

18 **Abstract:** Carnivore reintroduction is often expected to revert community and ecosystem
19 properties to their natural states via risk effects and the direct killing of prey. Because large
20 carnivore extirpation and reintroduction are usually believed to have symmetric and offsetting
21 effects, fulfilling this “assumption of reciprocity” is crucial to realizing the potential of large
22 carnivores to passively restore community structure and ecosystem function. We were unable to
23 find any study in which the assumption of reciprocity was rigorously tested in predator-prey
24 systems featuring large carnivores, their ungulate prey, and primary producers through a
25 comprehensive literature search. We therefore used studies involving (1) the reintroduction of
26 any native apex predator (including but not limited to large mammalian carnivores); and (2) the
27 removal of any introduced apex predator (also including but not limited to large mammalian
28 carnivores) to examine the assumption of reciprocity. Reintroduction of native apex predators
29 did not affect any of four trophic groups (mesopredator, omnivore, herbivore, primary producer)
30 in a positive or negative way, but removal of introduced apex predators consistently increased
31 the abundance and biomass of mesopredators. Further, outcomes of apex predator reintroduction
32 and removal were variable across systems, regardless of system complexity (ranging from single
33 predator-single prey to multiple predator-multiple prey systems). We suggest that the assumption
34 of reciprocity—in which predator extirpation and reintroduction are believed to have consistent,
35 counterbalancing effects—is unsupported by current evidence, and perhaps unrealistic. We
36 discuss potential directions for research that might illuminate when and why the assumption of
37 reciprocity would be valid.

38

39 **Keywords:** apex predator, large carnivore, prediction, reciprocity, restoration, trophic cascade

40

41 **1. Introduction**

42 Predation is one of nature's most important processes, shaping population abundance,
43 community structure, and ecosystem dynamics. Regional distributions of large carnivores have
44 changed in the past century, owing to both the widespread extirpation of some species and
45 subsequent recovery of others (Chapron et al., 2014; Estes et al., 2011; Gompper et al., 2015;
46 Ripple et al., 2014). The reintroduction of large carnivores may trigger trophic cascades by
47 reducing prey densities or altering prey behavior (Bakker and Svenning, 2018; Ripple et al.,
48 2014; Svenning et al., 2016). Attempts to reintroduce large carnivores to ecosystems therefore
49 are heralded not only as an end in themselves, but also for their potential to restore community
50 structure and ecosystem function via trophic cascades (Andriuzzi and Wall, 2018; Beschta and
51 Ripple, 2009; Newsome and Ripple, 2015; Ordiz et al., 2013).

52 The assumption that large carnivore reintroductions will result in consistent, cascading
53 effects is critical for realizing any higher-level restorative effects, albeit rarely tested (Allen et
54 al., 2017; Ford and Goheen, 2015). We refer to the notion that large carnivore extirpation and
55 reintroduction have symmetric, counterbalancing effects as the "assumption of reciprocity" (Fig.
56 1), a special case of resilience (*sensu* Holling, 1973) in which altered communities, ecosystems,
57 or both return to historical states following reintroduction of large carnivores. Extirpation and
58 reintroduction of large carnivores are often envisioned as natural experiments that mimic
59 removal and addition experiments, thereby providing insight into whether, how, and why large
60 carnivores impact higher-level ecological patterns and processes (Allen et al., 2017; Ford and
61 Goheen, 2015).

62 Despite the frequent assumption of reciprocity, however, a number of contextual factors
63 may reorganize communities and ecosystems in ways that prevent reversion to a historical state

64 (discussed below; see Ford et al., 2015; Marshall et al., 2013). These factors include shifts in
65 environmental conditions, shifts in land-use patterns, or conservation interventions during the
66 period of carnivore reintroduction. For example, although most agree that the reintroduction of
67 wolves into the Greater Yellowstone Ecosystem begat a series of trophic cascades that altered
68 Yellowstone's biotic communities (Beschta and Ripple, 2016; Ripple and Beschta, 2012), wolf
69 reintroduction coincided with increased drought (Middleton et al., 2013), regeneration after an
70 expansive series of wildfires (Romme et al., 2011), and recolonization by beavers (Smith and
71 Tyers, 2012), rendering it difficult to determine precisely the extent to which subsequent changes
72 to Yellowstone's biotic communities can be attributed to wolves. As a result, a nuanced view of
73 the restorative potential for large carnivores via cascading trophic effects is required: predators
74 can have different effects at different times and in different places (Haswell et al., 2017; Paine,
75 1966; Vaughn and Young, 2010). Our ability to predict the impacts of large carnivore
76 reintroduction should thus depend on a host of contextual details (Agrawal et al., 2007; Ford and
77 Goheen, 2015; Heithaus et al., 2009; Ritchie et al., 2012).

78 One such source of contingency is the degree of reticulation in food webs. Reticulate
79 food webs involve at least some functional overlap, wherein reduced consumption of prey (i.e.,
80 animals for predators, plants for herbivores) stemming from predator extirpation is compensated
81 for by other, functionally redundant, predators in the community (Polis and Strong, 1996; Strong,
82 1992). In predator-prey systems defined by multiple species of large carnivores, multiple species
83 of prey, or both, any cascading effects of large carnivore extirpation or reintroduction are likely
84 dampened relative to simpler systems lacking reticulation (i.e., food chains with a single large
85 carnivore and a single species of prey; Borer et al., 2005; Shurin et al., 2002; Trussell et al.,
86 2017). Reintroduction of large carnivores should therefore have the most pronounced impacts in

87 relatively simple predator-prey systems, or in predator-prey systems where extirpated large
88 carnivores or the herbivorous prey on which they depend exhibit minimal functional overlap
89 with those large carnivores or herbivorous prey that persist (Otieno et al., 2019; Pringle et al.,
90 2016).

91 Assuming that large carnivore extirpation alleviates top-down control on at least some
92 species of prey, three conditions must be true for the assumption of reciprocity to be upheld:

93 **Condition 1:** Prey populations (typically ungulate populations, with respect to large carnivores)
94 decrease or redistribute themselves on the landscape when large carnivores are reintroduced
95 (Creel et al., 2005; Elmhagen and Rushton, 2007; Fortin et al., 2005).

