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Note

Phenotypic Selection Exerted by a Seed Predator Is Replicated in Space and Time and among Prey Species

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abstract: Although consistent phenotypic selection arising from biotic interactions is thought to be the primary cause of adaptive diversification, studies documenting such selection are relatively few. Here we analyze 12 episodes of phenotypic selection exerted by a predispersal seed predator, the red crossbill (*Loxia curvirostra* complex), on five species of pines (*Pinus*). We find that even though the intensity of selection for some traits increased with the strength of the interaction (i.e., proportion of seeds eaten), the relative strength of selection exerted by crossbills on cone and seed traits is replicated across space and time and among species. Such selection (1) can account for repeated patterns of conifer cone evolution and escalation in seed defenses with time and (2) suggests that variation in selection is less the result of variation intrinsic to pairwise biotic interactions than, for example, variation in relative densities of the interacting species, community context, and abiotic factors.

Keywords: biotic interactions, geographic variation, *Loxia curvirostra*, phenotypic selection, *Pinus*, temporal variation.

Introduction

Consistent directional and divergent selection should typify episodes of adaptive diversification (Rieseberg et al. 2002). Indeed, studies that have focused on traits underlying adaptive diversification often find evidence implicating replicated patterns of selection (Nosil and Crespi 2006; Reznick et al. 2008; Martin and Pfennig 2012). In three-spine sticklebacks (*Gasterosteus aculeatus*), for which selection arising from resource competition has contributed to their diversification in multiple lakes (Schluter 2000), divergent selection has been detected repeatedly among lakes (Bolnick and Lau 2008). Extensive surveys further indicate that directional selection appears to be "remarkably consistent" over time (Morrissey and Hadfield 2012), and fluctuations in selection are often insufficient to reduce the cumulative impact of directional selection (Kingsolver and Diamond 2011). Nevertheless, examples of fluctuating selection seem numerous (e.g., Hairston and Dillon 1990; Grant and Grant 2002; Siepielski et al. 2009; Bell 2010; Thompson 2013), and shifts in the form of the interaction from, for example, mutualisms to antagonisms provide further evidence of fluctuating selection within biotic interactions (Thompson 2013). Indeed, selection arising from biotic interactions has often been characterized as fluctuating (Ehrlén and Münzbergová 2009; Thompson 2013).

Additional studies examining the consistency of selection are warranted, especially arising from biotic interactions, because they are thought to be the principal drivers of geographic variation and patterns of species diversity (Thompson 2005, 2013; Schemske 2009). In particular, it is unclear to what extent variation in selection is the result of shifts in the direction of selection because of attributes intrinsic to the pairwise species interactions (i.e., their trait-fitness relationships) or because of changes in the abundances of individual populations altering the intensity of selection between pairs of species (Benkman 2013), shifts in the trait distributions of interacting species, and alterations in the species assemblage in which the interaction is embedded (Thompson 2013). Characterizing the effects of these various components will aid us in understanding the causes and prevalence of fluctuating selection. In addition, previous comparative studies examining the consistency of selection have focused on individual traits (Siepielski et al. 2009, 2013; Morrissey and Hadfield 2012), yet the convergence of form or suites of characters as found, for example, in pollination syndromes (Fenster et al. 2004; Rosas-Guerrero et al. 2014) and within ecomorphs of anoles (Losos 2009; Mahler et al. 2013) often must represent the outcome of repeated patterns of selection among suites of characters (e.g., Nosil and Crespi 2006; Fenster et al. 2015). Consequently, studies addressing whether the overall patterns of selection across traits are replicated are also needed.

