











The ecology and evolution of seed predation by Darwin's finches on *Tribulus cistoides* on the Galápagos Islands

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Abstract. Predator–prey interactions play a key role in the evolution of species traits through antagonistic coevolutionary arms races. The evolution of beak morphology in the Darwin's finches in response to competition for seed resources is a classic example of evolution by natural selection. The seeds of *Tribulus cistoides* are an important food source for the largest ground finch species (*Geospiza fortis*, *G. magnirostris*, and *G. conirostris*) in dry months, and the hard spiny morphology of the fruits is a potent agent of selection that drives contemporary evolutionary change in finch beak morphology. Although the effects of these interactions on finches are well known, how seed predation affects the ecology and evolution of the plants is poorly understood. Here we examine whether seed predation by Darwin's finches affects the ecology and evolution of *T. cistoides*. We ask whether the intensity of seed predation and the strength of natural selection by finches on fruit defense traits vary among populations, islands, years, or with varying finch community composition (i.e., the presence/absence of the largest beaked species, which feed on *T. cistoides* most easily). We then further test whether *T. cistoides* fruit defenses have diverged among islands in response to spatial variation in finch communities. We addressed these questions by examining seed predation by finches in 30 populations of *T. cistoides* over 3 yr. Our study reveals three key results. First, Darwin's finches strongly influence *T. cistoides* seed survival, whereby seed predation varies with differences in finch community composition among islands and in response to interannual fluctuations in precipitation. Second, finches impose phenotypic selection on *T. cistoides* fruit morphology, whereby smaller and harder fruits with longer or more spines exhibited higher seed survival. Variation in finch community composition and precipitation also explains variation in phenotypic selection on fruit defense traits. Third, variation in the number of spines on fruits among islands is consistent with divergent phenotypic selection imposed by variation in finch community composition among islands. These results suggest that Darwin's finches and *T. cistoides* are experiencing an ongoing coevolutionary arms race, and that the strength of this coevolution varies in space and time.

Key words: adaptive divergence; coevolutionary arms race; geographic mosaic; phenotypic selection; plant defense; trophic interactions.

INTRODUCTION

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Antagonistic interactions play a major role in the evolutionary diversification of traits that mediate species interactions (Thompson 1999, Vamossi 2005, Paterson

et al. 2010). Plant–herbivore interactions have long been used as a model to understand the evolution and ecology of antagonistic interactions (Ehrlich and Raven 1964, Fritz and Simms 1992, Agrawal 2011). Plants employ a wide diversity of mechanical and chemical defense strategies to avoid the negative effects of herbivores, including seed predators (Crawley 1983, Carmona et al. 2011). In turn, herbivores and predators use a variety of strategies to counteract plant defenses, including behavioral, morphological, and physiological offensive traits (Karban and Agrawal 2002). Selection that favors traits that better protect plants against herbivores and predators can lead to contemporary evolutionary changes in plant defense traits (Agrawal et al. 2012, Züst et al. 2012, Didiano et al. 2014). Here, we study the effect of seed predation by Darwin’s finches on plant ecology, and its potential role in the evolution of seed defense traits by natural selection.

The interaction between Darwin’s finches and their food plants on the Galápagos Islands is a famous and well-studied example of contemporary evolution (Grant and Grant 2014). Previous studies in a group of Darwin’s finches known as ground finches show that evolutionary changes in beak size and shape are driven by the availability and distribution of seeds (Lack 1947, Grant 1986, Grant and Grant 1995). Ground finches are primarily seed predators and poor seed dispersers; they usually crush the seeds before ingesting them, and their feces and gut samples rarely contain viable seeds (Buddenhagen and Jewell 2006, Guerrero and Tye 2009). In general, ground finches are opportunistic feeders that eat a large variety of seed species, but when resources are limited following droughts, finches become dependent on the seeds of a smaller number of plant species that are often harder and more difficult to open (Grant and Grant 1995, De León et al. 2014). The ability to exploit those seeds is largely influenced by beak size and shape (Lack 1947, Grant and Grant 1995, De León et al. 2011). Because seeds are a major part of their diet, and because ground finches exhibit preferences for certain seeds, it is anticipated that finches have an important effect on the ecology and evolution of plants on the Galápagos Islands. However, despite the well-developed literature on the interactions between Darwin’s finches and plants (Boag and Grant 1981, Schluter and Grant 1984, Price 1987, Grant and Grant 1999, De León et al. 2014), the ecological and evolutionary consequences of seed predation by finches on plants remains largely unexplored.

