

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.

46

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.

167

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 ($\Delta \text{AIC} = 1.81$ 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 ($\Delta \text{AIC} = 1.66$). 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)

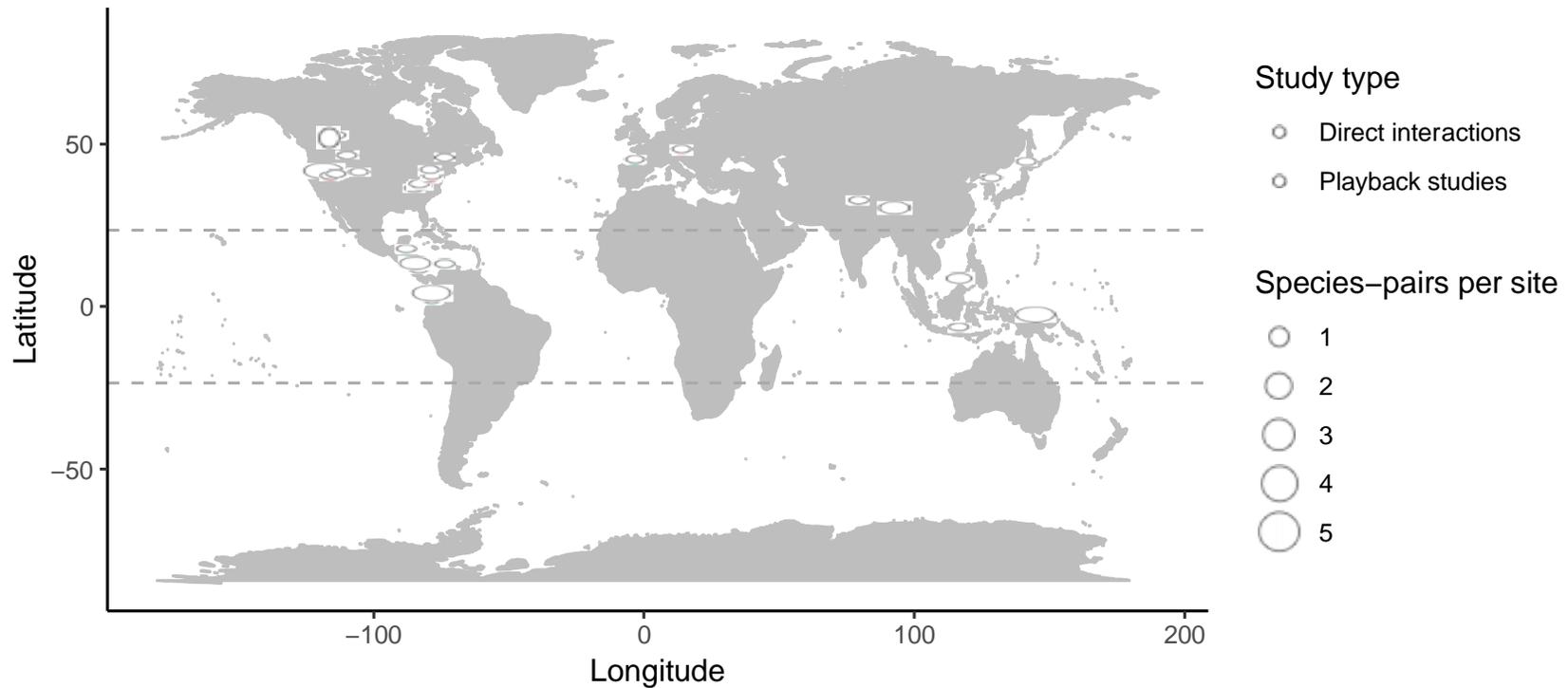
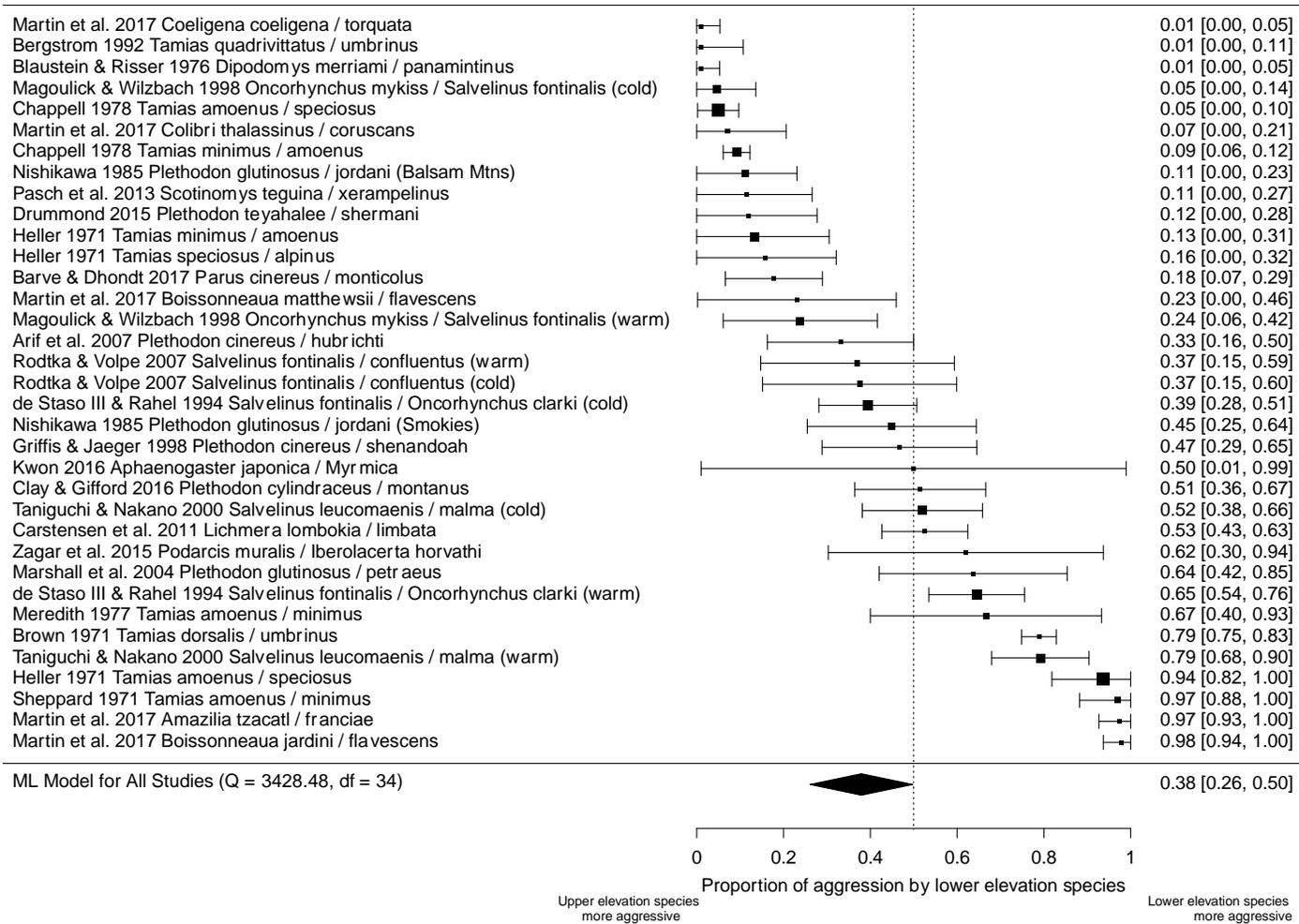


