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Leach, K., Montgomery, W. I., & Reid, N. (2015). Biogeography, macroecology and species' traits mediate competitive interactions in the order Lagomorpha. *Mammal Review*, 45(2), 88-102.
<https://doi.org/10.1111/mam.12035>

Published in:
Mammal Review

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

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This is the accepted version of the following article: Leach, K, Montgomery, WI & Reid, N 2015, 'Biogeography, macroecology and species' traits mediate competitive interactions in the order Lagomorpha' *Mammal Review*, vol 45, no. 2, pp. 88-102, which has been published in final form at <http://onlinelibrary.wiley.com/doi/10.1111/mam.12035/abstract>.

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1 REVIEW

2 **Biogeography, macroecology and species' traits mediate competitive interactions in the**
3 **order Lagomorpha**

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12 **ABSTRACT**

13 1. In addition to abiotic determinants, biotic factors, including competitive, interspecific
14 interactions, limit species' distributions. Environmental changes in human disturbance, land
15 use and climate are predicted to have widespread impacts on interactions between species,
16 especially in the order Lagomorpha due to the higher latitudes and more extreme
17 environmental conditions they occupy.

18 2. We reviewed the published literature on interspecific interactions in the order Lagomorpha,
19 and compared the biogeography, macroecology, phylogeny and traits of species known to
20 interact with those of species with no reported interactions, to investigate how projected
21 future environmental change may affect interactions and potentially alter species'
22 distributions.

23 3. Thirty-three lagomorph species have competitive interactions reported in the literature; the
24 majority involve hares (*Lepus* sp.) or the eastern cottontail rabbit (*Sylvilagus floridanus*).

25 Key regions for interactions are located between 30-50°N of the Equator, and include eastern
26 Asia (southern Russia on the border of Mongolia) and North America (north western USA).

27 4. Closely related, large-bodied, similarly sized species occurring in regions of human-
28 modified, typically agricultural landscapes, or at high elevations are significantly more likely
29 to have reported competitive interactions than other lagomorph species.

30 5. We identify species' traits associated with competitive interactions, and highlight some
31 potential impacts that future environmental change may have on interspecific interactions.
32 Our approach using bibliometric and biological data is widely applicable, and with relatively
33 straightforward methodologies, can provide insights into interactions between species.

34 6. Our results have implications for predicting species' responses to global change, and we
35 advise that capturing, parameterizing and incorporating interspecific interactions into
36 analyses (for example, species distribution modelling) may be more important than
37 suggested by the literature.

38

39 Submitted: 8 September 2014

40 Returned for revision: 21 October 2014

41 Revision accepted: 12 January 2015

42 Editor: KH

43

44 **Key words:** Biotic interactions, climate change, competition, leporids, pikas.

45 **Running head:** Competitive interactions in the order Lagomorpha

46

47 **INTRODUCTION**

48 Biotic interactions underpin a wide range of ecosystem processes and can occur between
49 individuals of the same species (intraspecific interactions), or among individuals belonging to
50 different species (interspecific interactions; Connell 1983, Chase et al. 2002). Interactions can
51 take place at the local scale, for example, predation, parasitism, competition, and disturbance, or
52 at the regional scale, for example, dispersal, speciation, extinction, and expansions or
53 contractions of species' ranges (Cornell & Lawton 1992, Amarasekare 2003). Competitive
54 interactions are variously defined, but most definitions incorporate limited resources, for
55 example: "the negative effects that one organism has upon another by consuming or controlling
56 access to a resource that is limited in availability" (Keddy 2001). Strong competitive
57 interspecific interactions at the same trophic level are likely to be due to occupied or partially
58 occupied niche space which influences species' coexistence (Cornell & Lawton 1992).
59 Competition can be symmetrical, whereby there are equivalent negative effects, or
60 asymmetrical, whereby there is a clear winner or loser (Connell 1983, Schoener 1983). Three
61 mechanisms are known: (i) interference competition is when an individual directly affects
62 another, for example, by using aggression (Birch 1957); (ii) exploitation competition is when
63 individuals interact indirectly, usually competing for a common, limited resource (Keddy
64 2001); and (iii) apparent competition is when two individuals that do not compete directly for
65 resources affect each other indirectly, by being prey for the same predator (Chaneton & Bonsall
66 2000, Hatcher et al. 2006, DeCesare et al. 2010).

67 Competitive interactions tend to produce biogeographical patterns in species' distributions.
68 Competing species may meet at a sharp boundary with little or no overlap, whereas non-
69 competing species' ranges may show complete overlap (Flux 2008). Parapatry is when two
70 species have separate but contiguous ranges, with no physical barrier between them, and only
71 co-occur, if at all, in a narrow contact zone (Bull 1991, Gutiérrez et al. 2014). Ranges of

72 allopatric species are separated by a geographic barrier and, therefore, there can be no
73 interspecific interaction. Sympatric species share the same geographical space, but may compete
74 for access to similar habitats or resources. Alternatively, species occupying overlapping niches
75 may not compete, so that their coexistence is possible due to the partitioning of resources.
76 Exploitation competition may be evident if, for example, habitat use between species is
77 comparable; abrupt habitat shifts at their point of contact in sympatry are likely to mirror the
78 response to competition (Vidus-Rosin et al. 2011).

79 Traits of competitively interacting species have been studied in great detail (e.g. Schoener
80 1982, Luiselli 2006). Phylogenetic relatedness and its association with competition are often
81 studied. Darwin (1859) suggested that closely related species are more likely to exhibit
82 competition because they occupy similar ecological niches. Close relatedness of interacting
83 species has since been shown experimentally (Violle et al. 2011), but does not hold for some
84 taxa, for example, green algae (Venail et al. 2014). Species with larger body masses are more
85 competitive because they are able to utilise a larger share of resources (Brown & Maurer 1986)
86 and similarly sized species are typically more likely to interact (Leyequien et al. 2007).
87 Environmental traits can also influence competitive interactions, for example, competition is
88 more likely in urban environments with higher human population densities (Shochat et al. 2006),
89 and past climatic changes have probably caused large impacts on species' distributions and,
90 therefore, on interspecific interactions (Koblmüller et al. 2012). Interactions between species are
91 more common at high elevations (Jankowski et al. 2010), perhaps due to limited resources there,
92 and are more vulnerable to change due to the predicted effects of climate change at such
93 elevations (Chen et al. 2011), potentially changing species' ranges both directly and indirectly.
94 Thus, environmental change, caused by human disturbance, changes in climate, or changes in
95 land use, may have direct or indirect effects on the strength of biotic interactions, thus informing
96 our interpretation of their likely influence on species' distributions.