The effects of seed predation by finches on plants on the Galápagos Islands are expected to be mediated by both climate and the strength of species interactions. Predation pressure by finches on seeds during periods with high precipitation might be negligible owing to the high production of seeds, and the increased availability of other food resources such as insects (Grant and Boag 1980, Boag and Grant 1984, Price 1985, Gibbs and Grant 1987). However, during extended droughts, when seed production is reduced, selective seed predation by finches (Grant 1986, De León et al. 2014, Grant and Grant 2014) could greatly influence seed survival, plant

distributions, and the evolution of seed defense traits. Selection imposed by finches on seed defense traits is expected to play the most important role for plant species that are commonly exploited by finches. Caltrop (*Tribulus cistoides*) is one of the main food sources for some species of ground finches during dry periods, and it is credited with driving the evolution of beak morphology in the Medium Ground Finch (*Geospiza fortis*) during periods of drought (Grant and Grant 2006, 2014). The fruits of *T. cistoides* possess morphological features thought to provide defenses against predation, including multiple long spines and a hard protective tissue (Grant 1981; Fig. 1). Grant (1981) showed that, within a *T. cistoides* population on Daphne Major island, fruits with two spines were eaten more frequently than fruits with four spines, suggesting that finches impose selection on *T. cistoides* fruit morphology. However, selection on *T. cistoides* fruits has not been assessed across years or in populations on other islands, and the association between fruit morphology and seed survival in response to finch predation across the archipelago remains unclear.

An additional factor that might influence the effects of seed predation by finches on plants on the Galápagos Islands is variation in the composition of finch communities. Ground finches are broadly distributed within the archipelago and most of the islands harbor several species that differ in beak size and shape. Among ground finches, only the Large Ground Finch (*G. magnirostris*), the Large Cactus Finch (*G. conirostris*), and the Medium Ground Finch (*G. fortis*) are able to exploit *T. cistoides* seeds (Grant 1981, Grant and Grant 1982). These species, however, are not uniformly distributed across the islands. The contemporary faunas of some major islands have one of the large-beaked *G. magnirostris* and *G. conirostris* species and the small-beaked *G. fortis*, such as Santa Cruz and Isabela (Fig. 2), whereas others lack the large-beaked species, such as Floreana and San Cristóbal. This spatial variation in the finch community could have large ecological and evolutionary consequences because *G. magnirostris* are superior at feeding on *T. cistoides* seeds relative to *G. fortis* (Grant 1981), which could lead to divergent patterns of predation and selection imposed on fruit morphology across the Galápagos Islands.

Our study focuses on understanding the effects of seed predation by Darwin’s finches on the ecology and evolution of *T. cistoides*. We asked the following three questions: (1) Does seed predation by finches vary among populations, islands, finch community composition, and years? We expected seed predation to vary among years; due to variation in annual precipitation, and also in association with finch community composition (small-beaked finches are expected to eat fewer seeds of *T. cistoides* during wetter conditions). (2) Do finches impose selection on *T. cistoides* fruit morphology, and does selection vary among populations, islands, years, and with finch community composition? We expected the strength of selection on fruit morphology to vary over time in correspondence with precipitation, and spatially among



FIG. 1. (a) *Tribulus cistoides* fruits (schizocarps), from left to right: a green immature fruit, a mature dry fruit, and a fruit attached to a maternal plant. (b) Two sets of dry mericarps, corresponding to two fruits of different plants, showing variation in size and number of spines. Mericarps in the upper set are larger and have four spines while mericarps in the lower set are smaller and have only two spines. (c) Opened mericarp to expose seed compartments, one empty compartment and three compartments with seeds inside. (d) *Geospiza fortis* (Medium Ground Finch) holding a *T. cistoides* mericarp. Mericarps showing marks observed (e) when seeds are eaten by finches, (f) when seeds are eaten by insects, and (g) when seeds germinate. Photo credits: Marc T. J. Johnson (a [left and middle], c, and f), Andrew P. Hendry (b), Kiyoko M. Gotanda (d and e), and Sofía Carvajal-Endara (a [right] and g).