96 **Condition 2:** Biomass, growth, survival, or composition of primary producers shifts when prey
97 become rare or redistribute themselves on the landscape in response to large carnivore
98 reintroduction (Ford et al., 2014; Hebblewhite et al., 2005; Morris and Letnic, 2017). In other
99 words, a trophic cascade is triggered by the reintroduction of large carnivores.

100 **Condition 3:** The trophic cascade arising from Conditions 1 and 2 yields a return to one or more
101 historical states (or “reference points”; Sinclair et al., 2018) that existed before large carnivores
102 were extirpated.

103 In the simplest cases (one species of large carnivore, one species of ungulate prey,
104 primary producers), reciprocity occurs when Condition 1, 2, and 3 are true (i.e., a trophic cascade
105 occurs, and the magnitude of its effects are sufficient to return the community or ecosystem to its
106 historical state; Fig. 1A). Alternatively, the reintroduction of a large carnivore may not result in
107 reciprocity because of hysteresis. Hysteresis—in this context, the existence of variable
108 abundances or compositions of prey and primary producers given the presence of the same
109 species of large carnivore—occurs when neither Condition 1 nor Condition 2 are true (Stier et

110 al., 2016; Young et al., 2005; Fig. 1B). An alternative state may occur when either Condition 1
111 or Condition 2 is true, or when both Condition 1 and Condition 2 are true, but the effect of one or
112 both differs from their historical effects (Ford et al., 2015; Marshall et al., 2013; Ng'weno et al.,
113 2017; Fig. 1C).

114 To understand whether the assumption of reciprocity is upheld following large carnivore
115 reintroductions, we conducted a meta-analysis on data derived from keyword searches on the
116 published literature to identify studies involving the removal or addition of large carnivores.
117 Specifically, we sought studies on reintroductions of extirpated species of large carnivores to
118 parts of their historical ranges. Such studies were rare, however (n = 6 from our literature search;
119 see below), so we extended our search to include other apex predators, which we defined
120 operationally as any predator not consumed by other predators in the focal study. Because
121 reciprocity assumes symmetric and opposing effects of carnivore addition and removal, we also
122 included studies involving the removal of exotic apex predators from their introduced ranges. We
123 expected to find support for the aforementioned three conditions (i.e., that effects induced by the
124 reintroduction of native predators or the removal of invasive predators were reciprocal to
125 extirpation and introduction, respectively). Specifically, (1) reintroduction of native apex
126 predators reduces the abundance of their prey (distinguishing between herbivores, omnivores,
127 and mesopredators), in turn leading to increased primary producer abundance; and (2) removal of
128 introduced apex predators results in increased prey abundance and decreased abundance of
129 primary producers. We expected the strongest support for the assumption of reciprocity to exist
130 in cases involving a single species of predator consuming a single species of prey, with multiple
131 species of predators, prey, or both dampening any indirect effects of carnivores (Otieno et al.,
132 2019; Polis and Strong, 1996).

133

134 **2. Methods**

135 2.1. Literature Search

136 We searched peer-reviewed publications for manipulative or natural experiments that
137 quantified responses of both prey and primary producers to native predator reintroduction or to
138 the removal of invasive predators. We used the Web of Science Core Collection and the search
139 terms: (((((carnivor* OR predator*) AND (communit* OR ecosystem) AND (*coloniz* OR
140 reintroduc* OR removal* OR eradicat* OR restor* OR introduc* OR invas* OR exotic*) AND
141 (multiple state* OR multiple stable state* OR ecosystem function* OR alternate state* OR
142 alternative stable state* OR recover* OR resilience* OR stable state* OR regime shift* OR
143 hysteresis OR trophic cascade*)))))). The initial search resulted in 1,816 articles published up to
144 May 2018. We refined this list of papers to a final dataset comprising responses to reintroduction
145 and removal events (Table A.1, Table A.2) based on the following criteria: (1) reintroduction of
146 an extirpated native apex predator or removal of an introduced apex predator; and (2) abundance
147 or biomass data of both prey and primary producers for at least two of the following three
148 consecutive time steps: before extirpation or introduction of an apex predator, during extirpation
149 or invasion of apex predator, and after reintroduction or removal of apex predator. Data were
150 extracted from tables, text, and figures. All resulting data consisted of the latter two time steps
151 (i.e., during and after extirpation or invasion). Following Shurin et al. (2002), we used the final
152 sampling date as a proxy for the cumulative effects of predators. For studies that reported the
153 effects on multiple species of prey and primary producers in the same article, we extracted data
154 for each taxon at the finest possible resolution. Most data are therefore for species, but some are
155 for higher taxonomic levels. We then categorized studies as either apex predator reintroduction

156 or apex predator removal and classified taxa into trophic groups (primary producers [terrestrial
157 plants and algae], herbivores, omnivores, or mesopredators). We defined apex predators as any
158 predator in a food web that is not consumed by any other species in that food web. Therefore, our
159 operational definition of “apex predator” encompassed species that otherwise could qualify as
160 mesopredators in the presence of other species that consume them.

161

162 2.2. Meta-analysis

163 Because the historical states from the study systems in our dataset were not quantified,
164 we assumed that trophic responses by prey and primary producers would follow the patterns laid
165 out in the final paragraph of our Introduction: that (1) reintroduction of native apex predators
166 reduces the abundance of their prey (distinguishing between herbivores, omnivores, and
167 mesopredators), in turn leading to increased primary producer abundance; and (2) removal of
168 introduced apex predators results in increased prey abundance and decreased abundance of
169 primary producers. Predictions that follow these patterns are pervasive in the literature on large
170 carnivore reintroduction (e.g., Beschta and Ripple, 2009; Callan et al., 2013; Licht et al., 2010;
171 Malhi et al., 2016; Soule et al., 2003). To quantify our predicted trophic responses, we calculated
172 the effects of apex predator reintroduction or apex predator removal as the log response ratio
173 (LRR) of primary producer and prey densities (Hedges et al., 1999). The LRR is calculated as
174 $[\ln(Y_{\text{treatment}})/Y_{\text{control}}]$, where Y_{control} is the density or abundance of a species of primary
175 producer or prey prior to apex predator reintroduction or removal, and $Y_{\text{treatment}}$ is the density or
176 abundance of primary producer or prey following the reintroduction or removal of apex
177 predators. The log ratio represents the proportional change in a response variable, where a
178 positive LRR indicates that the reintroduction or removal of an apex predator increases the

179 abundance or biomass of prey or plants. We regressed LRRs against study duration to ensure the
180 final (cumulative) effects reported in studies did not represent transient dynamics (Hastings,
181 2004).