97 Interactions between species are extremely difficult to identify and quantify in the wild.
98 Consequently, the impacts of global change on biotic interactions have rarely been studied
99 (McCann 2007), but they are likely to be significant, due to related changes in phenology,
100 behaviour, physiology, abundance and the co-occurrence of multiple species throughout biomes
101 (e.g. Tylianakis et al. 2008). In the majority of cases, interactions are inferred from parapatry or
102 species replacement, but this inference is not conclusive, and interactions could be a result of
103 hybridization or adaptation to different habitats with no geographic overlap (Huey 1979).
104 Competitive interspecific interactions may be altered by changes in dominant plants or animals
105 under future environmental change; for example, increases in mean global temperatures could
106 affect seed dehiscence times and change competition between mammalian seed predators and
107 invertebrate seed dispersers (Ness & Bressmer 2005). In a hypothetical situation in which
108 species A, B and C are positioned along a resource gradient, with species A occupying the upper
109 end (a region of high resource availability), species C occupying the lower end (a region of low
110 resource availability), and species B occupying a niche between the two, any response to future
111 environmental change involving an increase in the availability of resources may lead to selection
112 favouring the more extreme species (A and C) and, hence, may lead to the expansion of their
113 distributions (impacting species B). For example, species B could broaden its niche space, or
114 new species could invade and occupy niche vacancies left by shifts in species A and/or C.
115 However, if environmental change were to reduce the availability of resource types, the ranges
116 of all three species may contract, which could increase the intensity of competition, and possibly
117 lead to local extirpations at their contact zones, or total extinction(s) (Post 2013).

118 Lagomorphs are an important group of mammals economically and scientifically, as they are
119 a major human food resource, model laboratory animals, valued game, significant agricultural
120 pests, and key elements in food chains that provide scientific insights into entire trophic systems
121 (Chapman & Flux 2008). Competition among species in the order Lagomorpha can involve

122 interference or exploitation for food or shelter (Vidus-Rosin et al. 2008). Interspecific
123 competition is common between lagomorph species and is often precipitated by the introduction
124 of non-native species (e.g. the European rabbit *Oryctolagus cuniculus*, the European hare *Lepus*
125 *europaeus*, and the eastern cottontail *Sylvilagus floridanus*), leading to suppression or expulsion
126 of native lagomorphs from certain habitats due to dominant behaviour and adaptive capabilities
127 of the antagonist (Hackländer et al. 2008). Intraspecific competition in lagomorphs (Somers et
128 al. 2012) and competition with other herbivores (Hulbert & Andersen 2001, Bakker et al. 2009),
129 on the other hand, has been rarely reported in the literature.

130 Lagomorphs are likely to be affected by environmental change because they occupy a wide
131 range of environmental conditions in all continents except Antarctica, and because they are
132 found at extreme elevations, from sea level to >5,000 m, and at very high latitudes, from the
133 Equator to 80°N (Chapman & Flux, 2008). A quarter of lagomorph species are listed in the
134 International Union for Conservation of Nature's (IUCN) Red List of Threatened Species
135 (www.iucnredlist.org); a notable number of species have highly restricted ranges, including 14
136 listed under the IUCN's Criterion B, with an extent of occurrence estimated to be less than
137 20,000 km². Environmental change is predicted to have significant effects on lagomorphs,
138 especially changes in climatic conditions (Ge et al. 2013, Mills et al. 2013), land use (Fa & Bell
139 1990) and human disturbance (Schmidt et al. 2012), and is likely to have significant effects on
140 lagomorph-lagomorph interactions. Research on parapatric hare species in Europe (Acevedo et
141 al. 2012) showed that, under future climate scenarios, the Iberian hare *Lepus granatensis* is
142 likely to be the beneficiary in competition with the European hare in their zone of contact in
143 Northern Iberia, and interactions between the mountain hare *Lepus timidus* and the European
144 hare are expected to contribute to the decline of the former in areas of co-occurrence in Northern
145 Europe (Acevedo et al. 2012), for example, in Sweden (Thulin 2003) and Ireland (Reid 2011).

146 We collate, review and assess all published data on lagomorph-lagomorph interactions, from
147 both experimental evidence and inference from parapatry or species replacement, and examine
148 the potential relationships between the environment and species' traits within different types of
149 interaction. We aim to investigate how future environmental change may affect such interactions
150 and potentially alter species' distributions. We predict greater competition between lagomorph
151 species at higher elevations, due to restrictions in suitable habitat and in the range of potentially
152 interacting species found in mountainous terrain, and in human-converted habitats, which are
153 frequently inhabited by lagomorphs due to the availability of food (e.g. grasses or crops) and
154 shelter (e.g. field margins and hedgerows providing cover) there. We expect the restricted range
155 of food available in and the uniformity of anthropogenic landscapes to intensify competitive
156 interactions. We also hypothesize that competitive interactions are more likely to occur between
157 closely related species (i.e. those with shorter-than-average pairwise phylogenetic distances)
158 with a small difference in body mass (i.e. those relatively similar in size). We use a combination
159 of bibliometric analyses and biological data to assess traits associated with competitive
160 interactions in an entire mammalian order, the Lagomorpha.

161 **METHODS**

162 **Capturing competitive interactions**

163 In the taxonomy we adopt, the Lagomorpha comprises 87 species in two families: the
164 Ochotonidae consists of one monotypic group in the genus *Ochotona* containing 25 species of
165 small, social pikas found at high latitudes, and usually high elevations; the Leporidae has 32
166 species of large, solitary, cursorial hares and jackrabbits in the genus *Lepus* and 30 species of
167 medium-sized, semi-social, fossorial rabbits in 10 genera (Chapman & Flux 2008; *Ochotona*
168 *nigritia* and *Ochotona gaoligongensis* were classed as morphs of *Ochotona forresti*, *Ochotona*
169 *muliensis* as a morph of *Ochotona gloveri*, *Ochotona himalayana* as a morph of *Ochotona*

170 *roylei* and *Ochotona huangensis* as a morph of *Ochotona thibetana* following the taxonomic
171 expertise of Dr Andrey Lissovsky, Zoological Museum of Moscow State University).

172 Data on interspecific interactions involving only lagomorphs were captured using the Web of
173 Knowledge, searched using the terms “lagomorph AND interaction” or “lagomorph AND
174 competition”. Additional search terms included pairwise combinations of all species whose
175 IUCN range polygons overlapped (using both scientific and common names) to identify the
176 possibility of interactions not returned in the initial search. All 3,741 possible pairs of the 87
177 species in our taxonomy were classified as: (i) allopatric, i.e. exhibiting no range overlap, and
178 lacking any published evidence of interspecific interactions; (ii) sympatric (i.e. with partially
179 coincident geographical ranges, defined as overlap in their IUCN range polygons), but with no
180 known interaction; or (iii) sympatric with interaction reported in the literature. Competitive
181 interactions were classed as either exploitation or interference.

182 Information on interactions may be biased by body size or taxonomic group due to variable
183 research effort (Brooke et al. 2014), and some pairwise interactions are likely to be
184 undocumented in the literature to date; thus, the current study may have been vulnerable to type
185 II errors or false negatives in identifying species’ interactions. Moreover, there may have been a
186 bias towards species showing interactions, due to researchers’ preference for reporting
187 significant effects: so-called ‘publication bias’ (Connell 1983). To take this potential bias into
188 consideration, instead of assuming no competition between species for which there was no
189 evidence of interaction, we defined category ii) as ‘sympatric with no known interaction’.

190 **Spatial analysis**

191 The geographical range (based on the IUCN polygon) for each of the 33 species that had at least
192 one documented interaction with another species was rasterised in ArcGIS 10.2 (ESRI,
193 California, USA) at 30 arc-second resolution (~1km² grid cells), with a value of 1 for presence

194 and 0 for absence. The invasive range of the eastern cottontail in Italy was not included because
195 IUCN polygons were only available for its native distribution. Rasterised data were summed to
196 show the global distribution of possible interactions between species known to interact with at
197 least one other species. Mean elevation (m) and latitude (°) occupied by each pair of species
198 known to interact were calculated at 30 arc-second resolution (~1km² grid cells).