islands in association with finch community composition: large-beaked finch species eat seeds more readily and likely impose differing selection on fruit morphology compared to communities with only small-beaked

finches. (3) Does *T. cistoides* fruit morphology differ among islands with contrasting finch community composition (i.e., the presence/absence of large-beaked finches)? We expected spatial variation in fruit morphology to

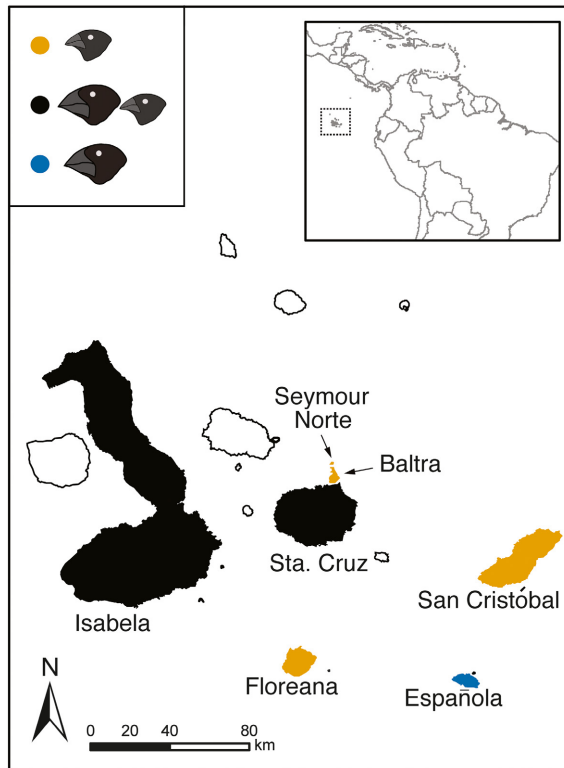


FIG. 2. Map showing the seven islands of the Galápagos archipelago where *Tribulus cistoides* fruits were sampled. Black and blue identify the islands where large-beaked finches are present: the Large Ground Finch (*Geospiza magnirostris*) is present on Isabela and Santa Cruz and the Large Cactus Finch (*G. conirostris*) is found on Española. Orange identifies the islands where these large-beaked finches are absent. The Medium Ground Finch (*G. fortis*) is present in all visited islands except in Española.

reflect spatial variation in finch community composition, which would be consistent with adaptive responses to divergent selective pressure. To address these questions, we examined variation in *T. cistoides* fruit morphology and patterns of seed predation in 30 natural populations across seven islands of the Galápagos archipelago over 3 yr, and performed a seed predation experiment in a population on one of the islands. Our study is one of the first to address the potential effect of seed predation by Darwin's finches on the evolution of Galápagos plants. We consider the importance of these results for understanding the potential coevolutionary interactions between Darwin's finches and the plants whose seeds they consume.

METHODS

Study site and system

The Galápagos archipelago is located in the Pacific Ocean approximately 1,000 km west of the Ecuadorian coast in South America, and it comprises 14 major

islands and many small islets (Geist 1996). We restricted our study to seven islands that vary in finch community composition (Fig. 2), and that harbor at least one of the three finch species that consume *T. cistoides* seeds: *G. fortis*, *G. conirostris*, and *G. magnirostris*. The diet of these three finch species varies according to the size and shape of their beaks, as well as the spatial and temporal availability of seeds (Schluter and Grant 1984; Grant and Grant 1999, De León et al. 2014). During dry periods, especially the droughts that accompany La Niña events, preferred foods are limited and, hence, *T. cistoides* seeds become a main food source for these finch species (Grant and Grant 2014).

