1   Mixed support for the idea that lower elevation animals are better competitors than their upper

2   elevation relatives

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24   Abstract

25   What factors set species' range edges? One general hypothesis, often attributed to Darwin and

26   MacArthur, is that interspecific competition prevents species from inhabiting the warmest

27   portions along geographic gradients (i.e., low latitudes or low elevations). A prediction arising

28   from the Darwin-MacArthur hypothesis is that lower elevation species are better competitors

29   than are related upper elevation species. I tested this prediction by conducting a meta-analysis

30   of studies that have measured behavioral competition between related species along

31   elevational gradients. I found that (1) interspecific aggression appears to be a reliable

32   indicator of interspecific competition; (2) as predicted, lower elevation species showed

33   stronger interspecific aggression, but only for tropical species-pairs tested with playback

34   experiments (nearly all songbirds); (3) for a broader range of taxa where authors directly

35   observed behavioral interactions, *upper* elevation species showed stronger interspecific

36   aggression; and (4) in general, larger species showed greater interspecific aggression. One

37   potential explanation for why upper elevation species often show more interspecific

38   aggression is that they tend to be larger (Bergmann's rule; larger body sizes in colder

39   environments). Supporting this possibility, tropical species tested with playback experiments,

40   which do not follow Bergmann's rule, were the only group that matched predictions arising

41   from the Darwin-MacArthur hypothesis. Hence, available evidence does not consistently

42   support the longstanding hypothesis that relative range position predicts the outcome of

43   interspecific competition. Instead, body size is a better predictor of behavioral competition.

44   Last, I consider these results in the context of the hypothesis that behavioral interactions may

45   impact rates of upslope range shifts associated with recent warming.

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47   Since Darwin, biologists have proposed that species interactions set species' warm range

48   edges, while climate sets species' cold range edges (Darwin, 1859; MacArthur, 1972). A

49   geographic prediction arising from this "Darwin-MacArthur" hypothesis is that species

50   interactions—often thought to be competition—limit species' ranges at low latitudes or low

51   elevations (Louthan *et al.*, 2015). While some comparative studies have revealed patterns

52   consistent with this prediction (Sunday *et al.*, 2012; Hargreaves *et al.*, 2014), others have

53   shown opposite patterns (Cahill *et al.*, 2014; Freeman *et al.*, 2018). Therefore, whether

54   competition (or other interactions) limit species' warm range edges in nature remains an open

55   question. One useful way to evaluate predictions arising from the Darwin-MacArthur

56   hypothesis is to examine interactions between related species that live in different latitudinal

57   or elevational zones. Here, I take this approach, focusing on competition along mountain

58   slopes: I conducted a meta-analysis to test the prediction that species living at low elevations

59   are better competitors than related species living at high elevations.

60   In this study, I focus on the behavioral component of competition (interference

61   competition). Interspecific interference competition is often mediated by interspecific

62   aggression (Schoener, 1983; Dhondt, 2011; Grether *et al.*, 2017), such that a better competitor

63   will tend to exhibit more interspecific aggression in an interaction with a related species. If so,

64   then the prediction arising from the Darwin-MacArthur hypothesis is that lower elevation

65   species should be more aggressive to upper elevation relatives than vice versa. To test this

66   prediction, I compiled a dataset of studies that have measured interspecific aggression

67   between species-pairs where the two species live primarily in different elevational zones. A

68   key assumption of my study is that interspecific aggression is a valid proxy for interspecific

69   competition; I find support for this assumption when analyzing the subset of studies that

70   measured both interspecific aggression and interspecific competition (Table 1, also see

71   Results).

72   A further motivation for testing general patterns of interspecific aggression as a

73   function of elevational position is that behavioral interactions have been hypothesized to

74   influence species' geographic responses to climate change. The idea is that while we might

75   generally expect species to shift upslope as a consequence of warming temperatures (as

76   indeed is happening in nature; Chen *et al.*, 2011; Lenoir & Svenning, 2015; Freeman *et al.*,

77   2018), behavioral interactions could lead to faster or slower shifts over short time scales. That

78   is, more aggressive lower elevation species might be able to rapidly colonize higher

79   elevations, in the process "pushing" upper elevation relatives to ever higher elevations at rates

80   faster than expected based solely on temperature changes; alternately, more aggressive upper

81   elevation species might be able to avoid range contractions at their lower elevation (warm)

82   range edge, persisting as "kings of the mountain", at least in the short term (Jankowski *et al.*,

83   2010). The possibility that behavioral interactions influence rates of warming-associated

84   upslope shifts has yet to be tested. Still, it is uncertain which of these situations—lower

85   elevation species more aggressive (consistent with the Darwin-MacArthur hypothesis) vs.

86   upper elevation species more aggressive—predominates in the real world. Hence, this meta-

87   analysis both tests a longstanding hypothesis in ecology, and also provides information that is

88   potentially relevant to understanding and predicting contemporary range shifts along

89   mountain slopes.