199 **Species' traits and environmental data**

200 Phylogenetic distance, the amount of time since the most recent common ancestor of both
201 species existed (Vellend et al. 2011), as a proxy for phenotypic differences between two species
202 (Cavender-Bares et al. 2009), was quantified for each pair (including allopatric, sympatric with
203 no known interaction and sympatric with interaction), to investigate whether closely related
204 species were more likely to interact competitively. A lagomorph phylogeny was extracted from
205 the mammalian supertree provided by Fritz et al. (2009). Likely clade membership for five
206 species not included in this phylogeny was determined from Ge et al. (2013), and missing tips
207 were grafted on using an expanded tree approach (Day et al. 2008). Pairwise phylogenetic
208 distances were calculated using the 'ape' package (Paradis et al. 2014) for R version 3.1.1.

209 Species' traits, including body mass (grams) and human population density (people/km²)
210 within each species' range, were taken from the PanTHERIA database (Jones et al. 2009).
211 Ecoregional climatic stability data was provided by Takuya Iwamura (Iwamura et al. 2013), and
212 was defined as “the proportion of an ecoregion which is predicted to be climatically stable under
213 [future] climate change.” The climatic stability index is calculated by estimating the overlap
214 between present and future climatic envelopes for each ecoregion, using results from seven
215 global circulation models. It ranges from 0 (no overlap between current and future climates) to 1
216 (complete overlap and high robustness to climate change; Watson et al. 2013).

217 For each species, the percentage of occurrence records in human-converted habitats was
218 included as a coarse measure of the threat to each species from human activities, following
219 Hoekstra et al. (2005). Converted habitats included cultivated or managed land and artificial
220 surfaces; areas were derived from a modified version of the Global Land Cover 2000 dataset
221 (Anonymous, 2003). The occurrence data used in this calculation comprised 41,874 records that
222 were either downloaded from the Global Biodiversity Information Facility data portal
223 (data.gbif.org), collated from experts or members of the IUCN Species Survival Commission
224 Lagomorph Specialist Group, and/or extracted from the literature for data-deficient species.
225 Taxonomic accuracy was ensured by checking all records against the latest IUCN taxonomy; if
226 names did not match after cross-referencing with taxonomic synonyms and previous names,
227 records were rejected. Spatial data accuracy was ensured by removing any records that were
228 obviously erroneous because they fell outside the extent of the IUCN geographic range polygon.
229 In addition, occurrences recorded with a spatial resolution of >2km were removed, and duplicate
230 records were eliminated. Species' traits considered (examined) but not included in the analysis
231 are listed in Appendix S1.

232 **Statistical analyses**

233 A linear regression was performed in R version 3.1.1 to test the relationship between the
234 dependent variable, elevation (m), and the number of possible pairwise interactions (rasterised
235 data from the *Spatial analysis* section). A Generalized Linear Model was used to evaluate
236 differences between pairs of species allocated to the three interaction types: (i) allopatric, (ii)
237 sympatric with no known interaction and (iii) sympatric with interaction, using a number of
238 species' traits as explanatory variables (phylogenetic distance, mean body mass, similarity in
239 body mass, mean ecoregional climatic stability, mean human population density and mean
240 percentage of occurrence records in human-converted habitats).

241 **RESULTS**

242 **Spatial patterns of interspecific interactions**

243 Of the 3,741 possible pairs between the 87 species of lagomorph, 3,489 were classed as
244 allopatric, 219 were classed as sympatric with no known interaction, and 33 were classed as
245 sympatric with documented interaction; of the 33 species involved in the 33 documented
246 interactions, nine were pikas, eight were rabbits and 16 were hares (Table 1). The distribution of
247 documented interspecific interactions was not uniform but clustered in eastern Asia (exclusively
248 pikas) and North America (rabbits, hares and jackrabbits; Fig. 1a). Six of the interactions
249 involved interference competition, and five of these (83%) involved the eastern cottontail. The
250 global distribution of possible pairwise interactions between lagomorph species (Fig. 1b) showed
251 that in large areas (~69% of the total global range of the order Lagomorpha), no documented
252 pairwise interactions exist (Fig. 1c); lagomorph species were 2.2 times more likely to occur in
253 allopatry than in sympatry, and 3.1 times more likely to be involved in just one pairwise
254 interaction than in multiple interactions. The mean number of potential pairwise interactions
255 globally was 1.51 ± 0.78 (SD). Only small areas of the globe contained the highest
256 concentrations of possible interactions; for example, there were six possible pairwise species
257 interactions in a 6,000 km² area in southern Russia on the border of Mongolia (Fig. 1c), with
258 interactions clustered around 30-50°N of the Equator (Fig. 1d). There was a significant positive
259 association between the number of possible pairwise interactions and elevation ($F_{3, 49917} = 731.8$,
260 $p < 0.001$; Fig. 2).

261 **Linking interactions to species' traits and environmental change**

262 Sympatric pairs of species with documented pairwise interactions had significantly shorter
263 phylogenetic distances between them than pairs of species that occurred in sympatry but had no
264 known interaction ($F_{2, 3738} = 19.8$, $p < 0.001$; Fig. 3a, see Appendix S2). Thus, within the order

265 Lagomorpha, sympatric species with documented competitive interactions were 2.3 times more
266 closely related than sympatric species with no known interaction.

267 The mean body mass of pairs of interacting sympatric species was significantly greater ($F_{2, 3738} = 22.3, p < 0.001$) than that of pairs of sympatric species that had no known interaction (Fig.
268 3b, Appendix S2). The mean body mass of pairs of allopatric species was lower than both.
269 However, whilst interacting species tended to be heaviest, analysis of the difference in body
270 mass between species in each pair showed that pairs of interacting species were significantly
271 closer in mass than pairs of allopatric species and sympatric species with no known interaction
272 (Fig.3c, Appendix S2).

274 There was no difference in mean ecoregional climatic stability between the pairwise
275 interaction types ($F_{2, 3738} = 0.03, p = 0.969$; Fig. 3d, Appendix S2). The mean ecoregional climatic
276 stability index value for the order Lagomorpha was 0.46 ± 0.14 , which is similar to, but slightly
277 higher than, the global average of 0.42 ± 0.03 .

278 Pairs of sympatric species were more likely to occur in regions of high human population
279 density, but due to the variability in human population density in regions supporting lagomorphs,
280 the difference between sympatric groups was not significant (Fig. 3e, Appendix S2). However,
281 there was a significant difference in mean human population density between the ranges of pairs
282 of allopatric species and those of sympatric species with a known interaction ($F_{2, 3738} = 5.02,$
283 $p < 0.001$; Fig. 3e). Interacting pairs of sympatric species occurred significantly more frequently
284 in human-converted habitats than pairs of sympatric species with no known interaction ($F_{2, 3738} =$
285 $6.3, p = 0.002$), and pairs of sympatric species with no known interaction were significantly more
286 frequently found in human-converted habitats than pairs of allopatric species ($F_{2, 3738} = 6.3,$
287 $p = 0.002$; Fig. 3f, Appendix S2).