Here we address whether the overall pattern of phenotypic selection exerted by a predispersal seed predator (red

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crossbill finches, *Loxia curvirostra* complex) on a suite of cone and seed traits of conifers is replicated in space and time, both within a given species of pine (*Pinus*) and between different pine species (fig. 1). Our previous studies show that although the overall selection experienced by pines varies depending on the occurrence and relative abundance of different seed consumers (e.g., Siepielski and Benkman 2004), the relative intensities of selection among different cone and seed traits are replicated in space and time for selection exerted by individual species, including crossbills (Benkman and Parchman 2013; Benkman et al. 2013), a moth (*Eucosma recissoriana*; Benkman et al. 2013), Clark's nutcrackers (*Nucifraga columbiana*), and American red squirrels (*Tamiasciurus hudsonicus*; Siepielski and Benkman 2007). Here we extend our earlier work to examine the patterns of selection exerted by crossbills on multiple species of pines. We find that the sets of selection gradients and selection differentials are consistent among studies and replicated in space and time and among species of pines, which presumably accounts for the repeated patterns of conifer and crossbill coevolution and the escalation of their arms race with time (Parchman et al. 2007; Benkman et al. 2010).

Methods

We used selection gradients and selection differentials estimated from data on predation by crossbills on the seeds of five species of pines (fig. 1) at eight sites over 12 time periods of study (table A1). Because we have described the data and their collection for a majority of these studies previously (references in table A1), we summarize the data and their collection (data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.c4018 [Benkman and Mezquida 2015]). For each study, we estimated the proportion of the seed crop eaten by crossbills by counting both the number of cones foraged on and the number of cones not foraged on by crossbills from either a subset of branches or the whole tree of between 45 and 120 trees. In all cases, the cones were closed, and sign of crossbill foraging (shredded scales) was obvious (fig. 1*E*). All or nearly all the seeds were eaten from each foraged-on cone for some species (*Pinus nigra*, *Pinus sylvestris*, and *Pinus uncinata*), whereas often only a portion of the seeds in a cone were eaten for other species (*Pinus contorta* and *Pinus ponderosa*). For the latter species, we estimated the proportion of seeds eaten and weighted the proportion of cones foraged on by the proportion of seeds per cone eaten to estimate the proportion of the tree's seed crop eaten. Absolute tree fitness relative to seed predation by crossbills was estimated as one minus the proportion of the seed crop consumed by crossbills. Relative fitness was estimated as tree fitness divided by the mean fitness of all trees in a given study. We collected two to five undamaged cones from each tree and measured the following traits of each cone to characterize these traits for each tree (Benkman et al. 2003): maximum length and width of the closed cone, cone mass without seeds, number of full (i.e., filled with female gametophyte) seeds, number of empty seeds, mass of five filled seeds without their wings, and thickness of five scales and length of three scales in the middle or distal part of the cone. Length measurements were made to the nearest 0.01 mm with digital calipers, and mass measurements were made on oven-dried (65°C for >36 h) cones and seeds to the nearest 0.01 mg with a digital scale. We calculated the ratio of seed mass to cone mass (a measure of the amount of energy devoted to reproduction relative to seed defense; Benkman 1999) as the total seed mass in grams (number of full seeds multiplied by individual seed mass) divided by cone mass in grams. Measurements were averaged for each tree, as individual trees are the unit of selection.

Selection gradients were estimated using linear multiple regression between relative fitness and cone and seed traits, standardized to a mean of 0 and a variance of 1 (Lande and Arnold 1983). To avoid multicollinearity, we examined correlation coefficients between traits and checked variance-inflation-factor scores from regression models. We removed two cone size variables (length and width) because of their high variance-inflation-factor scores (range of scores for cone length: 3.6–7.3; cone width: 3.2–12.1) and excluded seed mass/cone mass because it was a composite trait. Selection differentials were estimated using least squares linear regressions between relative fitness and each of the nine standardized cone and seed traits, following Lande and Arnold (1983).

We used several methods to evaluate the consistency of selection. First, we used the random-effect meta-analysis model of Morrissey and Hadfield (2012) to assess the consistency of the linear selection gradients and differentials. We examined only linear selection gradients and linear selection differentials because even in the relatively few occasions that we have detected nonlinear selection, selection was directional (e.g., Mezquida and Benkman 2010). The random factor in our models was the cone and seed traits, and our replicates were 12 sets of selection gradients or differentials for each cone and seed trait. Because selection intensity varies with the proportion of the seed crop eaten (Mezquida and Benkman 2014), we controlled for it in the analyses. We fitted the models in a Bayesian framework using the R package MCMCglmm (Hadfield 2010) with flat improper priors on both variances. This estimate of consistency measures the proportion of the total variance accounted for by among-trait variation and is analogous to repeatability (Morrissey and Hadfield 2012).