Tribulus cistoides (Zygophyllaceae) is a perennial prostrate herb native to subtropical and tropical Africa and now is widespread in tropical and subtropical arid coastal habitats around the world (Porter 1972). Broadly distributed across the Galápagos archipelago, it is usually found in arid lowlands and coastal regions, where it grows in discrete patches close to roads, trails, and shorelines (Porter 1971). *Tribulus cistoides* plants can flower at any time of year on the Galápagos Islands, but most of its vegetative growth occurs during the wet season (from January to May), they produce fruits called schizocarps (Fig. 1a), which contain five individual segments referred to as mericarps that typically separate from one another as the fruit dries (Fig. 1b) (Wiggins and Porter 1971). Each *T. cistoides* mericarp is a hard fibrous structure that includes from one to seven seeds contained within individual compartments (Fig. 1c). Mericarps typically have four spines (two upper and two lower sharp protuberances), but the size and position of spines varies greatly among individual plants, and some mericarps completely lack some or all spines (Fig. 1b). The spiny mericarps are also a means of seed dispersal (Porter 1972); fruits adhere easily to animals, such as the feet of seabirds (Wiggins and Porter 1971). Ocean currents and humans are considered important vectors of long-distance dispersal, whereby fruits travel long distances by getting attached to shoes and rubber tires (Holm et al. 1977).

To extract the seeds, finches pick up mericarps from the ground after they have dropped from the plant. The finches often hold the mericarp laterally between their mandibles, and apply pressure by closing their beak, moving the upper and lower mandibles sideways to each other, to crack the mericarp wall, sometimes stabilizing the mericarp against a rock or the ground (Fig. 1d, see Video S1). The mericarps are very durable and long lived and this, combined with the very distinct damage left by finch predation, makes it possible to determine which mericarps have been depredated even months after a predation event. Specifically, finches remove the ventral surface of the hard mericarp tissue protecting the seeds, exposing the empty seed compartments from which seeds are removed (Fig. 1c), often one compartment at a time (Video S1) (Grant 1981). Mericarps depredated by finches (Fig. 1e) are easily distinguished from mericarps

consumed by insects, which make smaller circular “drill” holes (Fig. 1f), and from mericarps from which seeds have germinated, which are apparent as empty seed compartments are still partially enclosed by the mericarp wall (Fig. 1g), without the rough damage characteristic of seed predation by finches (Fig. 1e). Other than finches and insects, no other common predators of *T. cistoides* seeds are found on the Galápagos Islands. Unopened mericarps of *T. cistoides* were found in the gizzard contents of a Galápagos dove (*Zenaida galapagoensis*); however, *T. cistoides* fruits are not a typical part of the diet of this species (Grant and Grant 1979).

Population sampling and experimental design

To explore impacts of seed predation by finches, we sampled nearly 7,000 mericarps from 30 *T. cistoides* populations across seven islands of the archipelago over 3 yr (2015–2017). Considering only ground finch species that consume *T. cistoides* seeds, finch seed-predator communities on three of the selected islands (Santa Cruz, Isabela, and Española) include large-beaked finch species (*G. magnirostris* or *G. conirostris*), whereas finch communities on the other four islands (San Cristóbal, Floreana, Baltra, and Seymour Norte) lack large-beaked finch species (Fig. 2). The medium-beaked species, *G. fortis*, is present on all sampled islands except Española (Fig. 2). Sampling was performed between the months of February and March, corresponding to the end of the dry season and beginning of the wet season (Fig. 3a), which is when the finches' preferred food is expected to be most scarce and their consumption of *T. cistoides* seeds becomes highest. On four of the islands (Santa Cruz, Isabela, San Cristóbal, and Floreana), we repeated sampling annually from 2015 to 2017. During this period, the archipelago experienced strong climatic variation, including an El Niño event that occurred in 2015 (Stramma et al. 2016) and resulted in higher precipitation relative to the preceding and subsequent years (Fig. 3b).