288

289 **REVIEW AND DISCUSSION**

290 Closely related, large-bodied, similarly-sized species occurring in regions of human-modified,
291 typically agricultural landscapes, or at high elevations, were significantly more likely to exhibit
292 competitive interactions than other species within the order Lagomorpha. The greatest changes
293 in species' ranges are likely to occur either at high elevation, where the effects of climate
294 warming are pronounced (Chen et al. 2011), or in human-modified habitats, which are already
295 subject to significant threats and pressures (McCarthy et al. 2010). This suggests that interacting
296 species, which are found more commonly in human-modified habitats and at high elevation, are
297 likely to be highly susceptible to future environmental changes. Moreover, the average
298 ecoregional climatic stability index for regions inhabited by lagomorphs, although slightly
299 higher than the global average, indicates only medium robustness of those regions to future
300 changes in climatic conditions. Larger mammalian species are predicted to be especially
301 vulnerable to future climatic changes (McCain & King 2014). Many of the responses to climate
302 change in large mammals, e.g. the Eurasian elk *Alces alces*, are in fact positive, but large species
303 are nevertheless vulnerable to change. In addition, we expect closely related species to show
304 similar responses to environmental change, although idiosyncratic responses are predicted to be
305 more likely (Tafani et al. 2013).

306 **Experimental evidence of competition**

307 Thirty-three pairwise interspecific interactions were identified within the order Lagomorpha, but
308 the evidence for the majority of these competitive interactions was from opportunistic, isolated
309 field observations inferred from parapatry or species replacement. Only one study to date
310 (Probert & Litvaitis 1996), provides experimental evidence of competition in lagomorphs:
311 interference competition between the eastern cottontail and the New England cottontail
312 *Sylvilagus transitionalis*, due to their utilisation of the same habitat and food resources (e.g.

313 Johnston 1972), has led to the expansion of the former and a decline in abundance of the latter. It
314 is possible that the eastern cottontail is a better competitor than the New England cottontail due
315 to inbreeding in transplanted locations which, by increasing the genetic variability of offspring,
316 has functionally enabled occupation of a broad range of habitats (Litvaitis et al. 2008) and also
317 because it is approximately 20% larger. The experimental trial by Probert and Litvaitis (1996),
318 however, showed that eastern cottontails were dominant in only 42% of trials, suggesting that
319 factors other than physical dominance may explain their colonisation of habitats. Eastern
320 cottontails are likely to be dominant because they use open habitats (Smith & Litvaitis 2000),
321 can detect predators at greater distances (Smith & Litvaitis 1999), and have better dispersal
322 capabilities (Probert & Litvaitis 1996) than New England cottontails.

323 Interference competition, as recorded by Probert and Litvaitis (1996), is attributable only to a
324 very small proportion of reported pairwise interactions between lagomorph species. This
325 suggests that most species lack aggressive antagonistic behaviour towards other lagomorphs.
326 Most notably, the eastern cottontail exhibits strong evidence for interference competition by
327 commonly displacing other species from shared habitats (Litvaitis et al. 2008). Our results
328 suggest that the eastern cottontail occupies a region of average climate stability (~ 0.36), with
329 higher than average mean human population density (267 individuals/km²) and higher than
330 average occurrence within human-converted habitats (44%). Occupation of areas vulnerable to
331 anthropogenic change may lead to heightened aggression in competitive interactions between the
332 eastern cottontail and other lagomorphs, e.g. pygmy rabbits *Brachylagus idahoensis*, brush
333 rabbits *Sylvilagus bachmani*, forest rabbits *Sylvilagus brasiliensis*, mountain cottontails
334 *Sylvilagus nuttallii* and New England cottontails, but further comparative analysis of species'
335 traits may be required to identify the mechanisms behind its uniquely aggressive, competitive
336 interactions.

337

338 **Inferred competition based on parapatry or species replacement**

339 Competitive interactions are not easily identified in the wild, and even when they are, most
340 competition is inferred from parapatry or species replacement. Due to limited data, we
341 considered two species to be competitively interacting even if there was only one record
342 providing supporting evidence, i.e. either an experimental study or inference from parapatry or
343 species replacement. However, the weaknesses of inferring competition should be noted.
344 Parapatric distributions and species replacement are consistent with intraspecific competition,
345 but evidence is far from conclusive. Huey (1979) states that parapatry is often used as evidence
346 for competition, and parapatric distributions can in fact result from intense interspecific
347 competition, but they may also arise from hybridization or from adaptation of species to
348 different habitats that do not overlap geographically. Nevertheless, with scarcely any
349 experimental demonstration of competitive interactions in lagomorphs, information on parapatric
350 distributions and species replacement is all we have at present to review competition within the
351 order.

352 Hares of the genus *Lepus* are typically allopatric, but in a few notable cases they exhibit
353 parapatry. For example, in Europe there are five *Lepus* species: the Apennine hare *Lepus*
354 *corsicanus* and broom hare *Lepus castroviejoii* have restricted allopatric ranges, whereas the
355 European hare, mountain hare and Iberian hare have much wider ranges. Competition between
356 the latter three species is asymmetrical and in most cases the ranges are parapatric (Acevedo et
357 al. 2012). In the contact zone between Iberian and European hares, there is a decrease in
358 abundance of the latter (Gortázar et al. 2007), the European hare competes with the Apennine
359 hare (Angelici et al. 2008) and there tends to be contraction of mountain hare ranges, in extent
360 and elevation, in contact zones with the European hare (Thulin 2003, Reid 2011). In most of the
361 European hare's native range, the mountain hare seems to be restricted to high elevations and
362 forests, as it is driven away from lowland grassland plains (Thulin 2003, Flux 2008), but in

363 Ireland, Finland, Russia and Sweden, the European hare, which was introduced in the late 19th
364 and early 20th centuries, is found in sympatry with the mountain hare (Flux 2008). In Ireland,
365 introduced European hares and endemic Irish hares *Lepus timidus hibernicus* occupy similar
366 habitats in sympatry (Reid & Montgomery 2007). They would probably show strong
367 interspecific competition if resources were limiting (Reid 2011), but this is highly unlikely as the
368 majority of available habitat is grassland and thus optimal for both species. Nevertheless, the
369 European hare has actively displaced the Irish hare within its core invasive range, creating a
370 zone of European hare allopatry (Caravaggi et al. 2014).

371 ‘Extinction by hybridization’ was originally described by Rhymer and Simberloff (1996) as a
372 possible effect of hybridization between native and introduced species. If there were a large
373 number of hybrid events between female mountain hares and male European hares, then species-
374 specific litters would be lost in mountain hare populations, causing a loss of range and decline in
375 population density (Thulin 2003). In Sweden, where the two species hybridize in sympatry, the
376 mitochondrial DNA (mtDNA) from mountain hares is transferred to European hares, but this
377 pattern gradually disappears in areas of allopatry (Thulin & Tegelström 2002). Only one
378 researcher to date (Lind 1963) has examined competition between mountain hares and European
379 hares; competitive exclusion of mountain hares and significant differences in food preference
380 and habitat utilisation were found. However, European hares and mountain hares have often
381 been observed feeding side by side (Hewson 1990).