Second, we used sign tests to determine whether the selection exerted by crossbills was consistent in direction on each of the cone and seed traits across the 12 species/site/year estimates of selection. Shifts in the sign of selection

Figure 1: Photographs of cones from the five species of pines for which phenotypic selection exerted by crossbills was measured. *A*, *Pinus nigra*. *B*, *Pinus sylvestris*. *C*, *Pinus uncinata*. *D*, *Pinus contorta latifolia*. *E*, *Pinus ponderosa scopulorum*. *F*, Red crossbill (*Loxia curvirostra* complex) from the South Hills, Idaho. Seeds in two of the *P. p. scopulorum* cones (*E*) have been fed on by crossbills.

are expected for traits under weak selection simply from sampling error (Morrissey and Hadfield 2012); thus, we distinguish between traits under relatively weak and strong selection. If shifts in the sign of selection are limited mostly to traits under weak selection, the frequency of shifts in the sign of selection should be inversely related to the absolute value of selection on a trait (Kingsolver and Diamond 2011). We tested for such an inverse relationship by examining the correlation between the probability that the direction of selection differed between different estimates for the same trait (ranges from 0, where selection is uniform in direction among estimates, to 0.5, where half of the estimates are positive and half are negative) and the absolute value of the selection gradients (median $|\beta|$) and the selection differentials (median $|s|$). Because the probability that the direction of the selection differentials differs was 0 for six of the nine traits, we used Spearman's rank correlation to test for the inverse relationship for the selection differentials.

Third, we used regressions between each set of linear selection gradients and between each set of selection differentials to further test for consistency in the overall pattern of selection across traits both within and among the five pine species (see Benkman and Parchman 2013; Benkman et al. 2013). Correlation coefficients provide a measure of the consistency of the overall pattern of selection among suites of traits, where the larger the correlation, the more consistent the relative intensities of selection among the different traits. Figure 2*A*, 2*C* illustrates comparisons of the relationships between the selection exerted on two pine species. We tested each of the regressions between sets of selection differentials to determine whether they were significant; we corrected *P* values for multiple testing using Hommel's method, which is a powerful modification of the Bonferroni correction (Shaffer 1995). Because the residual distributions of these regressions were unknown, we used nonparametric bootstraps ($n = 1{,}000$) to calculate 95% confidence intervals for the regression coefficients to account for uncertainty in the estimates of the selection differentials (Benkman et al. 2013). For each bootstrap replicate, we resampled the original data, calculated the selection differentials for each trait in the resampled data sets (as above), and performed a linear regression on the bootstrap selection differentials. We also calculated *P* values on the hypothesis that the coefficient $b_i = 0$, using the method described in Davison and Hinkley (1997).

Results

All lines of evidence indicate that the pattern of selection exerted by crossbills on cone and seed traits was consistent both within and among the five species of pines. First, the consistency of the directional selection gradients was 0.692 (95% credible interval: 0.379–0.948) and of the selection differentials was 0.728 (95% credible interval: 0.515–0.918), using the random-effect model of Morrissey and Hadfield (2012) and controlling for the proportion of the seed crop eaten by crossbills. These results imply that variation in selection on a trait among species/sites/years was relatively less than variation in selection among traits.