90

91   Methods

92   I searched the literature to find studies that measured interspecific aggression between species

93   that live in different elevational zones along mountain slopes. I conducted a Web of Science

94   search on 18 April 2019 with the keywords "behav*" OR "aggress*" AND "elevation*" OR

95   "altitu*" AND "compet*. This search returned 561 studies. I retained studies that met the

96   following two criteria: (1) They measured aggressive interactions between two closely related

97   species (typically congeners), and (2) The two species in question inhabit roughly parapatric

98   elevational zones during the breeding season (or all year long), with one species

99   predominately living at lower elevations and the other at higher elevations. Disappointingly,

100   this Web of Science search failed to return several older relevant papers that are routinely

101   cited within this literature (e.g., Brown, 1971; Heller, 1971). Because my overall goal was to

102   compile a comprehensive dataset, I located additional appropriate studies by (1) inspecting

103   citations within papers identified by the Web of Science search, and (2) following citation

104   webs. The final dataset included 57 estimates of interspecific aggression for 47 unique

105   species-pairs from 34 studies. While the majority of estimates came from the temperate zone

106   (absolute latitude > 23.4; N = 36), the tropics (absolute latitude < 23.4; N = 21) were also well

107   represented (Figure 1). Taxonomically, the dataset consists of estimates for birds (N = 28),

108   mammals (N = 12, mostly chipmunks from western North America), amphibians (N = 7, all

109   *Plethodon* salamanders from the Appalachian Mountains in eastern North America), fishes (N

110   = 8, all salmonids from temperate regions), reptiles (N = 1) and insects (N = 1).

111   Upon examining relevant studies, I found a fundamental distinction between instances

112   where authors directly observed interspecific aggression (N = 35), and those where authors

113   measured aggressive behaviors in response to the simulated presence of a heterospecific (N =

114   22). Direct interaction studies measured aggression during contests in laboratory behavioral

115   trials or at food sources placed in the environment (e.g., feeders). In contrast, simulated

116   interaction studies measured aggression in response to song playback experiments, and were

117   nearly always (21 out of 22) conducted on songbirds. Importantly, direct interaction vs.

118   simulated playback studies (hereafter "direct" and "playback") reported different metrics of

119   interspecific aggression. I was unable to analyze these different metrics in a single meta-

120   analytic model. Direct studies reported either the winner of aggressive contests or the number

121   of aggressive behaviors exhibited during such contests. For these direct studies, I summarized

122   interspecific aggression between the species-pair as a proportion—the proportion of contests

123   won by the lower elevation species, or the proportion of total aggressive behaviors exhibited

124   by the lower elevation species. Here, larger proportions indicate that the lower elevation

125   species tends to win contests or exhibits more aggressive behaviors. This quantity can be

126   directly used to test the prediction that lower elevation species are more aggressive to upper

127   elevation relatives than vice versa. In contrast, playback studies reported aggression scores in

128   response to a simulated heterospecific intruder (typically PC1 scores from a multivariate

129   analysis of behavioral responses to playback, less often a univariate metric of aggression such

130   as closest approach to the speaker). For these playback studies, I summarized interspecific

131   aggression between the species-pair as an effect score—the difference in mean aggression

132   scores between lower elevation and upper elevation species. Here, positive values represent

133   cases where the lower elevation species showed more interspecific aggression than did the

134   upper elevation species. Again, this difference can be directly used to test the prediction that

135   lower elevation species are more aggressive to upper elevation relatives than vice versa. For

136   all studies, when results were presented only in figures, I extracted data using

137   WebPlotDigitizer (Rohatgi, 2017).

138   My principal aim in this study is to assess if lower elevation species show more

139   interspecific aggression to upper elevation relatives than the reverse. I tested this idea by

140   fitting mixed effect meta-analytic models using the "metafor" package (Viechtbauer, 2010) in

141   R (R Development Core Team, 2017). I fit distinct models for direct and playback studies.

142   These models weight individual estimates by the inverse of their squared standard errors, and

143   incorporate the estimated variance among the study-specific effect sizes. Because my dataset

144   included some species-pairs with multiple estimates of interspecific aggression (i.e., the same

145   species-pair was measured in different studies), I included species-pair as a random effect in

146   all models. For both direct and playback studies, I explored whether patterns differed between

147   latitudinal zones or taxonomic groups by fitting secondary models that included either

148   latitudinal zone or taxa as a moderator variable, and compared model fit using AIC. I did not

149   fit a secondary model with taxonomic group for playback studies because nearly all playback

150   studies were conducted on birds (21 out of 22 cases). The null expectation for the direct

151   studies model is that the lower elevation species should win 50% of contests or exhibit 50%

152   of observed aggressive behaviors. For playback studies, the null expectation is that lower and

153   upper elevation species should have similar interspecific aggression scores, such that the true

154   mean difference in aggression score is 0.

155   Last, I tested how body size was related to both interspecific aggression and

156   elevational position. I extracted body size data (masses for birds and mammals, snout-vent-

157   length for salamanders) from papers or, when not presented in papers, from reference volumes

158   (Dunning, 2007; Wilman *et al.*, 2014) or personal communication with authors. I then used

159   binomial tests to evaluate (1) if larger species showed more aggression to smaller species than

160   vice versa (as expected, see Martin & Ghalambor, 2014), and (2) if upper elevation species

161   tend to be larger than lower elevation species (as expected given Bergmann's rule). For these

162   analyses, I did not include playback studies where neither species showed interspecific

163   aggression (defined as cases where response to song from the putative competitor was

164   statistically indistinguishable from response to a negative control, a song from a totally

165   unrelated species that is not expected to elicit any response). In sum I analyzed body mass for

166   33 unique species-pairs where at least one species showed interspecific aggression.