382 Species displacement through hybridization is not a new phenomenon restricted to secondary
383 contact after anthropogenic introductions of alien species into the ranges of old adversaries;
384 ‘ancient hybridisation’ is prevalent within the order Lagomorpha such that many species actually
385 share mitochondrial or nuclear haplotypes revealing the ‘ghosts of a hybrid past’ (Paulo Célio
386 Alves, *pers. comms.* citing Wilson & Bernatchez 1998). Mountain hare mtDNA lineages are
387 found throughout Europe within European hares, Iberian hares and broom hares (Melo-Ferreira

388 et al. 2009). Such ancient hybridization is likely to have occurred during the last glacial
389 maximum when the mountain hare's range would have extended further south than today.
390 Moreover, European hares, Iberian hares and Apennine hares are also known to have hybridized
391 in ancient times (Pietri et al. 2011). The phenomenon is pervasive, being present also in Asia
392 (Liu et al. 2011) and North America. For example, snowshoe hare *Lepus americanus* mtDNA
393 lineages in the Greater Pacific Northwest exhibit hybrid introgression from black-tailed
394 jackrabbits *Lepus californicus*, despite the minimal overlap of their current geographic ranges
395 (Cheng et al. 2014, Melo-Ferreira et al. 2014). For the purposes of this study, ancient
396 hybridization and introgression will not be considered any further as they do not represent on-
397 going competitive behavioural interactions.

398 The majority of competitive interactions occurred between hares in the genus *Lepus* and
399 involved a few key species, e.g. the European hare. Replacement of white-sided jackrabbits
400 *Lepus callotis* by black-tailed jackrabbits and desert cottontails *Sylvilagus audubonii* has been
401 observed (Best & Henry 1993); antelope jackrabbits *Lepus alleni* have been replaced by black-
402 tailed jackrabbits in some habitats (Chapman & Flux 1990); snowshoe hares in Wisconsin, USA
403 were replaced by white-tailed jackrabbits (Leopold 1947); and white-tailed jackrabbits were
404 replaced by black-tailed jackrabbits (Flinders & Chapman 2003). The Abyssinian hare *Lepus*
405 *habessinicus* and the European hare replace the cape hare *Lepus capensis* in some habitats
406 (Chapman & Flux 1990; Flux 2008), but the Abyssinian hare has been replaced by the African
407 savannah hare *Lepus microtis*, scrub hare *Lepus saxatilis*) and Ethiopian hare *Lepus fagani* in
408 others (Chapman & Flux 1990). The African savannah hare is replaced by the scrub hare (Flux
409 2008), and the Manchurian hare *Lepus mandshuricus* and European hare are replaced by the
410 Tolai hare *Lepus tolai* in Russian Asia (Fadeev 1966, Chapman & Flux 1990, Smith & Xie 2008,
411 Sokolov et al. 2009). Competition amongst hares is inferred in many cases because a species is
412 observed occupying the preferred habitat of another species in its absence, but it can also be

413 inferred due to the rare and transient nature of sympatric hare co-occurrence (Flux 1981). Hare
414 species often exhibit parapatric distributions and only tend to occur, if at all, temporarily in the
415 same habitat (Acevedo et al. 2012). Despite a lack of any experimental demonstration of
416 competitive exclusion in lagomorphs, this may nevertheless be a very powerful determinant of
417 geographical and local ranges (Flux 1981, Thulin 2003).

418 Large areas, globally, were occupied by lagomorphs for which there was no evidence of
419 interaction, suggesting that allopatry or parapatry is the usual situation, and that interspecific
420 contact is globally restricted and occurs only in relatively narrow contact zones. However, our
421 spatial analysis would not reveal that species could occupy the same range but be functionally
422 separated by habitat, e.g. mountain hares and European hares are separated by elevation within
423 parts of their contact zone (Thulin 2003). Thus, not all sympatric species will have the
424 opportunity to interact directly and, if they do, interactions may occur in a smaller range than
425 that suggested by our spatial analysis. In addition, population dynamics rather than competition
426 may cause a decline in the abundance of one species, leading to movement of the more abundant
427 species and hence replacement of one species by another in a particular habitat.

428 Hares and rabbits frequently co-occur, but rarely interact. The European hare and the
429 European rabbit form one of the most commonly studied and observed systems with respect to
430 competition. Before anthropogenic introductions, the European hare was restricted to central
431 Europe and the Asian steppes, and the European rabbit to the Iberian Peninsula (Flux 1994), but
432 overlap in the ranges of these two species is now widespread, and coexistence occurs in many
433 introduced populations (Flux 2008). Allopatry is seen at regional scales due to habitat
434 preferences (e.g. Petrovan 2011), and there is widespread belief that the species avoid each other
435 (e.g. Cox 1976). However, in most areas of their range they graze side by side, showing
436 significant dietary overlap (e.g. Katona et al. 2004). Various reports from the early 20th century

437 note physical attacks of rabbits on hares both in captivity and in the wild (Gayot 1868, Millais
438 1906), but more recent observations indicate that aggressive antagonism is rare (e.g. Flux 2008).

439 Rabbits from other genera, for example *Bunolagus*, *Poelagus* and *Pronolagus*, coexist with
440 hares without physical aggression, and there appear to be no antagonistic interactions between
441 rabbits and jackrabbits (Orr 1940, Flux 2008). However, competition with the black-tailed
442 jackrabbit may affect the distribution of the desert cottontail (AMCELA (Mexican Association
443 for Conservation and Study of Lagomorphs) et al. 2008) and competition may have occurred in
444 at least some areas between the mountain cottontail and the snowshoe hare (Frey & Malaney
445 2006), although more studies are needed to confirm this interaction. Leporids, for example the
446 black-tailed jackrabbit, eastern cottontail and desert cottontail, may compete with pygmy rabbits
447 for burrows (e.g. Pierce et al. 2011), cape hares may displace the riverine rabbit *Bunolagus*
448 *monticularis* in marginal habitat (Duthie 1989) and competition between introduced eastern
449 cottontails in Italy and European hares and rabbits is likely, due to marked differences in habitat
450 selection for feeding and resting in sympatric and allopatric areas (Vidus-Rosin et al. 2011,
451 2012), but has yet to be observed (e.g. Bertolino et al. 2013). In addition, aggressive competitive
452 interactions are documented between the eastern cottontail, brush rabbit and mountain cottontail
453 in North Dakota, USA (Chapman & Verts 1969, Genoways & Jones 1972) and between the
454 eastern cottontail and the forest rabbit in expanding savannah and scrub habitats of South
455 America (Chapman & Flux 1990).

456 Two species of pika in North America, the American pika *Ochotona princeps* and the
457 collared pika *Ochotona collaris*, show no overlap in range, whereas the ranges of the twenty-
458 three Asian pikas exhibit large degrees of overlap, yet most have no reported interaction in the
459 published literature. The plateau pika *Ochotona curzoniae* excludes the Daurian pika *Ochotona*
460 *dauurica* and the Gansu pika *Ochotona cansus* from open alpine meadows (Chapman & Flux
461 1990, Su 2001, Zhang et al. 2001), and Kozlov's pika *Ochotona koslowi* is excluded from the

462 Guldsha valley, Pakistan, by the plateau pika *Ochotona curzoniae* and the Ladak pika *Ochotona*
463 *Ladacensis* (Büchner 1894). In sympatric areas, alpine pikas *Ochotona alpina* and northern pikas
464 *Ochotona hyperborea* compete for shelter, and northern pikas are smaller in sympatry than in
465 allopatry (Chapman & Flux 1990). Interference competition has been reported between Pallas's
466 pikas *Ochotona pallasii* and steppe pikas *Ochotona pusilla* in peak population years (Sokolov et
467 al. 2009). Pallas's pika is more successful due to its aggressiveness and dispersal ability
468 (Smirnov 1974).