182 Although the precision of LRR estimates varied between studies in our data set, we did
183 not weight values by their precision, nor did we scale LRRs to the duration of experiments for
184 the reasons articulated by Shurin et al. (2002). Namely, 9 of 20 studies in our data set were
185 unreplicated, and 7 others did not report variance or other metrics of variability. Eliminating
186 studies without variance estimates would have reduced our sample size and possibly biased our
187 data set (Englund et al., 1999). Using unweighted LRR estimates would weaken our power to
188 detect differences among systems (i.e., inflating Type II error), but does not bias our estimates of
189 effect sizes (Gurevitch and Hedges, 1999; Hedges et al., 1999).

190 To assess variation in responses among taxa, we first split the data into two treatments
191 (reintroduction studies and removal studies) and visualized the LRR across trophic groups. We
192 then tested for differences in LRRs among trophic groups within each treatment type using one-
193 way Kruskal-Wallis rank sum tests and tested whether the median LRR for trophic groups was
194 significantly different from zero using Wilcoxon rank sum tests and Bonferroni corrections for
195 multiple comparisons.

196 Next, we examined changes in LRRs among trophic groups within four types of predator-
197 prey systems (single predator/single prey, single predator/multi-prey, multi-predator/single prey,
198 and multi-predator/multi-prey systems). Differences in LRRs among trophic groups within each
199 treatment x study system combination was evaluated with one-way Kruskal-Wallis non-
200 parametric rank sum tests. We then tested whether the average LRR for trophic groups within

201 each treatment x study system combination was significantly different from zero using Wilcoxon
202 rank sum tests and Bonferroni corrections for multiple comparisons.

203 Finally, we related LRRs among trophic groups within each treatment to the time since
204 apex predator reintroduction or removal using ordinary least-squares linear regression. We also
205 related LRRs of both prey species and primary producers to the number of prey species in each
206 system using ordinary least-squares regression.

207

208 **3. Results**

209 The final dataset included 142 observations from 20 studies (Table A.1). The 20 studies were
210 distributed among 6 ecosystem types (islands, deserts, forests, grasslands, lentic freshwater, and
211 marine), comprised 7 reintroduction studies and 13 removal studies, and represented 124 unique
212 taxa ranging from primary producers to mesopredators. Log response ratios were unrelated to the
213 time elapsed following reintroduction or removal efforts (Fig. A.1).

214 Both reintroduction and removal studies were characterized by a high degree of
215 variability (Fig. 2), suggesting idiosyncratic responses of trophic groups to the reintroduction of
216 native apex predators or to the removal of introduced apex predators. Within treatments, we
217 found no statistically significant differences in LRR among trophic groups (Fig. 3; reintroduction
218 studies: $H = 6.48$, $df = 3$, $P = 0.09$; removal studies: $H = 6.42$, $df = 3$, $P = 0.09$), indicating that
219 trophic groups do not consistently differ in their response to the reintroduction or removal of
220 apex predators. No trophic group responded directionally to the reintroduction of native apex
221 predators (Fig. 3A), but mesopredators responded positively to the removal of introduced apex
222 predators ($Z = 287$, $P = 0.01$; Fig. 3B).

223 Of the 20 studies in our dataset, 7 were single predator, single prey systems, 13 involved
224 a single predator and multiple prey species, and none involved multiple predators and multiple
225 prey systems or systems with multiple predators with a single species of prey (Table A.1). The
226 number of prey species in a system had no effect on the magnitude of either prey or primary
227 producer LRRs (Fig. A.2). Within each treatment x study system combination, we found no
228 significant differences in LRR among trophic groups (Fig. 4). Further, Wilcoxon signed-rank
229 tests revealed that only mesopredators in removal studies with single predator-multiple prey
230 systems had mean LRR values significantly different from zero ($Z = 254$, $P = 0.003$; Fig. 4).
231 Together, these results suggest that outcomes of apex predator reintroduction and removal are
232 highly variable across both simple and multi-species predator-prey systems.

233

234 **4. Discussion**

235 Responses of trophic groups to the reintroduction and removal of native and apex predators
236 varied widely. We quantified responses of four trophic groups—mesopredators, omnivores,
237 herbivores, and primary producers—to the reintroduction of native apex predators, and to the
238 removal of introduced apex predators. Mesopredators responded most strongly to removal and
239 reintroduction of apex predators, although assessment of responses by mesopredators to the
240 reintroduction of apex predators was limited by sample size (Fig. 2B). Among species
241 interactions, this “mesopredator release” is unusual in its universality: it occurs almost invariably
242 when apex predators are removed from a system (Prugh et al., 2009). If functional overlap occurs
243 between apex predators and mesopredators, responses of herbivores and primary producers may
244 be dampened following removal (or introduction) of apex predators. In contrast, because only

245 apex predators are capable of consuming mesopredators, mesopredators may be the only trophic
246 group that responds consistently to removal (or introduction) of apex predators.

247 Contingent outcomes of species interactions are common, and our results demonstrate
248 that they are pervasive following reintroduction and removal of apex predators. Though we were
249 unable to test for the full assumption of reciprocity because of a shortage of historical reference
250 point data, predicting the direction of trophic responses is a necessary first step toward reaching
251 that goal. Our study demonstrates that simply predicting the direction of trophic responses is
252 challenging—responses by lower trophic levels to apex predator removal and reintroduction are
253 often not predictable (Fig. 1, Fig. 2). For example, recolonization of Laikipia, Kenya by African
254 wild dogs (*Lycaon pictus*) suppressed densities of primary prey (Guenther's dik-dik [*Madoqua*
255 *guentheri*]) which suppressed growth of some species of trees, but wild dog recolonization did
256 not translate to a trophic cascade. Ford et al. (2015) hypothesized that some combination of
257 increased rainfall and compensatory browsing by other ungulates attenuated the effects of wild
258 dog recolonization on these trees. Similarly, Marshall et al. (2013) demonstrated that shifts in
259 stream hydrology driven by beaver extirpation prevented the restoration of willows (*Salix* spp.)
260 in many areas following the return of wolves to the Greater Yellowstone Ecosystem. Although
261 wolf (*Canis lupus*) reintroduction reduced elk (*Cervus elaphus*) abundance, a lowered water
262 table and resulting changes in nutrient availability gave rise to an alternative stable state in
263 beaver-free areas that was resilient to shifts in elk abundance stemming from wolf reintroduction.
264 In sum, pinpointing the effects of apex predator reintroduction and removal is often complicated
265 by shifting abiotic conditions.

