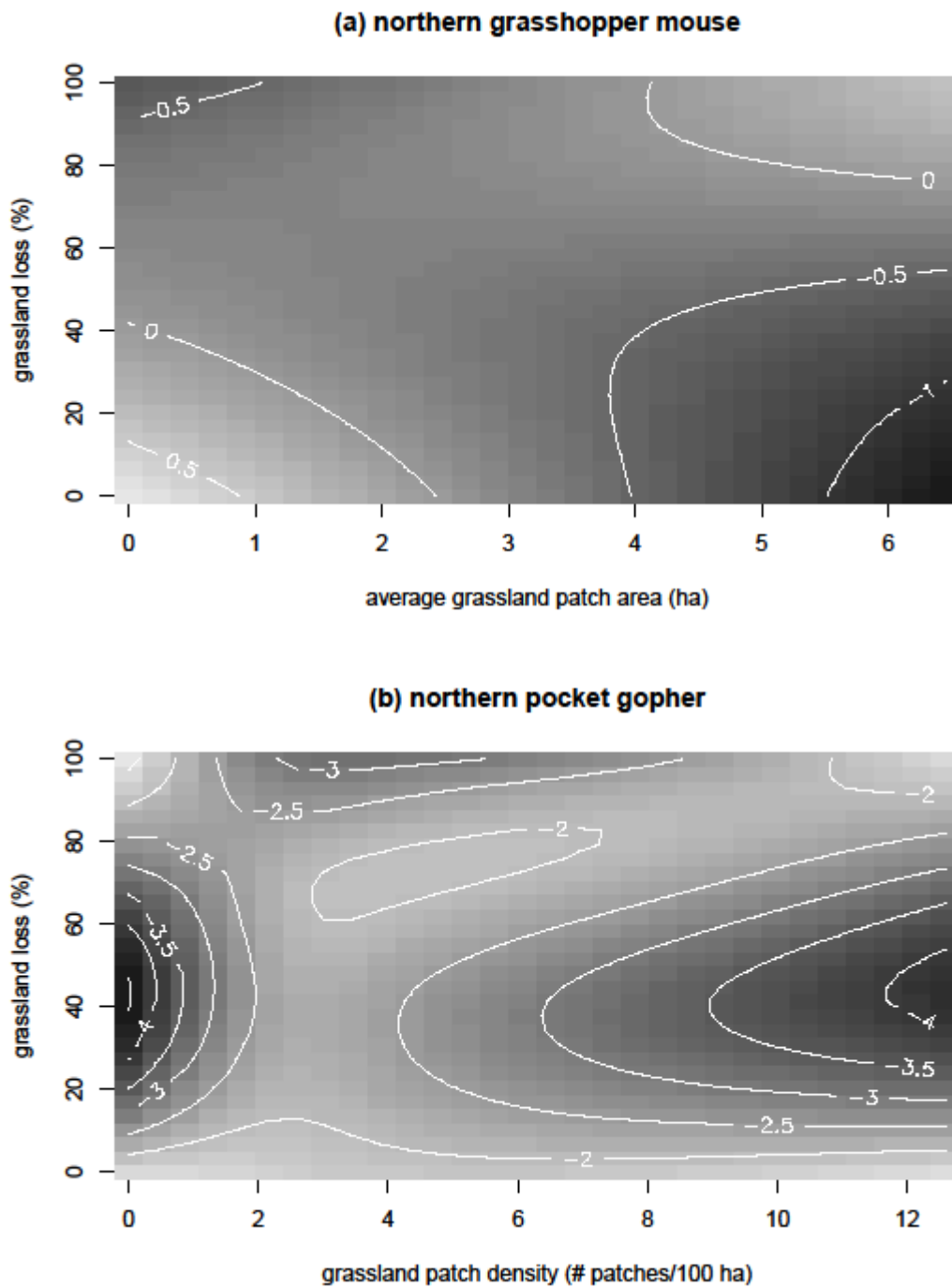


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