469 Two invasive interactions were identified in our literature review: between the European and
470 the mountain hare in Sweden and Ireland (Thulin 2003, Reid, 2011), and between the European
471 hare and the forest rabbit in Argentina (Novillo & Ojeda 2008). Inclusion of these species into
472 the analysis did not have substantial effects on the overall patterns observed; however, we did
473 find that these invasive interactions occupied regions with higher than average human population
474 density and human-converted habitats, and regions which were on average more climatically
475 unstable. Other researchers have found increased occurrence of invasive species in areas of high
476 human population density (e.g. McKinney 2001), and our finding indicates that the interactions
477 between these lagomorph species pairs may be heavily influenced by future human disturbance
478 as well as by climatic changes (e.g. Schmidt et al. 2012). Invasive interactions between the
479 eastern cottontail and native Italian lagomorphs are also possible, however at present there is no
480 available IUCN polygon for the invasive range and competition is yet to be observed (e.g.
481 Bertolino et al. 2013).

482 **Conclusion**

483 Our results have implications for predicting lagomorph responses to global change, and suggest
484 that capturing, parameterizing and incorporating interspecific interactions into analyses may be
485 more important than suggested by the literature, for example, when applying species distribution

486 modelling (Acevedo et al. 2012). Future behavioural observation studies should focus on areas
487 of sympatry, particularly those areas in which *Lepus* species occur in a narrow contact zone or in
488 species-rich regions (most notably, the hotspots in southern Russia on the border of Mongolia
489 and north western USA), to increase our knowledge of competitive interactions in the order
490 Lagomorpha. The combination of bibliometric analyses and biological data used in this study
491 allowed us to identify traits associated with competitively interacting species and highlight the
492 potential impacts of future environmental change. This approach is widely applicable, and with
493 relatively straightforward methodologies, can provide significant insights into interactions
494 between species.

495

496 **ACKNOWLEDGEMENTS**

497 This project was funded by Quercus, Northern Ireland's Centre for Biodiversity and
498 Conservation Science supported by the School of Biological Sciences, Queen's University
499 Belfast. We thank Michael Barbour, Kai Collins, Christy Bragg, Deyan Ge, David Hik, Dana
500 Lee, Andrew Smith, Franz Suchentrunk, Zelalem Tolesa and Weihe Yang for contributing
501 species' occurrence data. Particular thanks go to Andrey Lissovsky for taxonomic expertise and
502 for contributing data. We also thank two anonymous reviewers and Nancy Jennings for
503 comments that greatly improved the manuscript.

504

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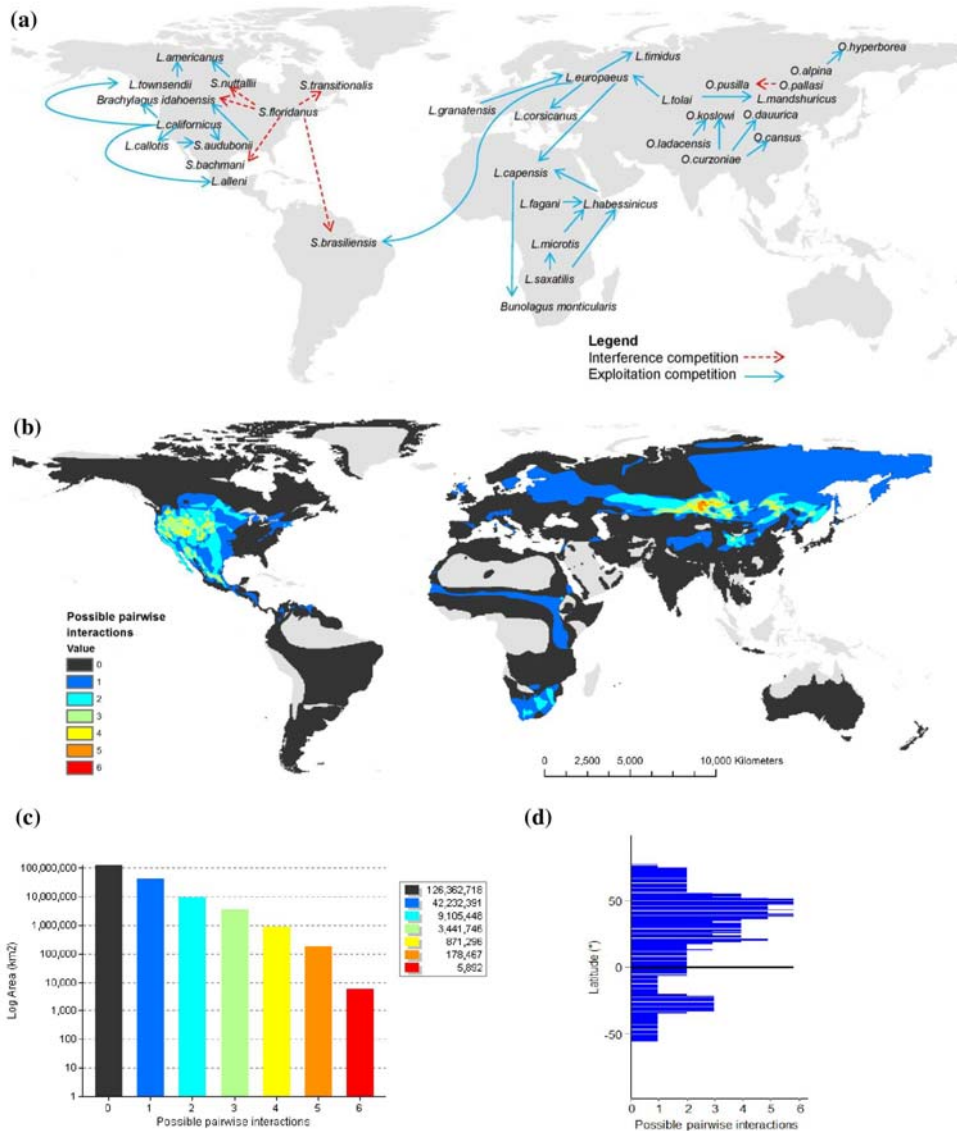
763 **Table 1.** Summary of the 33 competitive interactions documented in the order Lagomorpha,
764 involving 33 species. Type of competitive interaction (exploitation or interference), resource
765 competing for, and a citation for the interaction are also listed. Invasive interactions are
766 highlighted in bold.