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168   Results

169   Interspecific aggression between related species along mountain slopes appears to be fairly

170   common in nature. This is somewhat surprising, especially for playback studies. It is perhaps

171   to be expected that individuals will behave aggressively when placed in a small laboratory

172   arena with a single resource (i.e., most direct studies). But there is little expectation that

173   simply broadcasting the song of a relative—a song that typically sounds obviously different

174   from the focal species' own song—should elicit an aggressive response. Nevertheless, the

175   majority of species-pairs tested with playback studies in my dataset (15 out of 20) showed

176   interspecific aggression, and interspecific aggression was as strong as intraspecific aggression

177   in one-third of cases (7 out of 22; denominators differ because these inferences depend on

178   experimental design, which varied among studies). Further, strong interspecific aggression

179   appears to indicate competitive dominance, at least within this dataset. In the 10 studies that

180   measured both interspecific aggression and interspecific competition, the more aggressive

181   species was the better competitor in 9 out of 10 cases (binomial test; $p = 0.021$; Table 1).

182   I found mixed evidence that lower elevation species are more aggressive to upper

183   elevation relatives than vice versa. For direct studies, the *upper* elevation species tended to

184   win most contests or exhibit more aggressive behaviors in contests (Figure 2), the opposite of

185   the predicted relationship. Competing models that included latitudinal zone or taxa as

186   moderator variables provided poorer fits to the data (Δ AIC = 1.81 and 8.42, respectively). In

187   contrast, in playback studies, lower elevation species did tend to exhibit more interspecific

188   aggression (Figure 3), with an overall mean effect size that narrowly overlapped the null

189   expectation of zero. A model that included latitudinal zone (tropical vs. temperate) provided a

190   better fit to the data than a model without this moderator variable (Δ AIC = 1.66). In the

191   model that included latitudinal zone, the estimate for tropical species-pairs was positive and

192   did not overlap zero, indicating that the tendency for lower elevation species to be more

193   aggressive in playback studies was associated with the tropics (Figure 3; the estimate for the

194   subgroup of temperate zone species-pairs was approximately zero). While most studies

195   conducted either direct observations or playback experiments, there were two studies that

196   measured interspecific aggression using both direct observations and playback experiments,

197   and these two studies both reported congruent results between the two methodologies (Pasch

198   *et al.*, 2013; Barve & Dhondt, 2017).

199   I found evidence that body size drives observed patterns of interspecific aggression.

200   Larger species tended to show stronger interspecific aggression (24 out of 33 species-pairs;

201   binomial test; $p = 0.014$). However, overall, upper elevation species were not larger more

202   often than by chance (18 out of 33 upper elevation species-pairs were larger; binomial test; p

203     $= 0.72$). The association between size and elevational position differed somewhat between

204   datasets (see Table 2), with upper elevation species tending to be larger in studies that directly

205   observed behaviors (13 out of 21) but not in playback studies from the tropics (5 out of 11)

206   [there were only three playback studies from the temperate zone that showed interspecific

207   aggression; the upper elevation species was larger in two of these three cases].

Figure 1. Map of studies that measured interspecific aggression between lower vs. upper elevation species. Studies that directly observed aggressive interactions are shown in pink; those that used playback to simulate interactions are shown in blue. Many studies report data for multiple species-pairs from the same site, illustrated by the size of the circle. The Tropics of Cancer and Capricorn (at 23.4° N and S, respectively) delimit the tropics, and are illustrated with dashed lines. This map was made using the package "ggmap" (Kahle & Wickham, 2013)
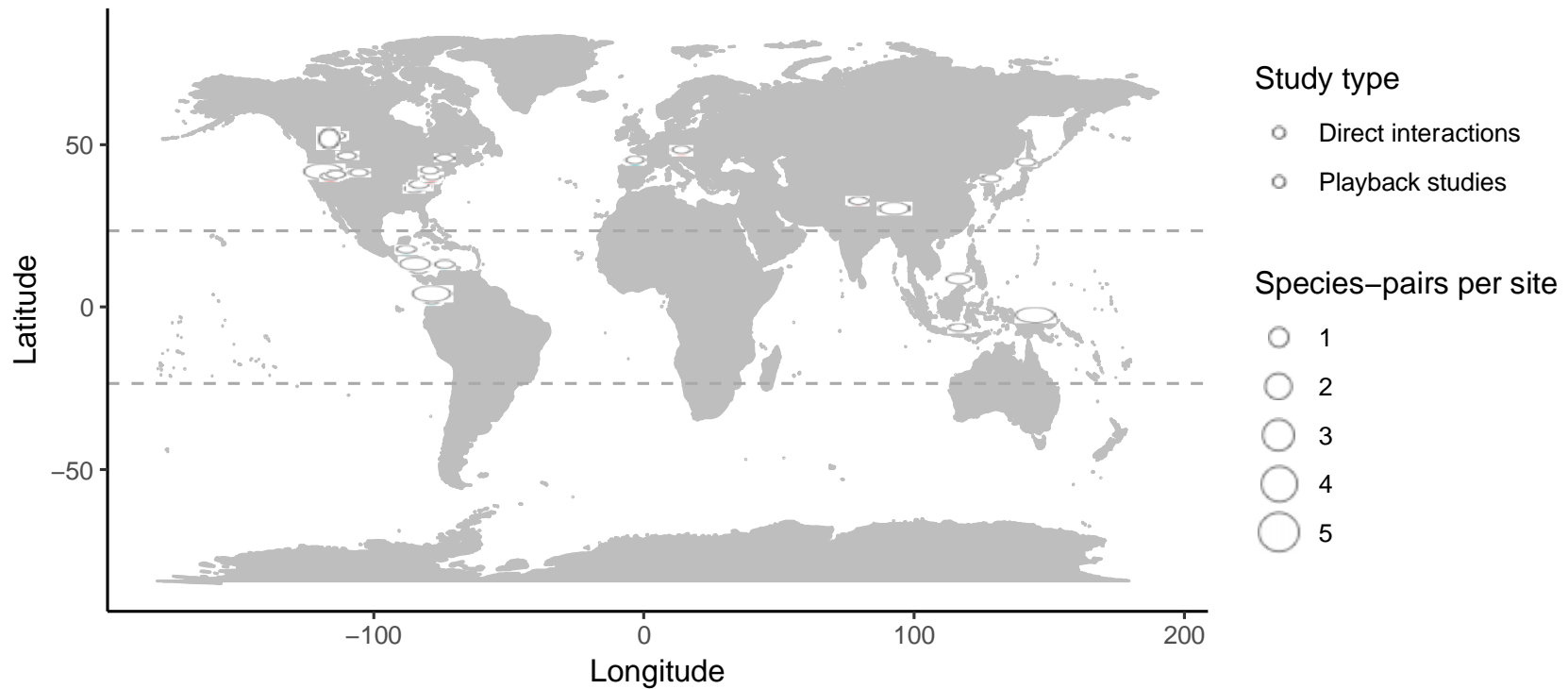
Figure 2. Results of studies that directly observed interspecific aggression (N = 36). The summary metric is the proportion of contests won, or aggressive behaviors exhibited, by the lower elevation species (± SE); this score would be 1 if the lower elevation species won all contests or exhibited 100% of all observed aggressive behaviors. Studies are identified by their author(s), year, and the scientific names of the species-pair.