Second, shifts in the sign of selection on traits were infrequent, except for those experiencing the weakest selection. Selection gradients were always or nearly always (11 of 12 cases) positive or negative for the three cone traits having the largest selection gradients (cone mass, scale thickness, and number of full seeds; sign tests, $P \leq .006$; median $|\beta| = 0.055$–0.157), whereas the direction of the selection gradients on the other traits fluctuated (scale length, number of empty seeds, and individual seed mass; sign tests, $P \geq .39$; median $|\beta| = 0.005$–0.022). As the absolute value of the selection gradients for the different cone and seed traits (median $|\beta|$) increased, the probability that the direction of selection (ln-transformed) differed between different estimates decreased ($r = -0.98$, $P = .0003$). An inverse relationship was also found between the absolute value of the selection differentials for the different cone and seed traits (median $|s|$) and the probability that the direction of selection differed between different estimates (Spearman $\rho = -0.82$, $P = .007$). Selection differentials were always positive for the six size-related cone, scale, and seed traits (72 of 72 cases; sign tests, $P = .0005$ for each trait; median $|s| = 0.100$–0.173); usually positive for the number of empty seeds (10 of 12 cases; sign tests, $P = .04$; median $|s| = 0.017$); and negative for the ratio of seed mass to cone mass (11 of 12 cases; sign tests, $P = .006$; median $|s| = 0.074$), and they oscillated around 0 for the number of full seeds (6 positive and 6 negative; sign tests, $P = 1.0$; median $|s| = 0.019$).

Third, all 11 pairwise within-species regressions for the sets of linear selection differentials for the nine cone and seed traits were significant ($P < .05$), and 53 of the 55 (96%) between-species regressions were significant ($P < .05$). The correlation coefficients for these regressions were consistently high (fig. 2*C*, 2*D*; median *r* values were 0.93 for within-species regressions and 0.87 for between-species regressions) and were on average larger than those for the selection gradients (fig. 2*A*, 2*B*; median *r* values were 0.70 for within-species regressions and 0.80 for between-species regressions), consistent with the higher estimate for the consistency of selection for the selection differentials (0.728) than for the selection gradients (0.692). Two sets of selection gradients (*Pinus nigra* [Greece] and *Pinus uncinata* in 2009; see table A1) were responsible for the 11 lowest correlation coefficients, and 18 of the 25 *r* values < 0.7 (fig. 2*B*). Thus, with the exception of two studies, the similarity in the selection gradients between different pairs of studies was high.

Although the relative intensity of selection among traits was consistent among most studies, there was considerable variation in the intensity of selection within certain traits