266 We found no evidence that functional redundancy among prey species affects either prey
267 or primary producer responses to the reintroduction or removal of apex predators (Fig. 2.A), but

268 this may result from studies centering on relatively common species rather than uncommon ones.
269 In predator-prey systems characterized by large carnivores and multiple species of ungulate prey,
270 prey communities tend to be comprised of one or a few species that are sufficiently numerous to
271 escape top-down control and several less common species for which predation limits abundance
272 (e.g., Chirima et al., 2013; Georgiadis et al., 2007; Owen-Smith et al., 2005; Sinclair and Fryxell,
273 1985). Because numerically dominant species strongly influence community structure and
274 ecosystem function, the reintroduction of large carnivores may simply reduce populations of
275 secondary species of prey that already were uncommon before large-carnivore reintroductions
276 and are less likely than common species to control plant populations. Researchers also have a
277 strong tendency to simplify complex systems when studying trophic relationships (Montgomery
278 et al., 2019), and uncommon species are less likely to be included in studies of trophic
279 relationships due to logistical concerns (e.g., added difficulty and cost in surveying individuals
280 and accurately estimating abundance). Both of these phenomena could yield the muted outcomes
281 from apex predator reintroduction or removal we observed (Fig. 2, Fig. 3).

282 Our inferences regarding the assumption of reciprocity are constrained by a lack of
283 experimental evidence involving both large carnivores and trophic cascades (Allen et al., 2017;
284 Ford and Goheen, 2015), as well as more tractable mesocosm manipulations. To properly
285 evaluate the assumption of reciprocity, data on large carnivores (or other apex predators), prey,
286 and primary producers are required for three distinct time steps: one in which native apex
287 predators exist (i.e., a historical state), a time step in which native apex predators have been
288 extirpated, and a time step in which apex predators have been reintroduced and attain population
289 sizes comparable to the historical state. The vast majority of studies in the literature focus on the
290 latter two time steps and did not report historic reference point data prior to apex predator

291 reintroduction (or removal, in the case of introduced apex predators). Though baseline data on
292 historical reference points is very challenging to quantify in most systems, it is occasionally
293 possible to generate reasonable estimates of important variables—e.g., tree density using
294 historical photographs of known landscapes. Filling this knowledge gap is critical for
295 understanding whether extirpation and reintroduction have symmetrical, offsetting impacts.

296 Shifts in environmental conditions are increasingly likely as the time periods over which
297 apex predators are extirpated increase, and it may take some time for altered environmental
298 conditions to revert to historical reference points after predator reintroduction. Consequently,
299 there is strong potential for transient dynamics during the extirpation and reintroduction of apex
300 predators, where populations within trophic groups will have not yet reached equilibrium
301 abundances at the end of a study (Hastings, 2001). The extent to which the assumption of
302 reciprocity is upheld should therefore depend on the amount of time over which a native apex
303 predator is extirpated or, conversely, an introduced apex predator is present. In an attempt to
304 address the possibility of transient (non-equilibrium) dynamics, we analyzed responses of trophic
305 groups as a function of time elapsed since the reintroduction or removal of apex predators. We
306 found no evidence that the effects of apex predator reintroduction or removal are influenced by
307 time in the studies in our data set (Fig. A.1), indicating that the results reported for the majority
308 of studies in our meta-analysis do not reflect transient dynamics.

309 Reintroduction of large carnivores can inject optimism into conservation efforts typically
310 characterized by reactive approaches. Many questions concerning the ecology of large carnivore
311 reintroduction remain unanswered (see Table 1), however, particularly concerning the
312 consistency (and thus predictability) of higher-level effects generated by such reintroductions.
313 Professionals in our field might consider the conservation importance of large carnivore

314 reintroduction (which few ecologists would question) as distinct from the cascading impacts of
315 large carnivore reintroduction, which can be significant (Letnic et al., 2009; Ripple and Beschta,
316 2012), muted (Elmhagen and Rushton, 2007; le Roux et al., 2018), or virtually non-existent
317 (Ford et al., 2015). Removing or reintroducing apex predators from ecosystems does not appear
318 to have predictable restorative effects, but solid confirmation will require additional rigorous
319 tests of this assumption of reciprocity.

320

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326

327 **Appendix A: Supplementary Data**

328 Table A.1: Data for: Reciprocity in restoration ecology: when might large carnivore
329 reintroduction restore ecosystems?

330

331 Table A.2: Literature cited in Table A.1.

332

333 Fig. A.1: Regressions between log response ratios (LRRs) and time elapsed since (A) apex
334 predator reintroduction, or (B) apex predator removal for four trophic groups. Time elapsed since
335 apex predator reintroduction or removal is not correlated with the abundance or biomass of any
336 trophic group. This suggests that inconsistency in trophic responses to apex predator
337 reintroduction and removal is not due merely to too little time elapsed for full responses to
338 become apparent.

339

340 Fig. A.2. Regressions between log response ratios (LRRs) of prey and primary producer species
341 and the number of prey in a study system. The number of prey species in a study is not correlated
342 with the abundance or biomass of either prey or primary producers.

343

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- 537

538 **Figures and Tables:**

539

540 **Table 1.** Outstanding questions regarding the ecology of large carnivore reintroductions.