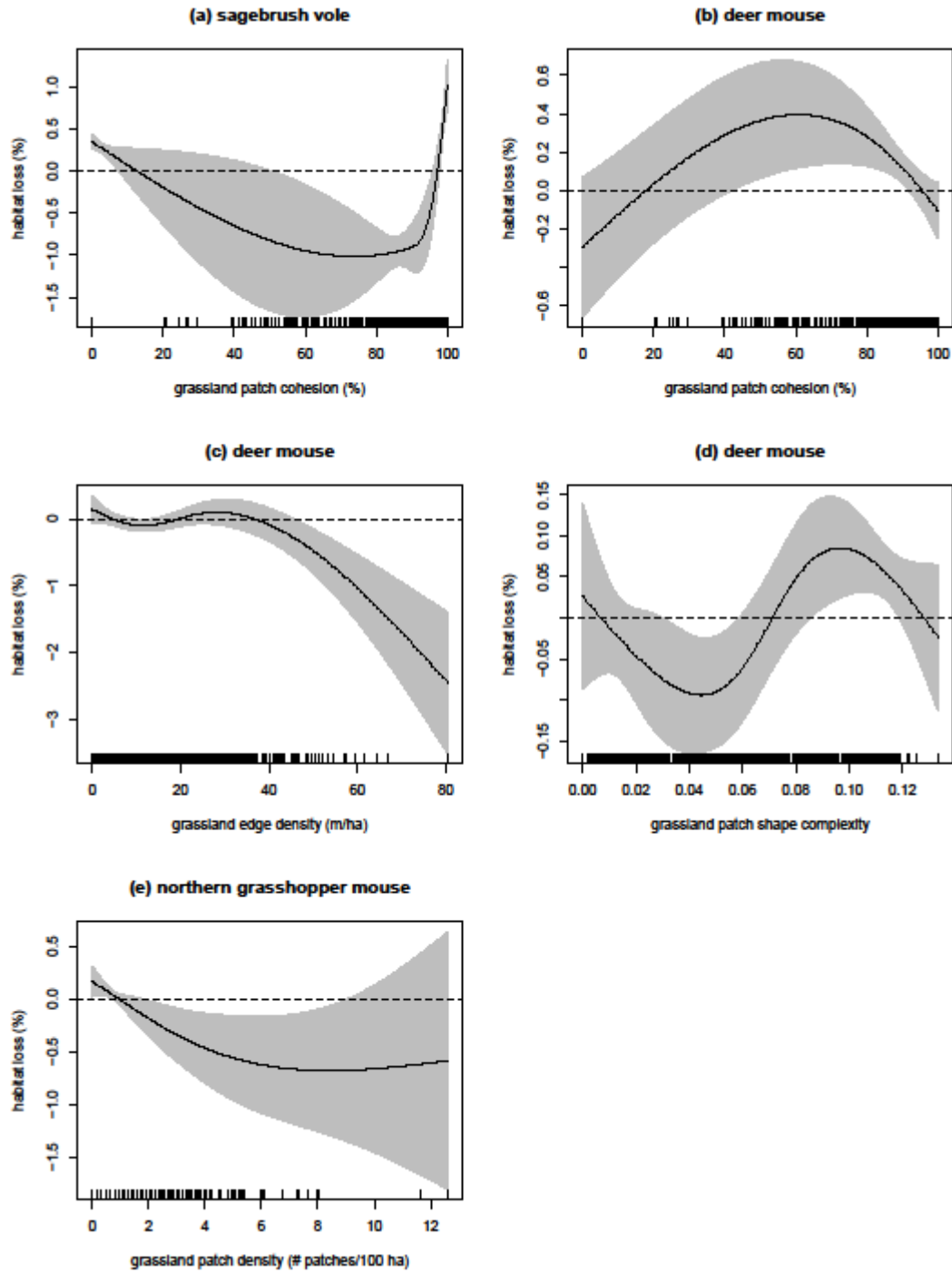


Figure 5.