The number of *T. cistoides* populations sampled varied among islands (one to eight populations) due to spatial variation in the abundance of plants, with a “population” considered to be a discrete patch of *T. cistoides* plants separated by at least 500 m from any other patch. Information about the populations sampled each year (island, geographic coordinates) is provided in Appendix S1: Table S1. From each population, we collected approximately 100 mericarps chosen haphazardly across the area; we made every effort to select mericarps “blindly” to avoid biases, so that mericarps represented a random subset of the morphological traits present in the population as much as possible. Most mericarps are expected to be from the previous season, but it is possible that some mericarps were >1 yr old. A total of 6,391 mericarps were collected across all islands, populations, and years. For each mericarp, we used digital calipers to measure mericarp length (mm), width (mm), and the

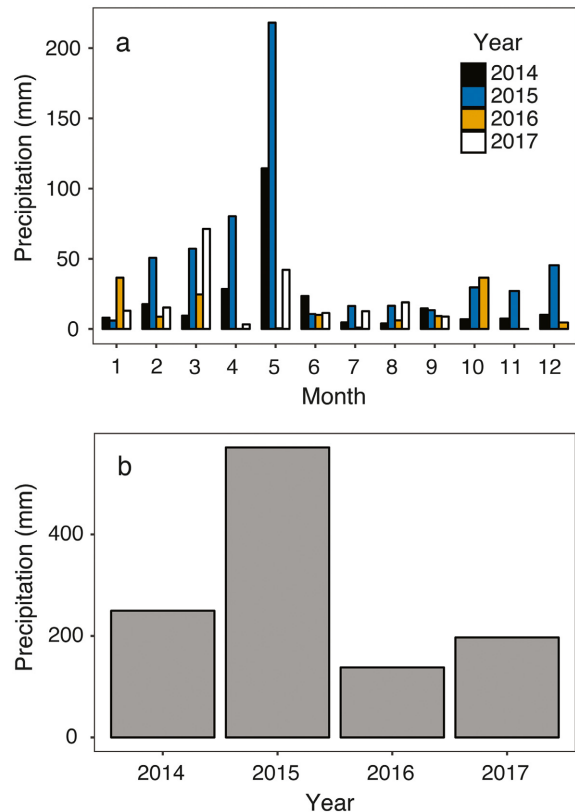


FIG. 3. Variation in (a) monthly and (b) annual precipitation (mm) from 2014 to 2017 on Santa Cruz island. Precipitation data were obtained from a meteorological station at the Charles Darwin Research Station (CDRS).

distance between the tips of the upper spines (upper spine size, mm) located toward the distal end of the mericarp, and we noted the presence or absence of lower spines and the number of seeds removed by finches (Fig. 4a). To estimate the total number of seeds originally produced in each mericarp we opened and counted the number of seeds in 752 mericarps, collected from five populations on Santa Cruz island in 2015. We evaluated the relationship between the number of seeds per mericarp and mericarp morphology by fitting the following allometric equation: number of seeds = $\log(\text{length}) + \log(\text{width}) + \log(\text{length}) \times \log(\text{width})$. We then used this model to predict the total number of seeds per mericarp ($R^2 = 0.48$).

To test whether there was variation in fruit morphology among individual plants for selection to act upon, we sampled mericarps from two *T. cistoides* populations (AB and EG) on Santa Cruz island during February 2015 (see geographic information in Appendix S1: Table S1). From each population, we sampled 15 individual plants, from each of which we collected four complete (i.e., uneaten) and mature fruits (schizocarps), with each schizocarp having four to five mericarps. In total,

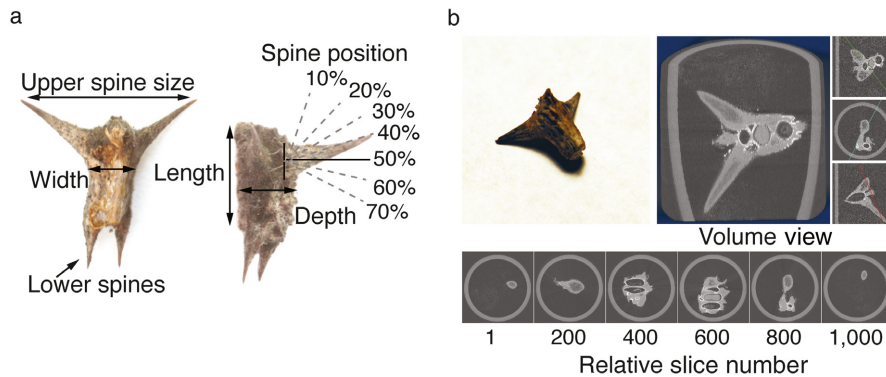


FIG. 4. (a) Mericarp traits and morphological measurements. (b) Micro-computed tomography (μ CT) image showing mericarp wall variation over its surface.