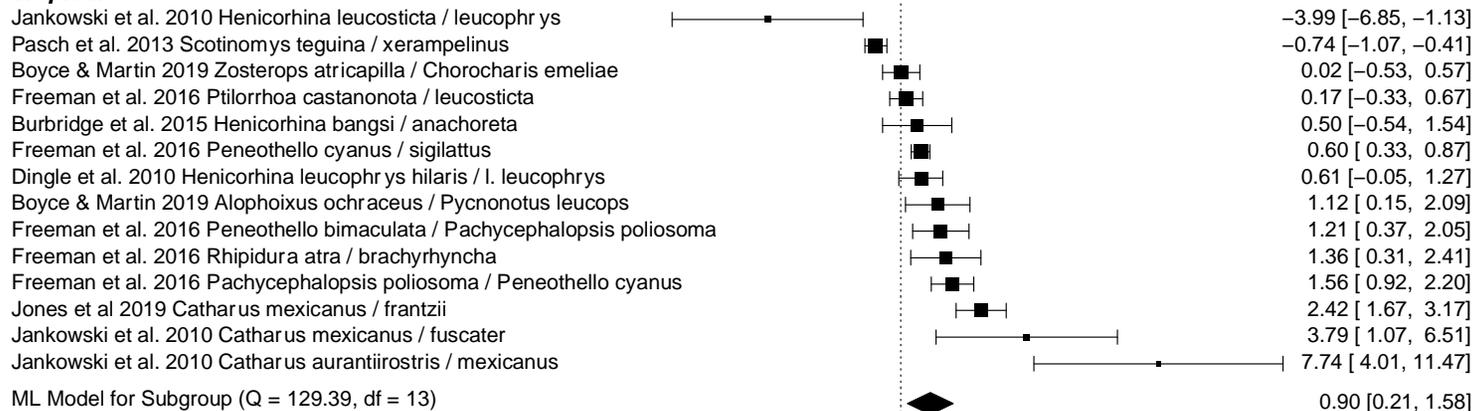
Figure 2. Results of studies that directly observed interspecific aggression (N = 36). The summary metric is the proportion of contests won, or aggressive behaviors exhibited, by the lower elevation species (\pm SE); this score would be 1 if the lower elevation species won all contests or exhibited 100% of all observed aggressive behaviors. Studies are identified by their author(s), year, and the scientific names of the species-pair.