541

542 **Figure 1.** A schematic illustrating the assumption of reciprocity, and alternative scenarios under

543 which the assumption is not met. (A) The assumption of reciprocity, in which lion recovery has

544 an equivalent and counterbalancing effect to lion extirpation. In this example, the ca. 30-year

545 extirpation of lions triggered an increase in their preferred prey (hartebeest); recovery of lions

546 returned hartebeest populations to levels comparable with the historical state. (B) A violation of

547 the assumption of reciprocity (hysteresis), in which lion recovery does not affect hartebeest

548 abundance. In this example, lion extirpation allowed hartebeest populations to increase in size

549 past a threshold below which they were limited top-down. (C) A violation of the assumption of

550 reciprocity (an alternative stable state), in which lion recovery has an anisotropic effect to

551 extirpation. In this example, fire suppression during the ca. 30-year period of lion extirpation

552 resulted in an increase in tree density, rendering lions more effective at killing hartebeest, and

553 resulting in fewer hartebeest relative to the historical state. Examples based on Ng'weno et al.,

554 2017, Ng'weno et al., in revision, and Ng'weno et al., in review.

555

556 **Figure 2.** Log response ratios (LRRs) of individual species, categorized into four trophic groups

557 (primary producer, herbivore, omnivore, mesopredator), following the (A) reintroduction of

558 native apex predators; or (B) removal of introduced apex predators. In panel A, the LRR is

559 calculated as $[\ln(Y_{\text{reintroduction}})/(Y_{\text{extirpation}})]$, such that positive LRRs indicate a positive response of

560 abundance or biomass of the individual species or trophic group following the reintroduction of

561 native apex predators. In panel B, the LRR is calculated as $[\ln(Y_{\text{removal}})/(Y_{\text{invaded}})]$, such that

562 positive LRRs indicate a positive response of abundance or biomass of the individual species or
563 trophic group following the removal of introduced apex predators. The observed variability in
564 LRR suggests idiosyncratic responses of trophic groups to the reintroduction of native apex
565 predators and to the removal of introduced apex predators.

566

567 **Figure 3.** Summary of log response ratios (LRRs) among four trophic groups (primary producer,
568 herbivore, omnivore, mesopredator) following the (A) reintroduction of native apex predators, or
569 (B) removal of introduced apex predators. Within treatments, we found no statistically
570 significant differences in LRR among trophic groups using one-way Kruskal-Wallis rank-sum
571 tests. *P*-values given in figure correspond to results from non-parametric Wilcoxon signed rank
572 tests and indicate that mesopredators and herbivores exhibit a positive numerical response to
573 predator removal actions.

574

575 **Figure 4.** Summary of log response ratios (LRRs) for trophic groups across predator-prey system
576 types from simple predator-prey systems (single species of predator, single species of prey),
577 versus more complex predator-prey systems (those with multiple species of predators, multiple
578 species of prey, or both) following (A) the reintroduction of native apex predators; and (B) the
579 removal of introduced apex predators. Within treatments, one-way Kruskal-Wallis rank-sum
580 tests found significant differences in LRR among trophic groups only in removal studies with a
581 single predator and multiple prey ($H = 7.68$, $df = 3$, $P = 0.05$). Asterisks in the figure correspond
582 to results from non-parametric Wilcoxon signed rank tests and indicate that only mesopredators
583 in removal studies with single predator-multiple prey systems ($Z = 301$, $P < 0.001$) and

584 herbivores in removal studies with multiple predators-multiple prey systems ($Z = 27, P = 0.03$),
585 had mean LRRs significantly different from zero.

586

587 Table 1

Outstanding Questions in Large Carnivore Reintroduction

Under what conditions do large carnivore removal and reintroduction have offsetting (reciprocal) effects on ecosystem structure or function?

Which regions and ecological processes are most sensitive to changing large carnivore abundance? Which are most resistant?

Do risk effects persist following removal of large carnivores, and for how long?
What functional traits of large carnivores and prey mediate the impacts of top-down control?

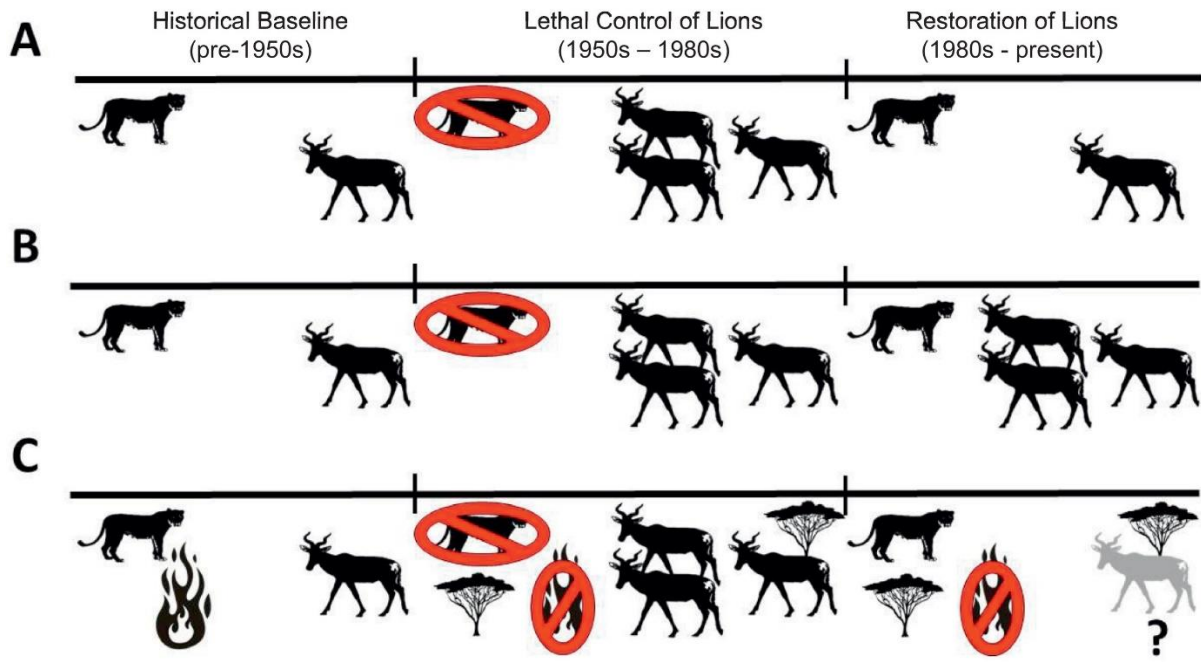
How does variation in environmental conditions and landscape characteristics mediate the impacts of top-down control?

Under what conditions does bottom-up control supersede top-down control?