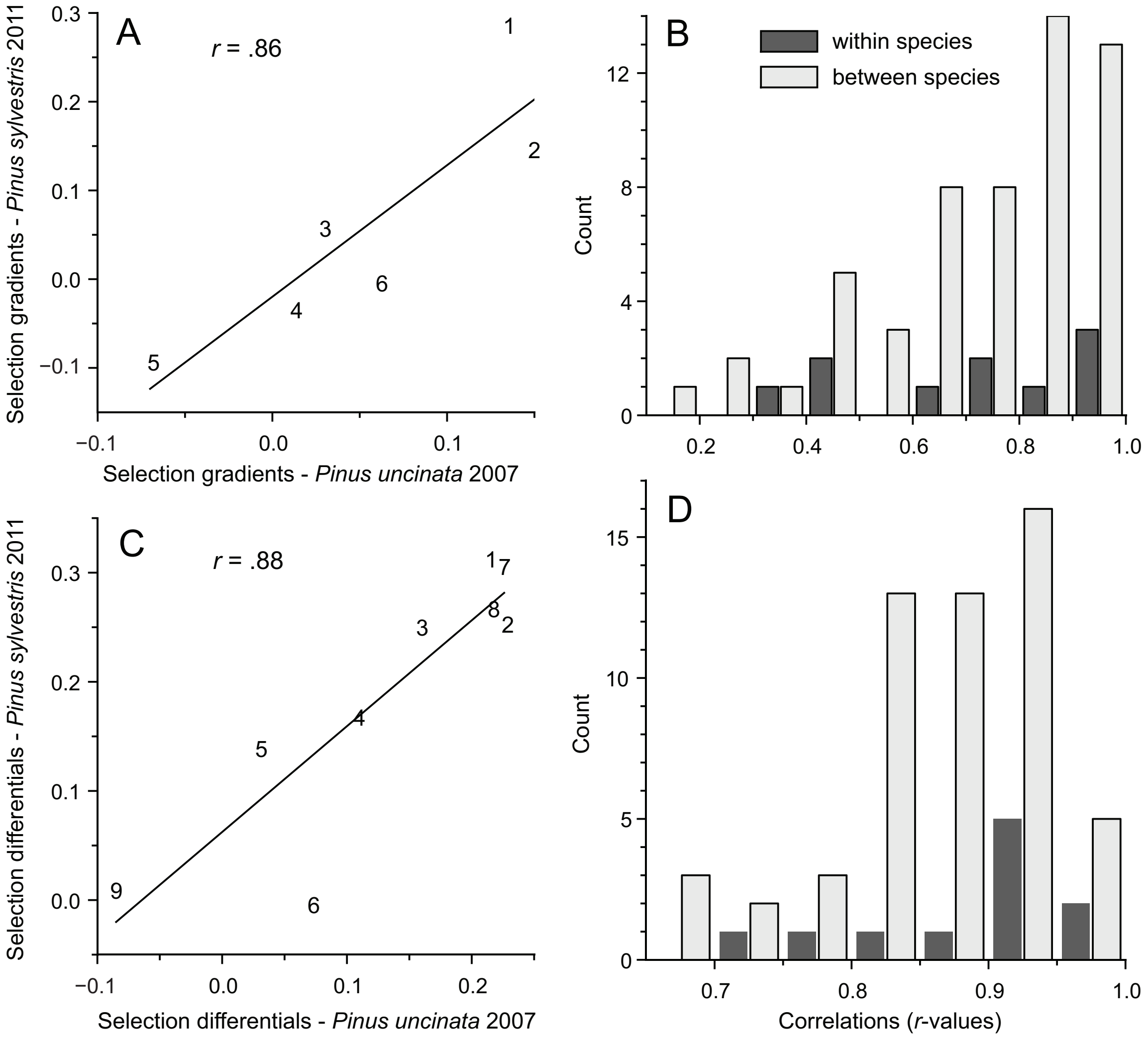

Figure 2: Examples of pairwise regressions between the selection gradients (*A*) and the selection differentials (*C*) for six and nine cone and seed traits, respectively, used to assess the consistency of selection exerted by crossbills on two species of pines (table A1). The lines are linear regressions, and the numbers signify the different cone traits: 1 = cone mass, 2 = scale thickness, 3 = scale length, 4 = individual seed mass, 5 = number of full seeds, 6 = number of empty seeds, 7 = cone length, 8 = cone width, 9 = seed mass/cone mass. Histograms of the correlation coefficients for the regressions between sets of selection gradients (*B*) and sets of selection differentials (*D*) using intervals of 0.1 and 0.05, respectively.

that was related to the proportion of the seeds eaten (fig. 3). The selection gradients increased significantly with increasing seed predation for cone mass ($P = .005$) and scale thickness ($P = .005$), the only traits that were the target or targets of selection (significant selection gradients [$P < .05$] in 11 of 12 multiple regressions). Such an increase in selection gradients also occurred for scale length ($P = .048$) but not for the number of empty ($P = .94$) and full ($P = .22$) seeds and seed mass ($P = .40$; fig. 3*A*). All the selection differentials increased significantly with increasing seed predation ($P < .05$), except the number of empty seeds ($P = .85$; fig. 2*B*) and seed mass/cone mass ($P = .50$; not shown). Presumably, most of these increases in selection differentials occurred because all but the number of empty seeds were usually phenotypically correlated with one or both of the two traits under direct selection (cone mass and scale thickness) and thereby experienced correlated (indirect) selection. The selection gradients for cone mass and scale thickness ranged mostly between 0.2 and 0.4 of the maximal values for selection (i.e., truncation selection; Benkman 2013), except at the lowest levels of seed predation (fig. A1).