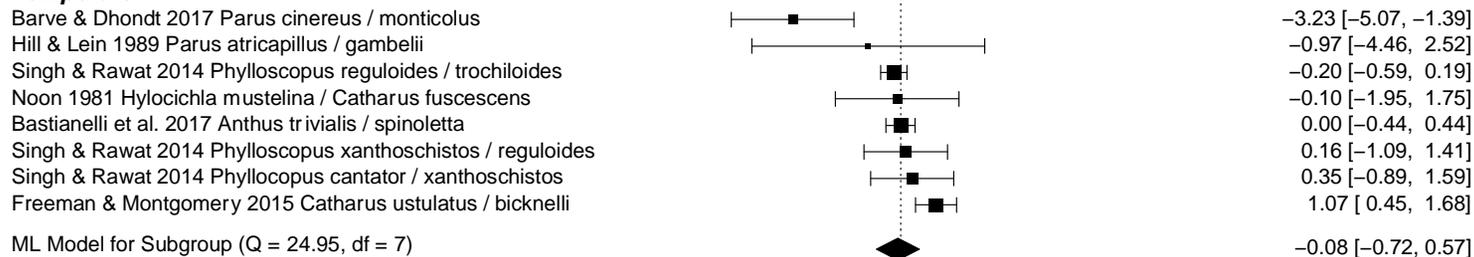
Upper elevation species more aggressive | Proportion of aggression by lower elevation species | Lower elevation species more aggressive

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 (\pm 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.

Tropical



Temperate



ML Model for All Studies (Q = 160.25, df = 21)

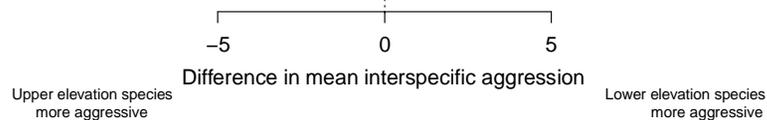


Table 1. Details for 10 studies that measured both interspecific aggression and interspecific competition between lower vs. upper elevation species. The methods used to infer aggression and competition are given as parentheticals. The key question is whether interspecific aggression indicates interspecific 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

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339

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