Study	Value
Martin et al. 2017 Coeligena coeligena / torquata	0.01 [0.00, 0.05]
Bergstrom 1992 Tamias quadrivittatus / umbrinus	0.01 [0.00, 0.11]
Blaustein & Risser 1976 Dipodomys merriami / panamintinus	0.01 [0.00, 0.05]
Magoulick & Wilzbach 1998 Oncorhynchus mykiss / Salvelinus fontinalis (cold)	0.05 [0.00, 0.14]
Chappell 1978 Tamias amoenus / speciosus	0.05 [0.00, 0.10]
Martin et al. 2017 Colibri thalassinus / coruscans	0.07 [0.00, 0.21]
Chappell 1978 Tamias minimus / amoenus	0.09 [0.06, 0.12]
Nishikawa 1985 Plethodon glutinosus / jordani (Balsam Mtns)	0.11 [0.00, 0.23]
Pasch et al. 2013 Scotinomys teguina / xerampelinus	0.11 [0.00, 0.27]
Drummond 2015 Plethodon teyahalee / shermani	0.12 [0.00, 0.28]
Heller 1971 Tamias minimus / amoenus	0.13 [0.00, 0.31]
Heller 1971 Tamias speciosus / alpinus	0.16 [0.00, 0.32]
Barve & Dhondt 2017 Parus cinereus / monticolus	0.18 [0.07, 0.29]
Martin et al. 2017 Boissonneaua matthewsii / flavescens	0.23 [0.00, 0.46]
Magoulick & Wilzbach 1998 Oncorhynchus mykiss / Salvelinus fontinalis (warm)	0.24 [0.06, 0.42]
Arif et al. 2007 Plethodon cinereus / hubrichti	0.33 [0.16, 0.50]
Rodtka & Volpe 2007 Salvelinus fontinalis / confluentus (warm)	0.37 [0.15, 0.59]
Rodtka & Volpe 2007 Salvelinus fontinalis / confluentus (cold)	0.37 [0.15, 0.60]
de Staso III & Rahel 1994 Salvelinus fontinalis / Oncorhynchus clarki (cold)	0.39 [0.28, 0.51]
Nishikawa 1985 Plethodon glutinosus / jordani (Smokies)	0.45 [0.25, 0.64]
Griffis & Jaeger 1998 Plethodon cinereus / shenandoah	0.47 [0.29, 0.65]
Kwon 2016 Aphaenogaster japonica / Myrmica	0.50 [0.01, 0.99]
Clay & Gifford 2016 Plethodon cylindraceus / montanus	0.51 [0.36, 0.67]
Taniguchi & Nakano 2000 Salvelinus leucomaenis / malma (cold)	0.52 [0.38, 0.66]
Carstensen et al. 2011 Lichmera lombokia / limbata	0.53 [0.43, 0.63]
Zagar et al. 2015 Podarcis muralis / Iberolacerta horvathi	0.62 [0.30, 0.94]
Marshall et al. 2004 Plethodon glutinosus / petraeus	0.64 [0.42, 0.85]
de Staso III & Rahel 1994 Salvelinus fontinalis / Oncorhynchus clarki (warm)	0.65 [0.54, 0.76]
Meredith 1977 Tamias amoenus / minimus	0.67 [0.40, 0.93]
Brown 1971 Tamias dorsalis / umbrinus	0.79 [0.75, 0.83]
Taniguchi & Nakano 2000 Salvelinus leucomaenis / malma (warm)	0.79 [0.68, 0.90]
Heller 1971 Tamias amoenus / speciosus	0.94 [0.82, 1.00]
Sheppard 1971 Tamias amoenus / minimus	0.97 [0.88, 1.00]
Martin et al. 2017 Amazilia tzacatl / franciae	0.97 [0.93, 1.00]
Martin et al. 2017 Boissonneaua jardini / flavescens	0.98 [0.94, 1.00]
ML Model for All Studies (Q = 3428.48, df = 34)	0.38 [0.26, 0.50]