Discussion

Our analyses indicate that the pattern of selection exerted by crossbills on pines was usually replicated from location

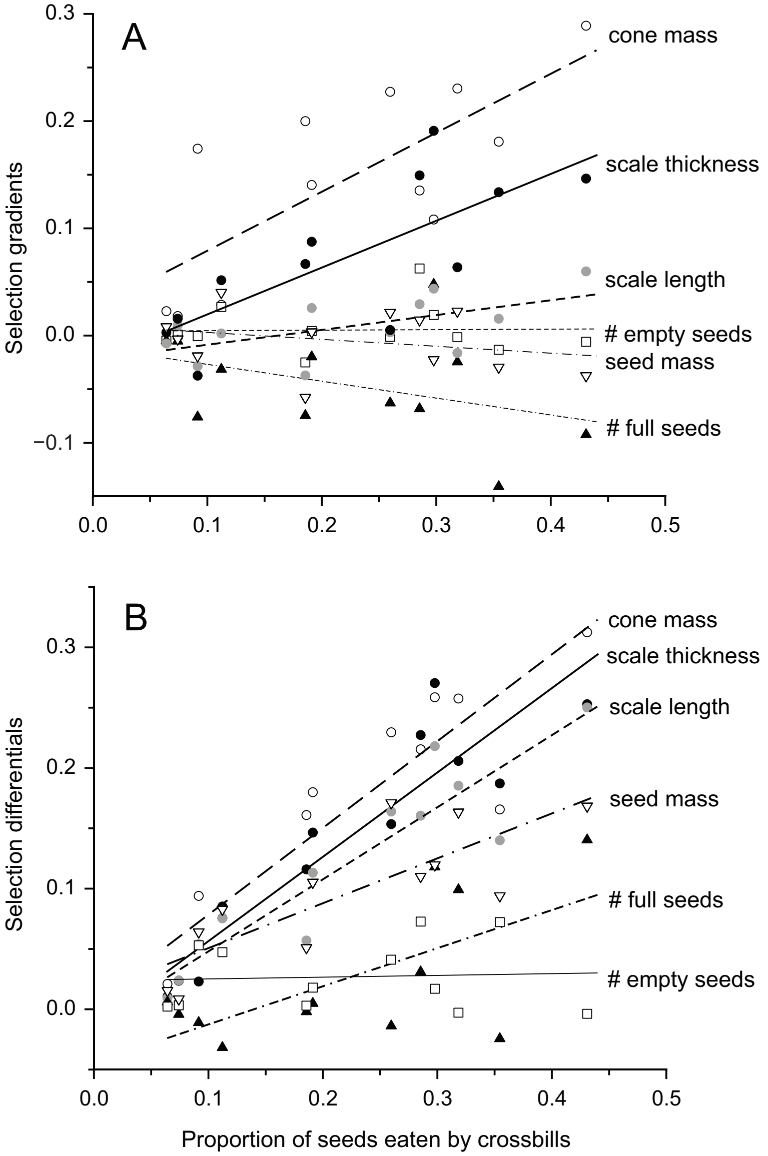

Figure 3: Selection gradients (*A*) and selection differentials (*B*) in relation to the proportion of seeds eaten by crossbills. The symbols and best-fit lines for each cone and seed trait are the same in each panel, with the names of the traits located along the right margin by the corresponding regression lines (and near their corresponding data symbols in *A*). Only the six traits used to estimate the selection gradients are shown. The solid lines represent regressions that are significant ($P < .05$).

to location, year to year, and species to species. Moreover, because the selection differentials measured in the wild were similar to those measured experimentally in aviaries for crossbills foraging on two species of pines in this study (*Pinus ponderosa* [Parchman and Benkman 2008] and *Pinus nigra* [Benkman and Parchman 2009]), our estimates of selection were unlikely to have been biased by local environmental conditions that influence both fitness (the probability that seeds are not eaten) and the phenotype of the cones and seeds (Rausher 1992). Such consistency of selection by crossbills is expected. Crossbills forage in a stereotypic manner to reach the seeds secured between the overlapping woody scales of conifer cones (Newton 1972; Benkman 1987), which results in the same cone features acting to deter crossbills (especially cone mass and scale thickness; Mezquida and Benkman 2014).