we sampled 583 mericarps for measurement of morphological traits including length, width, upper spine size, presence/absence of lower spines, and mericarp mass (to the nearest milligram using a digital balance GEM20; Smart Weigh, Jintan, China).

To experimentally test whether finches impose selection on mericarp morphology, we performed a seed predation experiment during March 2016. First, we collected 600 mature and intact mericarps from a *T. cistoides* population (EG) located on Santa Cruz island (see geographic information in Appendix S1: Table S1). We measured four traits from each mericarp (length, width, upper spine size, and presence/absence of lower spines), and gave each mericarp a unique mark with indelible ink so mericarps could be individually identified. We also applied an experimental removal of spines from a haphazard subset of the 400 mericarps by clipping either one or both of the upper spines, which allowed us to experimentally test the functional role of spines in defense. The marked mericarps were then exposed to natural finch predation on 40 circular plastic trays (~15 cm in diameter). The trays were placed across the area where the mericarps were collected, at least 30 cm apart from each other, and were monitored every three days. The mericarps were recovered after 30 d.

Finally, to evaluate the relationship between mericarp morphology and hardness, we used 102 mericarps collected in 2017 from three populations on Isabela island and seven populations on Santa Cruz island (Appendix S1: Table S1). For each mericarp, we measured hardness (0–100 value on a Shore D scale; Pam-push et al. 2011) using a handheld durometer (Asker, Super Ex, Type D, Kyoto, Japan). As the structure of the mericarp wall varies over its surface (Fig. 4b), we measured hardness at six locations on each mericarp (see detailed information in Appendix S2: Fig. S1). In addition, on each mericarp, we measured six morphological traits (length, width, depth, upper spine size, longest spine length, and spine position; Fig. 4a).

Statistical analyses

All statistical analyses were performed using R v. 3.4.2 (R Development Core Team 2008).

Does seed predation by finches vary among populations, islands, finch community composition, or years?—We used logistic linear mixed-effects models with the function *glmer* in *lme4* v. 1.1-14 package (Bates et al. 2015) to model the proportion of seed predation per population (proportion of mericarps with one or more seeds removed by finches). This model was fit as follows: predation per population = year + finch community composition + year \times finch community composition + island + error. Year, finch community composition, and their interaction were treated as fixed effects, whereas island was included as a random effect. Finch community composition was categorized as 0 on islands where large-beaked finch species (*G. magnirostris* and *G. conirostris*) were absent (Floreana, San Cristóbal, Baltra, and Seymour Norte), and 1 on islands where large-beaked finch species were present (Isabela, Santa Cruz, and Española). To examine the association of precipitation with seed predation during our study, we fit a similar model in which we replaced the fixed factor year with the total annual precipitation (mm) registered during the year that preceded each sampling. Precipitation measurements, obtained from a meteorological station placed on Santa Cruz island at the Charles Darwin Research Station (0°44′37.6″ S, 90°50′21.9″ W), were \log_{10} -transformed. We also fit the following model where the response variable was the proportion of seeds removed per mericarp, and mericarp was the unit of replication: proportion of seeds removed = year + finch community composition + year \times finch community composition + island + population(island) + error. In this analysis, the proportion of seeds consumed per mericarp was calculated as the ratio between the number of seeds removed from the mericarp

and the number of seeds predicted based on the traits of the mericarp. We included year and finch community composition as fixed effects, whereas island and population were included as nested random effects, with the parentheses denoting nested factors. Significance of fixed effects was assessed using a type II Wald's chi-squared test, and the significance of random effects was assessed with likelihood-ratio tests. P values were divided by two because tests of the significance of random effects are one-tailed given that variance > 0 (Littell et al. 1996). Finally, to evaluate more directly the effect of the finch community on seed predation per year (at the level of population and mericarps), we fit the logistic mixed-effects models separately for each year. We performed the analyses described above including all islands and excluding data from the three islands that were sampled only in 2016 (Española, Baltra, and Seymour Norte).