767

Competition	For...	Species	Replaced by...	Citation
Exploitation	Habitat	<i>Brachylagus idahoensis</i>	<i>Lepus californicus</i>	Pierce et al. 2011
Exploitation	Habitat	<i>Brachylagus idahoensis</i>	<i>Sylvilagus audubonii</i>	Pierce et al. 2011
Exploitation	Habitat	<i>Bunolagus monticularis</i>	<i>Lepus capensis</i>	Duthie 1989
Exploitation	Habitat	<i>Lepus alleni</i>	<i>Lepus californicus</i>	Chapman & Flux 1990
Exploitation	Habitat	<i>Lepus americanus</i>	<i>Lepus townsendii</i>	Leopold 1947
Exploitation	Habitat	<i>Lepus americanus</i>	<i>Sylvilagus nuttallii</i>	Frey & Malaney 2006
Exploitation	Habitat	<i>Lepus callotis</i>	<i>Lepus californicus</i>	Best & Henry 1993
Exploitation	Habitat	<i>Lepus capensis</i>	<i>Lepus habessinicus</i>	Flux 2008
Exploitation	Habitat	<i>Lepus capensis</i>	<i>Lepus europaeus</i>	Chapman & Flux 1990
Exploitation	Habitat	<i>Lepus corsicanus</i>	<i>Lepus europaeus</i>	Angelici et al. 2008
Exploitation	Habitat	<i>Lepus europaeus</i>	<i>Lepus tolai</i>	Sokolov et al. 2009
Exploitation	Habitat	<i>Lepus europaeus</i>	<i>Lepus granatensis</i>	Gortázar et al. 2007
Exploitation	Habitat	<i>Lepus habessinicus</i>	<i>Lepus microtis</i>	Chapman & Flux 1990
Exploitation	Habitat	<i>Lepus habessinicus</i>	<i>Lepus saxatilis</i>	Chapman & Flux 1990
Exploitation	Habitat	<i>Lepus habessinicus</i>	<i>Lepus fagani</i>	Chapman & Flux 1990
Exploitation	Habitat	<i>Lepus mandshuricus</i>	<i>Lepus tolai</i>	Chapman & Flux 1990, Smith & Xie 2008
Exploitation	Habitat	<i>Lepus microtis</i>	<i>Lepus saxatilis</i>	Flux 2008
Exploitation	Habitat	<i>Lepus timidus</i>	<i>Lepus europaeus</i>	Thulin 2003, Reid 2011
Exploitation	Habitat	<i>Lepus townsendii</i>	<i>Lepus californicus</i>	Flinders & Chapman 2003
Exploitation	Habitat	<i>Ochotona cansus</i>	<i>Ochotona curzoniae</i>	Chapman & Flux 1990
Exploitation	Habitat	<i>Ochotona dauurica</i>	<i>Ochotona curzoniae</i>	Zhang et al. 2001
Exploitation	Habitat	<i>Ochotona koslowi</i>	<i>Ochotona curzoniae</i>	Buchner 1894
Exploitation	Habitat	<i>Ochotona koslowi</i>	<i>Ochotona ladacensis</i>	Buchner 1894
Exploitation	Habitat	<i>Sylvilagus audubonii</i>	<i>Lepus californicus</i>	AMCELA (Mexican Association for Conservation and Study of Lagomorphs) et al. 2008
Exploitation	Habitat	<i>Sylvilagus audubonii</i>	<i>Lepus callotis</i>	Best & Henry 1993
Exploitation	Habitat	<i>Sylvilagus brasiliensis</i>	<i>Lepus europaeus</i>	Novillo & Ojeda 2008
Exploitation	Shelter	<i>Ochotona hyperborea</i>	<i>Ochotona alpina</i>	Chapman & Flux 1990
Interference	Habitat	<i>Brachylagus idahoensis</i>	<i>Sylvilagus floridanus</i>	Pierce et al. 2011
Interference	Habitat	<i>Ochotona pusilla</i>	<i>Ochotona pallasi</i>	Sokolov et al. 2009
Interference	Habitat	<i>Sylvilagus bachmani</i>	<i>Sylvilagus floridanus</i>	Chapman & Verts 1969
Interference	Habitat	<i>Sylvilagus brasiliensis</i>	<i>Sylvilagus floridanus</i>	Chapman & Flux 1990
Interference	Habitat	<i>Sylvilagus nuttallii</i>	<i>Sylvilagus floridanus</i>	Genoways & Jones 1972
Interference	Habitat/food	<i>Sylvilagus transitionalis</i>	<i>Sylvilagus floridanus</i>	Probert & Litvaitis 1996, Litvaitis et al. 2008

768

Fig. 1.



770

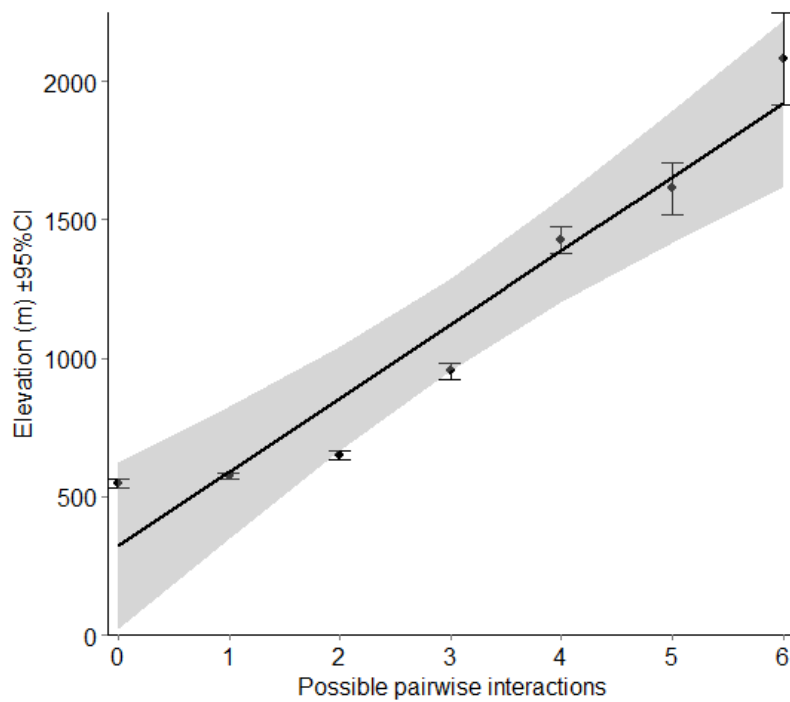
771 **Figure 1.** (a) Documented competitive interactions in the order Lagomorpha shown in their
 772 approximate geographic locations. Red arrows (dashed) indicate interference competition, blue
 773 arrows indicate exploitation competition. (b) Global distribution of possible pairwise
 774 competitive interactions between the 33 species in the order Lagomorpha that have documented
 775 interactions with other species. Pale grey areas indicate places where no lagomorph species are
 776 found. (c) Histogram of the area occupied by possible pairwise interactions between species
 777 documented to interact with others. (d) Histogram of the latitudes occupied by possible pairwise

778 interactions between species known to interact with others; the bold line represents the Equator.

779 In (b), (c) and (d), zero possible pairwise interactions indicates the occurrence of one species not

780 documented to interact with others.