Proportion of aggression by lower elevation species

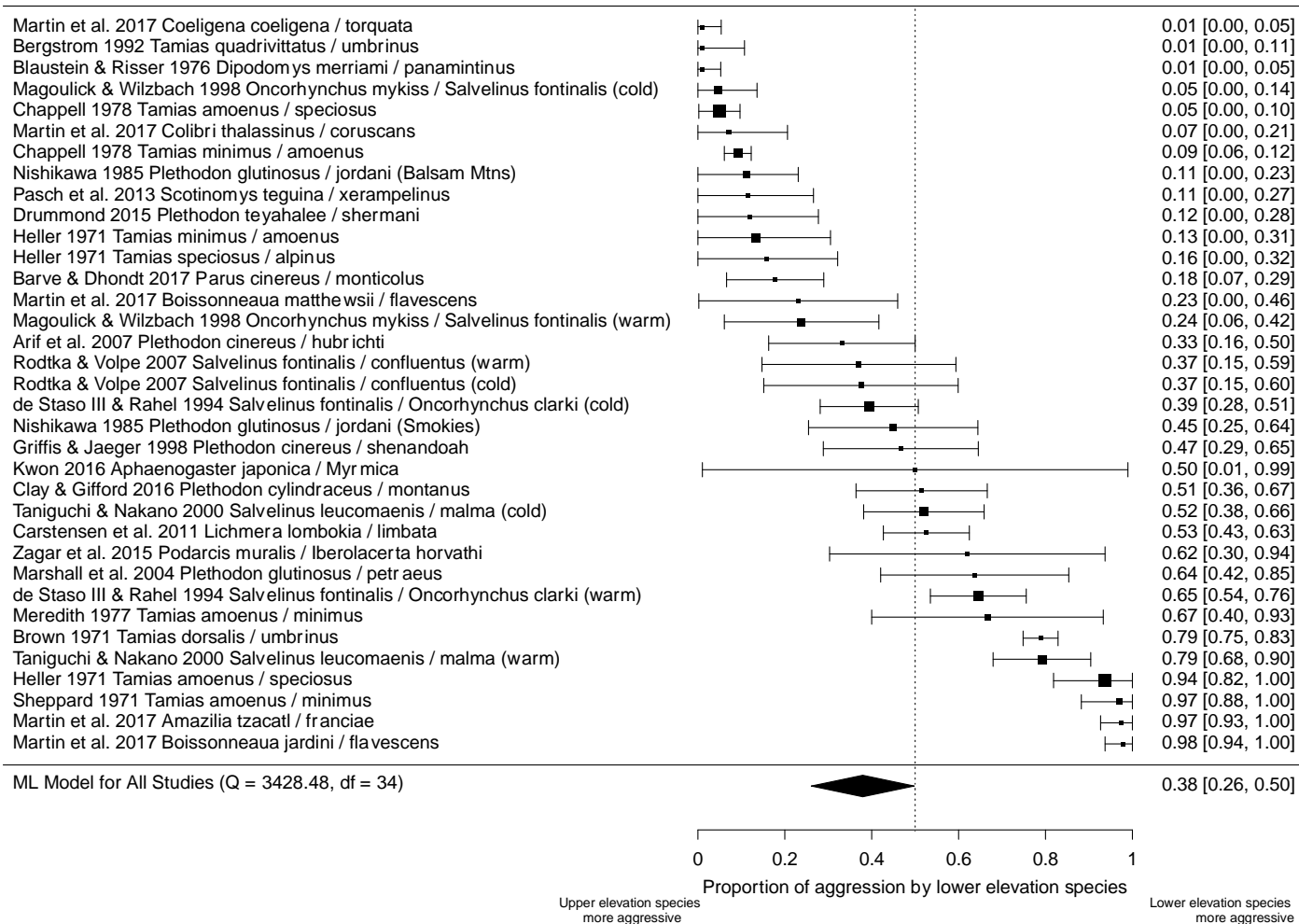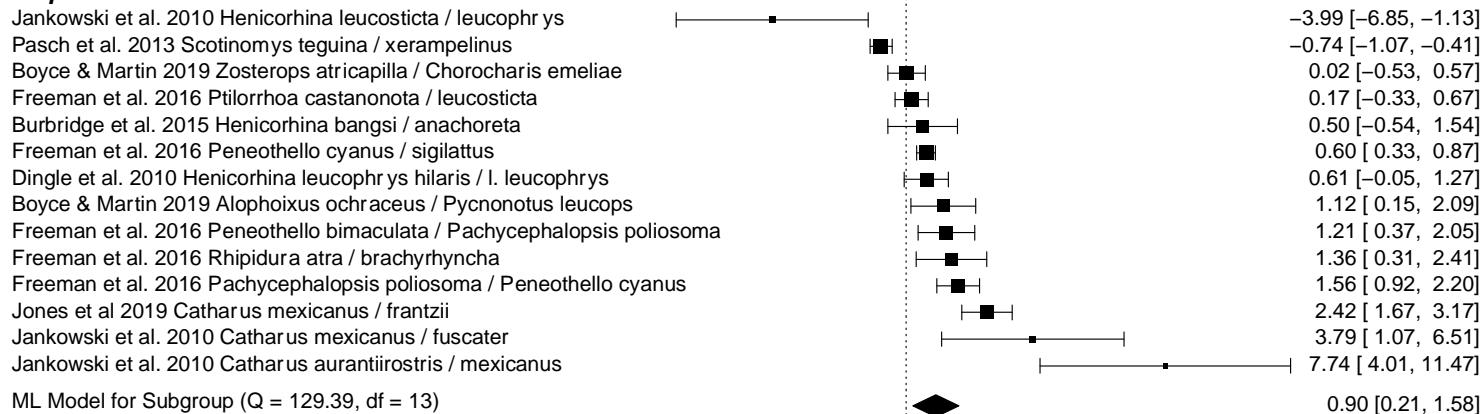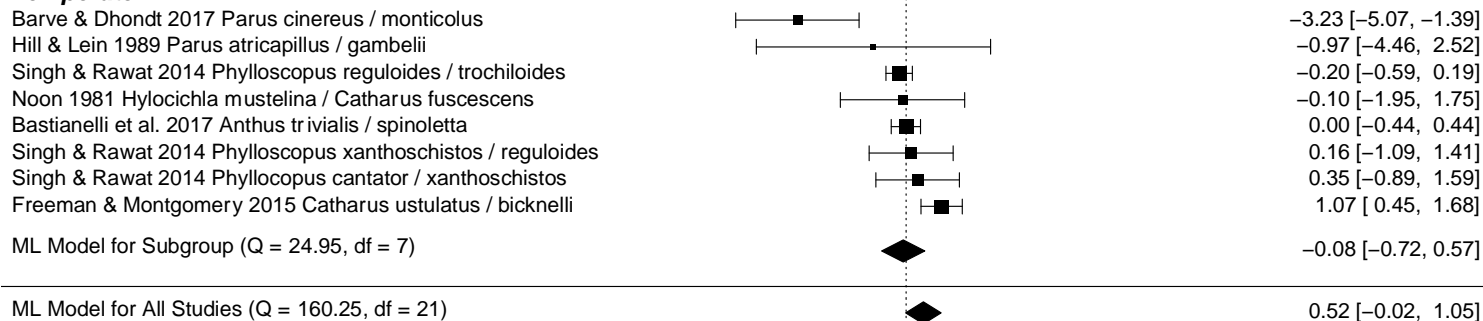Upper elevation species more aggressive   Lower elevation species more aggressive