Even though the overall form of selection in terms of the relative strengths of selection among traits was generally consistent among species/sites/years, the intensity of selection on certain traits varied. In particular, traits experiencing the strongest average selection also experienced the greatest variation in selection (selection gradient SD =

$0.026 + 0.464$ [selection gradient mean], $r^2 = 0.95$, $df = 4$, $P = .001$). Such a relationship has been found previously (Kingsolver et al. 2012; Morrissey and Hadfield 2012). What causes the variation in selection on the traits experiencing the strongest selection, however, remains an important question. For antagonistic interactions such as seed predation, the intensity of selection is predicted to increase with increasing strength of the interaction (fig. A1) because of a concomitant increase in the opportunity for selection (Benkman 2013). We found that selection on cone mass and scale thickness, which are logically and empirically the targets of selection (Benkman et al. 2010; Mezquida and Benkman 2014), increased in a manner implying that selection approximated 0.3 of the maximum possible selection for a given interaction strength (fig. A1). Interestingly, analyses of phenotypic selection in other systems (e.g., parasites and predators of a gall-forming insect, *Eurosta*) found a similar pattern of selection approximating 0.3 of the maximum across a wide range of interaction strengths (Benkman 2013). If future studies find similar results, the basis of this will be worth considering.

Shifts in the direction of selection occurred for traits only under the weakest selection (median $|\beta|$ and $|s|$ near 0), as found in extensive surveys by Kingsolver et al. (2012) and Morrissey and Hadfield (2012). These shifts in the direction of selection are in part the result of sampling error and have little evolutionary significance. The extent to which variation in selection among traits in other systems can be partitioned into traits that experience weak (if any) selection that varies minimally and traits that are the target(s) of selection and whose selection intensity varies with interaction strength or some other variable of biological significance remains largely unknown (but see Campbell and Powers 2015).

Variation in the intensity of selection was expected because most conifer cone crops vary in size from year to year, as do crossbill population sizes, causing the relative densities of consumer to prey and thus the levels of seed predation to vary (Summers 2011). Further contributing to measured variation in selection is the time of year when we measured selection. Crossbills usually begin foraging on a given year's seed crop in late summer, with the amount of seed predation increasing over time until the cones open and seeds are released. Because we sampled cones during different months depending on the study, the variation in the intensity of selection among species/sites/years in our comparisons does not necessarily have evolutionary consequences. Furthermore, we note that we are measuring only a component of fitness and not the probability of seeds recruiting, let alone lifetime reproductive success. If we had been able to use seed recruitment as our measure of fitness and isolate selection by crossbills, we would have probably detected weaker selection and perhaps less consistency in selection among cone and seed traits, because crossbill foraging preferences may shift as cone scales spread apart and large cone size and thick cone scales become less of an impediment to foraging crossbills (Benkman 1987; Summers et al. 2010). Nonetheless, given the overall consistency of selection and replicated patterns of cone evolution consistent with our measures of selection (Benkman et al. 2010), we believe that our measures represent well the form of selection often exerted by crossbills on pines and most likely on other species of conifers (see Parchman and Benkman 2002).

Given the high heritabilities of cone traits (Singh and Chaudhary 1993; Matziris 1998), selection by crossbills has the potential to lead to substantial and consistent evolutionary change within and among species of conifers, with escalating arms races between crossbills and pines the norm (Benkman et al. 2010). Because the traits experiencing selection are size related, many loci likely contribute to (polygenic) variation, and because the pine populations are vast, large numbers of mutations are likely to replenish this variation, and therefore the additive genetic variation underlying these traits is unlikely to be depleted from reoccurring selection (Barton and Keightley 2002). However, increasing seed defenses directed at crossbills pertain to increases in the allocation of resources to cones (structural defenses) at the expense of seeds. Consequently, conifers will increasingly experience counterselection because of allocation tradeoffs (Benkman 1999). This will limit the rate of cone evolution in response to selection exerted by seed predators. Nevertheless, with increasing time, the escalation in the defenses of pines and the offenses of crossbills have increased as expected for an ongoing coevolutionary arms race (Parchman et al. 2007; Benkman et al. 2010).