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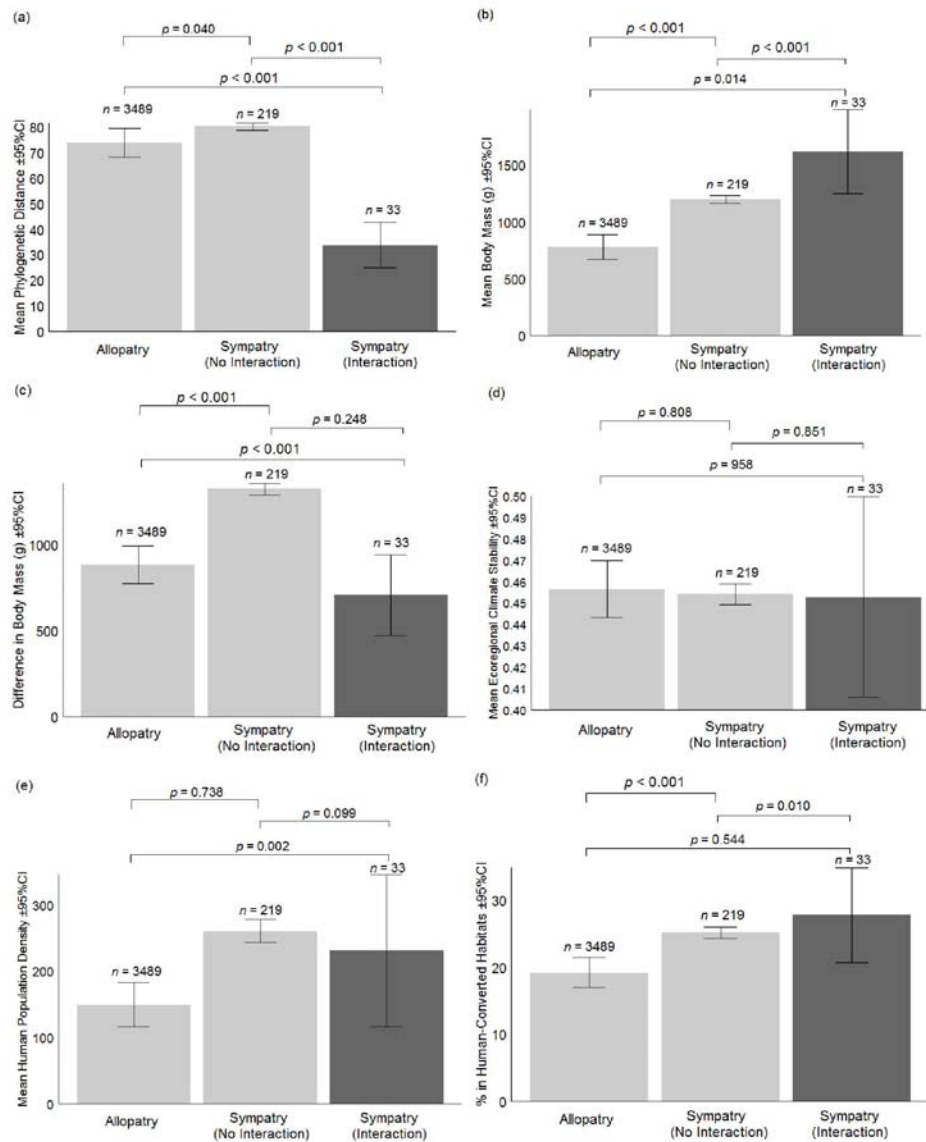
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783 **Figure 2.** Relationship between possible pairwise interactions in species of Lagomorpha

784 documented to interact with others and elevation (m), with $\pm 95\%$ confidence error bars. The

785 grey area surrounding the fitted linear regression line indicates the 95% confidence limits.

Fig. 3.



786

787 **Figure 3.** Mean phylogenetic distance (a), mean body mass (b), difference in body mass
 788 between each species in an interacting pair (c), mean ecoregional climate stability (d), mean
 789 human population density (e) and mean percentage of occurrence records in human-converted
 790 habitats (f) ±95% confidence intervals, for lagomorph species in allopatry (light grey), sympatry
 791 with no known interaction (light grey) and sympatry with an interaction (dark grey).

792

793 **SUPPORTING INFORMATION**

794 **Appendix S1.** Variables considered, but not included in the analysis.

- 795 • Activity cycle,
- 796 • Body length,
- 797 • Body mass at birth,
- 798 • Diet breadth,
- 799 • Elevational change (1930-2080),
- 800 • Gestation length,
- 801 • Habitat breadth,
- 802 • Home range size,
- 803 • Land use change (1980-2050),
- 804 • Land use change (1980-2070),
- 805 • Litter size,
- 806 • Litters per year,
- 807 • Poleward movement (1930-2080),
- 808 • Population density,
- 809 • Range decline (1930-2080).

810

811 **Appendix S2.** Results of Generalized Linear Models characterising phylogenetic distance, body
812 mass, difference in body mass, ecoregional climatic stability, human population density and
813 percentage of occurrence records in human-converted habitats for pairs of species of lagomorph
814 in allopatry, sympatry with no interaction and sympatry with an interaction. Significant *p* values
815 are in bold.

Response variable	Term	$\beta \pm \text{s.e.}$	<i>t</i>	<i>p</i>
Mean phylogenetic distance <i>F</i> _{2, 3738} =19.80 (<i>p</i> <0.001)	Sympatry-Interaction & Sympatry- No Interaction	39.971 ± 7.791	5.130	<0.001
	Sympatry-Interaction & Allopatry	-46.311 ± 7.729	-5.992	<0.001
	Sympatry-No Interaction & Allopatry	-6.340 ± 3.078	-2.060	0.040
Mean adult body mass (g) <i>F</i> _{2, 3738} =22.26 (<i>p</i> <0.001)	Sympatry-Interaction & Sympatry- No Interaction	-838.100 ± 162.500	-5.159	<0.001
	Sympatry-Interaction & Allopatry	419.790 ± 170.930	2.456	0.014
	Sympatry-No Interaction & Allopatry	-418.300 ± 68.080	-6.144	<0.001
Difference in adult body mass (g) <i>F</i> _{2, 3738} =26.81 (<i>p</i> <0.001)	Sympatry-Interaction & Sympatry- No Interaction	176.100 ± 152.000	1.159	0.248
	Sympatry-Interaction & Allopatry	-616.590 ± 171.230	-3.601	<0.001
	Sympatry-No Interaction & Allopatry	-440.470 ± 68.200	-6.458	<0.001
Mean ecoregional climate stability <i>F</i> _{2, 3738} =0.03 (<i>p</i> =0.969)	Sympatry-Interaction & Sympatry- No Interaction	0.004 ± 0.020	0.188	0.851
	Sympatry-Interaction & Allopatry	-0.001 ± 0.025	-0.053	0.958
	Sympatry-No Interaction & Allopatry	0.002 ± 0.010	0.243	0.808
Mean human population density <i>F</i> _{2, 3738} =5.02 (<i>p</i> <0.001)	Sympatry-Interaction & Sympatry- No Interaction	-81.760 ± 49.480	-1.653	0.099
	Sympatry-Interaction & Allopatry	-29.580 ± 88.508	-0.334	0.738
	Sympatry-No Interaction & Allopatry	-111.342 ± 35.253	-3.158	0.002
Mean % of occurrence records in human- converted habitats <i>F</i> _{2, 3738} =6.30 (<i>p</i> =0.002)	Sympatry-Interaction & Sympatry- No Interaction	-8.538 ± 3.269	-2.612	0.010
	Sympatry-Interaction & Allopatry	2.600 ± 4.283	0.607	0.544
	Sympatry-No Interaction & Allopatry	-5.940 ± 1.706	-3.482	<0.001

816