Figure 3. Results of studies that used playback experiments to measure interspecific aggression (N = 22), broken down into tropical and temperate zone subgroups. Effect sizes are calculated as the difference in mean interspecific aggression (± SE) between lower and upper elevation species, with positive values indicating cases where the lower elevation species exhibits stronger interspecific aggression than does the upper elevation species. Studies are identified by their author(s), year, and the scientific names of the species-pair.

Table 1. Details for 10 studies that measured both interspecific aggression and interspecific competition between lower vs. upper elevation species. The methods used to infer aggression and competition are given as parentheticals. The key question is whether interspecific aggression indicates interspecific competition. If the more aggressive species is also the better competitor, correspondence = "Yes". Studies are arranged by year of publication.

Study	Taxa	Location	Aggression	Competition	Correspondence
Blaustein & Risser 1976	Jumping mice	Nevada, USA	Upper elevation species more aggressive (behavioral trials)	Upper elevation species excludes lower elevation species (time series data from Price et al. 2000)	Yes
Chappell 1978	Chipmunks	California, USA	Upper elevation species more aggressive (contests at feeders)	Upper elevation species excludes lower elevation species (removal experiment)	Yes
Nishikawa 1985	Salamanders	North Carolina, USA	Upper elevation species more aggressive (behavioral trials replicated in two mountain ranges)	Upper elevation species excludes lower elevation species (removal experiment data from Hairston 1980, replicated in two mountain ranges)	Yes
De Staso III & Rahel 1994	Trout	Wyoming, USA	Upper elevation species more aggressive in cold water, lower elevation species more aggressive in warm water (behavioral trials)	Upper elevation species better competitor in cold water, lower elevation species better competitor in warm water (feeding rates)	Yes, including reversal at different temperatures
Griffis & Jaeger 1998	Salamanders	Virginia, USA	Lower elevation species = Upper elevation species (behavioral trials)	Lower elevation species excludes upper elevation species (removal experiment)	No
Magoulick & Wilzbach 1998	Trout	Pennsylvania, USA	Upper elevation species more aggressive (behavioral trials)	Upper elevation species better competitor (relative growth rates)	Yes
Taniguchi & Nakano	Salmon	Hokkaido, Japan	Lower elevation species more aggressive	Lower elevation species better competitor (relative growth rates)	Yes