In conclusion, determining whether selection is repeated is important, not only to help resolve the extent to which selection is consistent in form for a given set of pairwise biotic interactions (e.g., Nosil and Crespi 2006; Bolnick and Lau 2008; Martin and Pfennig 2012) but also to understand why and how variation in selection arises from biotic interactions. Selection from a given pairwise interaction could be consistent in direction, but the occurrence and abundance of other interacting species might vary, causing the direction and form of overall selection to shift (e.g., Weis et al. 1992; Benkman 1999; Thompson 2005; Strauss and Whittall 2006; Craig et al. 2007; Siepielski and Benkman 2007; Gómez et al. 2009; Campbell and Powers 2015). Alternatively, the form and direction of selection one species exerts on another vary depending on other features of the environment (Muola et al. 2010; Thompson 2013). For example, selection exerted on flowering phenology by a seed predator may vary from year to year because of variation in abiotic factors unrelated to flowering phenology, influencing the activity of ovipositing beetles (Ehrlén and Münzbergová 2009). In other systems, selection is consistent year after year because abiotic and other biotic factors do not alter the predator-prey interaction, and, unlike in the example of flowering phenology, the traits are clearly evolving in response to selection from the interaction (e.g., Mezquida and Benkman 2014). Distinguishing between alternative causes of variation in the form and direction of selection and assessing the situations in which each is more likely are critical for furthering our understanding of how geographic selection mosaics arise (Thompson 2005) and the mechanisms contributing most to stasis and adaptive diversification (Eldredge et al. 2005; Futuyma 2010; Uyeda et al. 2011; Thompson 2013). Based on our findings for crossbills and pines, we suspect selection arising from pairs of interacting species is often consistent across suites of characters.

Acknowledgments

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APPENDIX

Supplementary Figure and Table

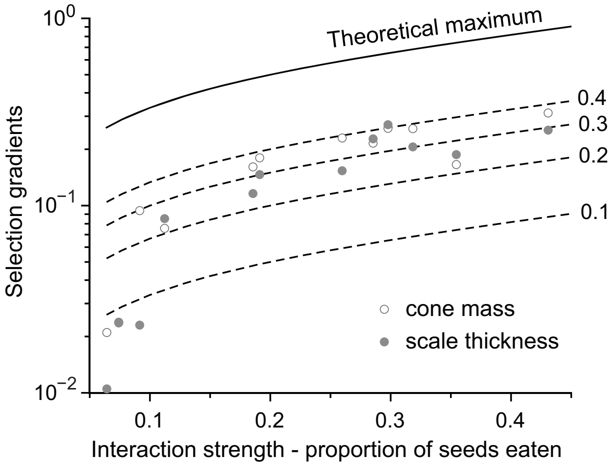

Figure A1: Relationships between selection gradients and proportion of seeds eaten (antagonistic interaction strength), showing the theoretical maximum (i.e., truncation selection; Benkman 2013) and dashed contours representing 0.4, 0.3, 0.2, and 0.1 of the maximum. Circles represent values for cone mass and scale thickness, which are the two traits logically and empirically the targets of selection (e.g., Mezquida and Benkman 2014). Note that the selection-gradient axis is on a $\log_{10}$ scale.

Table A1: Phenotypic selection data sets used in the analyses, including pine species, general location, year(s) when cone samples were collected and seed predation was estimated, sample sizes, and references for the data

Pine species	Location	Year(s)	Sample size (no. trees)	References
Pinus contorta	Little Rocky Mountains, Montana	2000	120	Benkman et al. 2003
P. contorta	South Hills, Idaho	2007–2008	87	Benkman et al. 2013
Pinus nigra	Pindos, Greece	2008	78	Benkman and Parchman 2013
P. nigra	Troodos Mountains, Cyprus	2006 and 2008	65 and 96	Benkman and Parchman 2009, 2013
Pinus ponderosa	Black Hills, South Dakota	2003	45	Parchman and Benkman 2008
Pinus sylvestris	Iberian System, Spain	2010–2011 and 2011–2012	70 and 70	E. T. Mezquida, unpublished data
Pinus uncinata	Western Pyrenees, Spain	2007	65	Mezquida and Benkman 2010
P. uncinata	Eastern Pyrenees, Spain	2008, 2009, and 2011	97, 100, and 70	Mezquida and Benkman 2014; E. T. Mezquida, unpublished data

Note: Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.c4018 (Benkman and Mezquida 2015).

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