588

589

590 Fig. 1

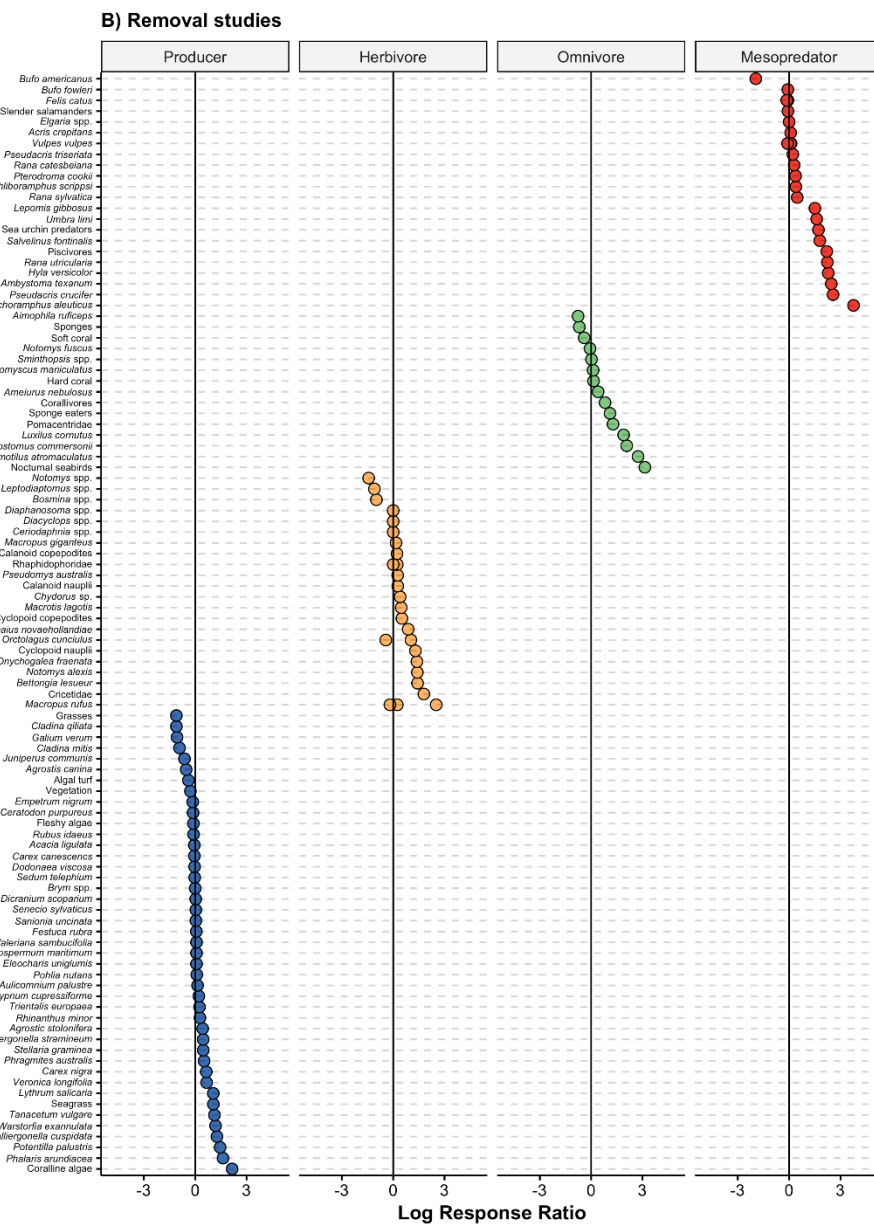
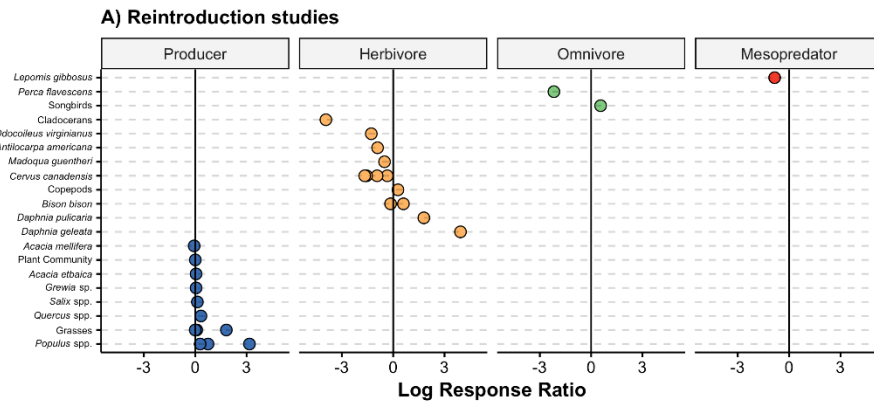