2000			(behavioral trials)		
Rodtka & Volpe 2007	Trout	Colorado, USA	Upper elevation species more aggressive (behavioral trials)	Upper elevation species better competitor (weight changes in experiments)	Yes
Pasch et al. 2013	Singing mice	Cartago, Costa Rica	Upper elevation species more aggressive (behavioral trials)	Upper elevation species excludes lower elevation species (removal experiment)	Yes
Drummond 2015	Salamanders	North Carolina, USA	Upper elevation species more aggressive (behavioral trials)	Upper elevation species excludes lower elevation species (thermal physiology and niche modeling data from Gifford & Kozak 2012)	Yes

Table 2. Patterns of body size, interspecific aggression, and elevational position for species-pairs from direct observation and playback studies. Relative size and relative interspecific aggression are coded as binary variables. Larger species tend to show more interspecific aggression than do smaller species (gray cells vs. white cells). In direct observation studies, but not playback studies (at least in the tropics), upper elevation species tend to be larger than lower elevation species (second column vs. first column). The numbers presented in this table sum to 35 (not 33) because two studies measured interspecific aggression using both direct observations and playback.

Direct observation studies

	Lower = bigger	Upper = bigger
Lower = more aggressive	5	2
Upper = more aggressive	3	11

Playback studies (tropical)

	Lower = bigger	Upper = bigger
Lower = more aggressive	6	3
Upper = more aggressive	0	2

Playback studies (temperate)

	Lower = bigger	Upper = bigger
Lower = more aggressive	1	1
Upper = more aggressive	0	1

208   Discussion

209   I found mixed support for the prediction arising from the Darwin-MacArthur hypothesis that

210   lower elevation species are more aggressive to their upper elevation relatives than vice versa.

211   While lower elevation species showed stronger interspecific aggression in playback studies

212   from the tropics, *upper* elevation species exhibited stronger interspecific aggression in studies

213   that directly observed aggression, across a range of latitudes. Playback experiments were

214   almost exclusively performed on forest-dwelling insectivorous birds, while direct observation

215   studies investigated a much broader swath of biological diversity. Hence, I interpret this

216   dataset as showing that insectivorous forest birds in the tropics show patterns consistent with

217   the Darwin-MacArthur hypothesis, while patterns for other taxa, including for birds that are

218   not tropical insectivores, are opposite to the prediction arising from the Darwin-MacArthur

219   hypothesis. These mixed results indicate that the Darwin-MacArthur hypothesis is not a

220   general explanation of aggressive interactions between related species along elevational

221   gradients.

222   I next examine three reasons why my results do not consistently agree with predictions

223   arising from the Darwin-MacArthur hypothesis, beginning with the possibility that my study

224   is inappropriately designed. The most obvious caveat to my approach is that I attempt to study

225   interspecific competition by analyzing patterns of interspecific aggression. That is, I assume

226   interspecific aggression indicates competitive ability. This assumption need not hold—e.g.,

227   the most aggressive person lifting weights in your neighborhood gym may not necessarily win

228   the local weightlifting competition. Nevertheless, this assumption does appear to be met in my

229   dataset, as the more aggressive species was the better competitor in 9 out of 10 cases where

230   researchers measured both variables ($p = 0.021$; Table 1). In addition, the subset of studies

231   that measured interspecific competition are perhaps the most appropriate raw material for

232   testing the Darwin-MacArthur hypothesis, but these "gold standard" studies fail to support

233   predictions arising from this hypothesis. Instead, the *upper* elevation species was

234   competitively superior to the lower elevation species in most cases where biologists measured

235   competition (7 out of 9, see Table 1; note that competitive dominance flipped with

236   temperature in one case).

237   Second, the evolution of larger body sizes at high elevations drivers could reverse

238   expectations for patterns of interspecific aggression between low and high elevation species.

239   That is, contra the Darwin-MacArthur hypothesis, we might expect *upper* elevation species to

240   show more aggression towards lowland species than vice versa when two conditions are

241   met— (1) larger species tend to win aggressive behavioral contests, and (2) species in colder

242   high elevations are larger. These conditions likely apply broadly. The pattern that larger

243   species tend to show more interspecific aggression than smaller species is strongly supported

244   (Martin & Ghalambor, 2014), and Bergmann's rule describes the well-known pattern that

245   species in colder environments are larger. Indeed, larger species in my dataset exhibited more

246   interspecific aggression in 73% of species-pairs ($p = 0.014$, see Table 2). In contrast, upper

247   elevation taxa were larger in only just over half—55%—of species-pairs in my dataset ($p =$

248   0.73, see Table 2). Intriguingly, there is a rough correspondence between whether species-

249   pairs show Bergmann's rule body size clines and whether they show patterns consistent with

250   predictions arising from the Darwin-MacArthur hypothesis. The only dataset that showed the

251   predicted pattern of stronger interspecific aggression from lower elevation species was for

252   tropical species-pairs (nearly all birds) from playback experiments, and there was no trend for

253   upper elevation species to be larger within this subset (see Table 2). This is consistent with

254 previous research showing that tropical birds do not generally follow Bergmann's rule

255 (Freeman, 2017). In contrast, upper elevation species did tend to be larger than lower

256 elevation species in taxa in the direct observation dataset (where upper elevation species

257 showed stronger interspecific aggression) and also for the small number of temperate zone

258 species (Table 2). Hence, one possibility is that the evolution of larger body sizes at higher,

259 colder elevations, at least in non-tropical birds, in conjunction with an advantage for larger

260 body size in interspecific interference competition, may explain why the Darwin-MacArthur

261 hypothesis does not generally apply to global patterns of interspecific aggression along

262 mountain slopes. Further research with larger sample sizes is necessary to test this possibility.