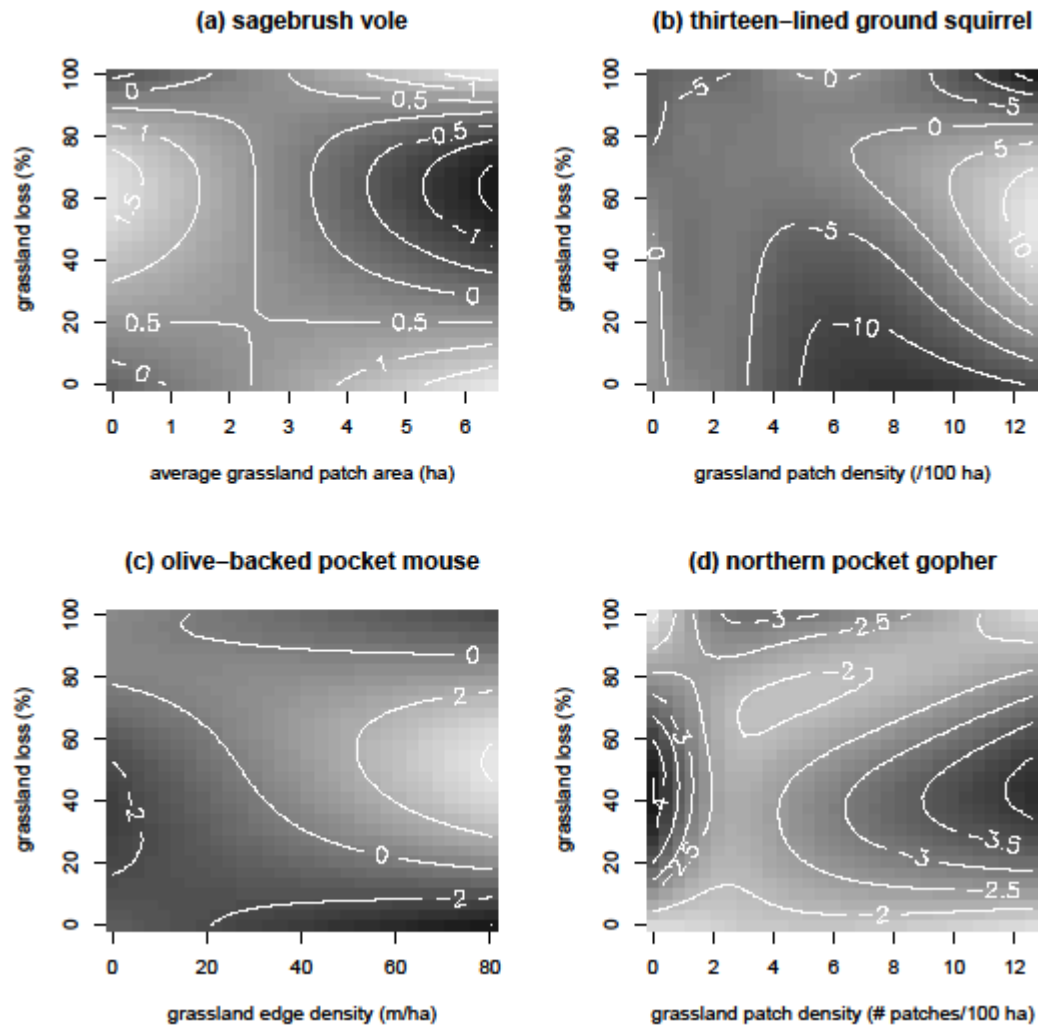


Figure 6.

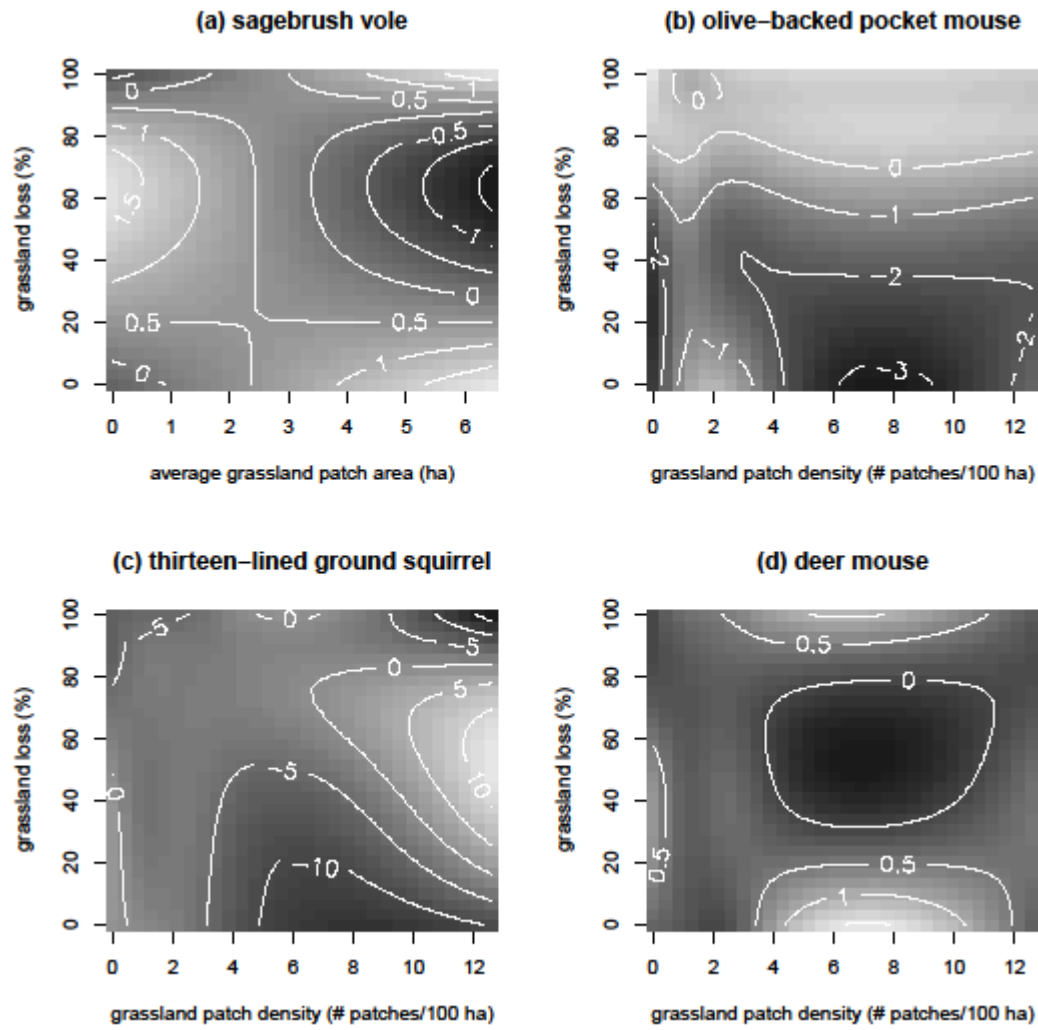


Figure 7.