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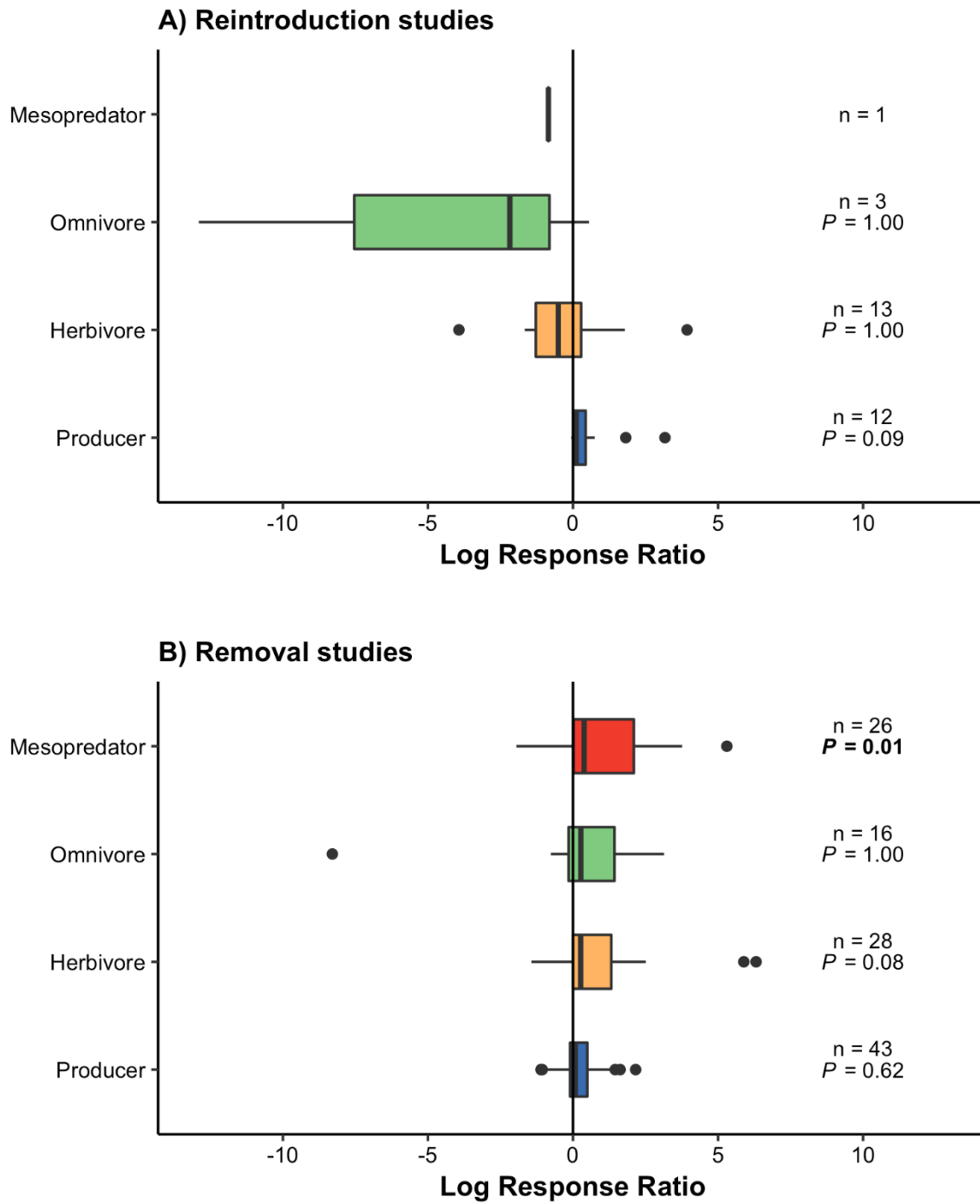
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594 Fig. 2.



596 Fig. 3

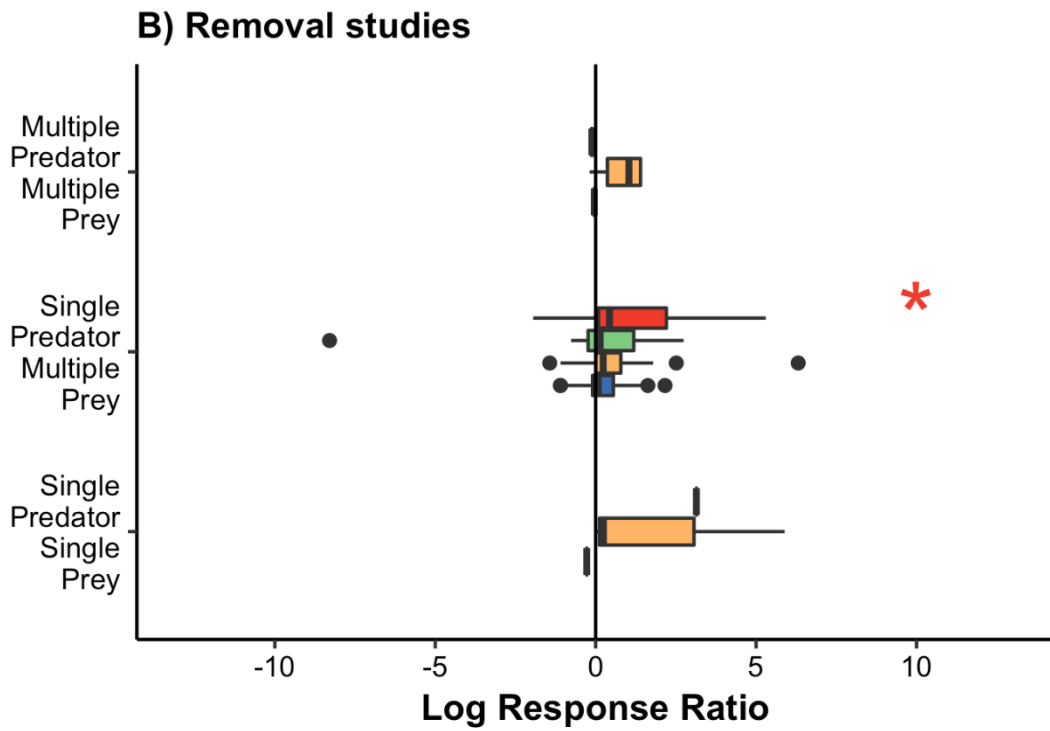
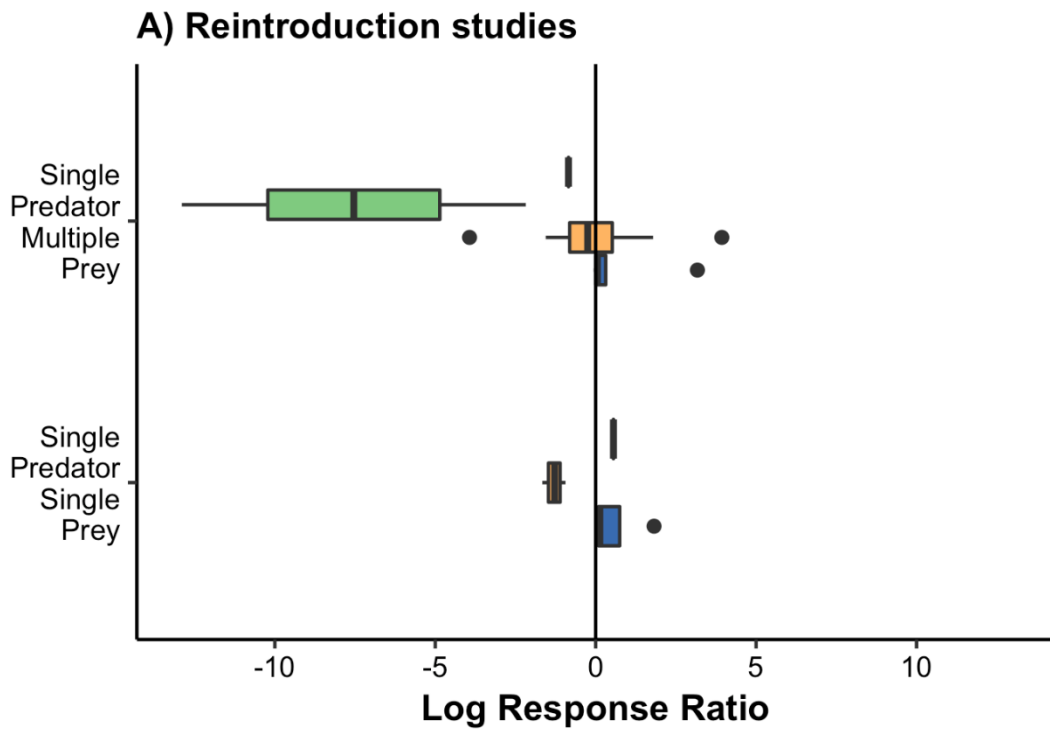