263   Third, the simple logic of the Darwin-MacArthur hypothesis may require further

264 refinement (see also Louthan *et al.*, 2015). Darwin's proposal was that harsh climates prevent

265 species from colonizing polar regions or high elevations, but that climate alone is unlikely to

266 prevent species from colonizing the tropics or low elevations (Darwin, 1859). Instead, Darwin

267 thought that tropical or low elevation species would have greater competitive ability relative

268 to related temperate zone or high elevation species. This greater competitive ability would

269 then prevent temperate zone/high elevation species from expanding at their warm range edge.

270 However, if this basic scenario holds, with species' warm range edges limited primarily by

271 competition (and not by abiotic harshness), then selection on individuals' competitive abilities

272 would be strong at their warm range edge. If so, we might actually expect the evolution of

273 increased competitive ability at species' *warm* range edges. One prediction of this idea might

274 be that shared range edges between lower vs. upper elevation species are located not where

275 the lower elevation species meets unfavorable climatic conditions, but instead where the

276 competitive balance tips between species adapted to different abiotic environments. In this

277   case we might expect flips in competitive abilities along the elevational gradient, with the

278   lower elevation species a better competitor at lower, warmer elevations, and the upper

279   elevation species a better competitor at upper, cooler elevations (condition-dependent

280   competition; see examples in Woodward, 1975; Taniguchi & Nakano, 2000; De Staso &

281   Rahel, 2004; Altshuler, 2006). In general, investigating how selection on competitive ability

282   varies across species' ranges is likely to offer fresh insights for when competition sets

283   species' range edges.

284

285   *Behavioral interactions and range shifts*

286   There have been widespread calls to incorporate species interactions when attempting to

287   understand or predict species' geographic responses to climate change (e.g., Araújo & Luoto,

288   2007; Alexander *et al.*, 2015). Behavioral interactions have the potential to be important for

289   range limits. Indeed, case studies show that interspecific aggression appears to promote recent

290   dramatic range expansions of native taxa (Duckworth & Badyaev, 2007; Wiens *et al.*, 2014).

291   Extended to climate-associated range shifts, the idea is that aggressive lower elevation species

292   could rapidly colonize elevations beyond their upper limit, "pushing" upper elevation

293   relatives upslope, or that aggressive upper elevation species could hold steady at their lower

294   limit as "kings of the mountain" despite warming. However, whether behavioral competition

295   influences range shifts associated with climate change remains an open question. Consistent

296   with a potential role for behavioral interactions in driving recent upslope shifts, I and

297   colleagues reported that three aggressive lower elevation species of tropical birds have

298   expanded their ranges upslope associated with recent warming while two non-aggressive

299   lower elevation species have failed to expand (Freeman *et al.*, 2016). But another empirical

300   example shows the reverse case—in the last century, a high elevation chipmunk (*Tamias*

301   *speciosus*) has dramatically shifted upslope in the Sierra Nevadas in California (Moritz *et al.*,

302   2008) despite being a better behavioral competitor than a related lower elevation chipmunk

303   (Heller, 1971). Clearly, many more studies are needed before we can confidently state that

304   behavioral interactions between lower vs. upper elevation species do (or do not) predict

305   species' distributional responses to recent climate change.

306

307   *Conclusions*

308   Probing the drivers of species' range edges—explaining why a species lives *here* but not

309   *there*—is a fundamental goal of ecology. More recently, this basic research has been reborn as

310   an applied question, as ecologists are tasked with predicting where species will live in a

311   warmer and climatically different future. The idea that general rules govern range limits is

312   alluring in both basic and applied contexts, and the proposal that species' warm range edges

313   are set by competition (here termed the Darwin-MacArthur hypothesis) is one such general

314   rule. In this paper I find mixed support for the prediction arising from this hypothesis that

315   lower elevation species are better competitors than their upper elevation relatives, at least for

316   behavioral competition. The "glass half empty" response to this finding would be to jettison

317   the Darwin-MacArthur hypothesis (conditioned on the relatively small sample size of this

318   study and the particular prediction being tested). However, an alternative "glass half full"

319   approach would be to add a wrinkle to the hypothesis—that lower elevation species may

320   indeed tend to be better behavioral competitors than their upper elevation relatives, but only

321   when they are similar in mass (i.e., when Bergmann's rule does not apply). Testing which of

322   these scenarios is better supported will require additional data. I was pleasantly surprised to

323   find as many studies measuring behavioral interactions between species-pairs along mountain

324   slopes as I did (57 estimates of interspecific aggression for 47 unique species-pairs from 34

325   studies), but more empirical data is needed to test whether Bergmann's rule modifies the

326   general expectation that competition sets warm range limits, or that behavioral interactions are

327   important in driving climate-associated range shifts, at least in the short term. My hope is that

328   this literature continues to expand, such that someone revisiting this topic in a decade's time

329   will be able to provide firm answers to these and related questions.

330

331   Acknowledgements

339

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