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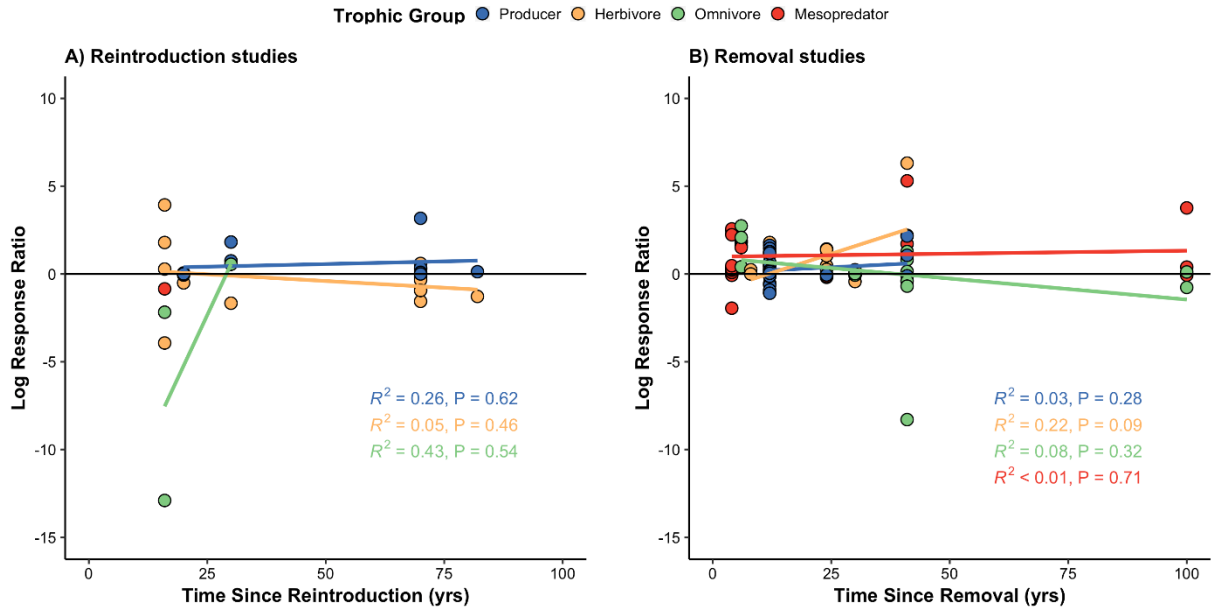
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599 Fig. 4

Trophic Group ■ Producer ■ Herbivore ■ Omnivore ■ Mesopredator



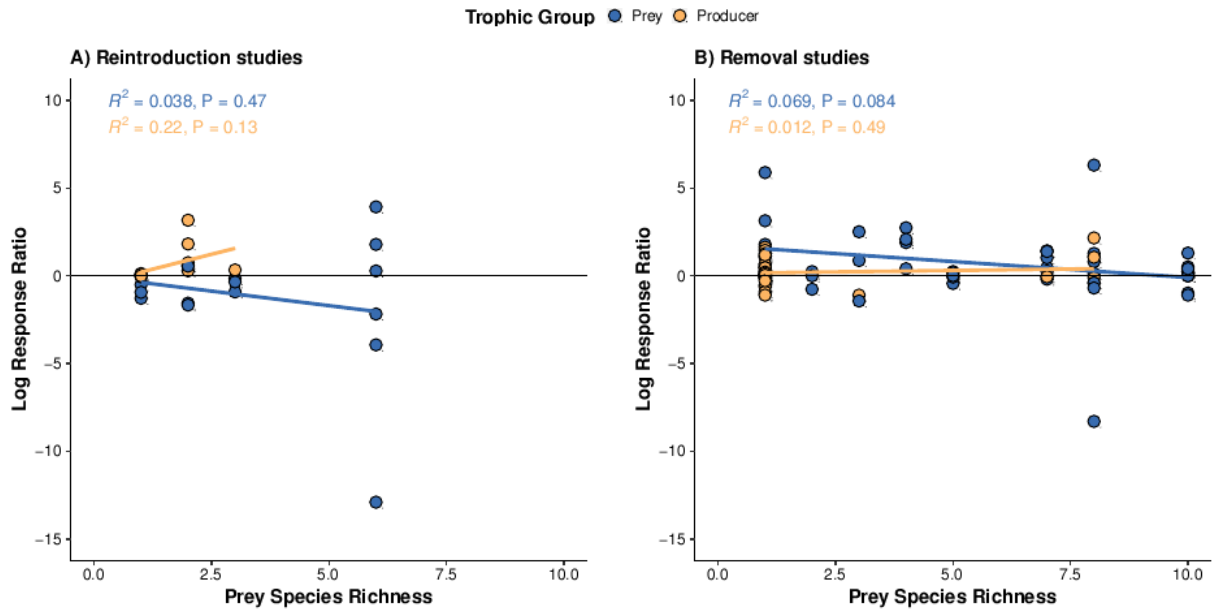
601 Fig. A.1



602

603

604 Fig. A.2



605