Do finches impose selection on T. cistoides fruit morphology and does selection vary among populations, islands, years, or with finch community composition?—We first confirmed that most mericarp traits examined (length, upper spine size, presence/absence of lower spines, and mass) exhibit substantial variation among individual plants, with the exception of mericarp width (Appendix S3: Table S1). Next, we measured phenotypic selection (sensu Lande and Arnold 1983) on mericarps sampled from natural populations using logistic mixed-effects models in the R package *lme4* v. 1.1-14 (Bates et al. 2015) to examine the relationship between *T. cistoides* fitness (seed survival) and fruit morphology (Janzen and Stern 1998). Estimates of *T. cistoides* seed survival included two variables: (1) a binary response, where 0 corresponded to a mericarp that had at least one seed removed and 1 to a mericarp that had no seeds removed, and (2) the proportion of seeds that survived finch predation per mericarp, calculated based on the estimated number of seeds per mericarp. Each of these response variables was considered in separate models, with mericarp traits treated as fixed effects.

Mericarp length, width, and upper spine size were \log_{10} -transformed to improve normality and standardized to a mean of 0 and a standard deviation of 1. Because of the correlation between mericarp width and length ($r = 0.43$), as well as a correlation between length and upper spine size ($r = 0.51$), we also performed a principal component analysis to obtain a principal component axis ($PC1_{Size}$) that captures covariation among these traits. We also included mericarp lower spines as a binary response variable, with 1 indicating the presence of a lower spine and 0 the absence of the trait. In addition, to test if selection on mericarp traits depended on year and finch community, we added the interaction between mericarp traits and these two factors, with island and population nested within island as random effects. To enable comparisons among years, we excluded the data from the three islands that were sampled only in 2016 (Española, Baltra, and Seymour

Norte) from this analysis. The full model was seed survival = $PC1_{Size} + \text{upper spine size} + \text{presence of lower spines} + \text{year} + \text{finch community} + \text{year} \times PC1_{Size} + \text{year} \times \text{upper spine size} + \text{year} \times \text{presence of lower spines} + \text{finch community} \times PC1_{Size} + \text{finch community} \times \text{upper spine size} + \text{finch community} \times \text{presence of lower spines} + \text{island} + \text{population(island)} + \text{island} \times PC1_{Size} + \text{island} \times \text{upper spine size} + \text{island} \times \text{presence of lower spine} + \text{error}$.

To avoid overparameterization of the models, reduced statistical power, and elevated type II error, we used the *dredge* function in the R package *MuMIn* v. 1.15.6 (Baron 2016) and *glmer* to compare the models resulting from all combinations of the fixed effects. This multi-model averaging approach provides the most comprehensive and powerful approach for finding the best-fitting models based on the lowest Akaike information criterion (AIC) values. The importance of each effect was evaluated from the best-fitting model selected for each response variable, with significance estimated using type II Wald's tests in the case of fixed effects, and likelihood-ratio tests in the case of random effects as described above. We averaged the subset of models with AIC values < 2 to estimate average coefficients for each independent variable using the function *model.avg*.

To explore whether finches imposed selection on mericarps in the seed predation experiment, we also used logistic mixed-effects models in which seed survival was coded as 0 when the recovered mericarp had one or more seeds removed, and 1 when the mericarp had no seeds removed. This model had mericarp as the unit of replication and took the following form: Seed survival = spine treatment + lower spines + $PC1_{Size}$ + tray. Spine treatment (a categorical variable coded as 0, 1, or 2 according to the number of large spines remaining on the mericarp), presence/absence of lower spines, and $PC1_{Size}$ (i.e., mericarp size) were included as fixed effects, and tray was included as a random effect. The significance of each fixed effect was evaluated using a type II Wald's test.

To evaluate the relationship between mericarp morphology and mericarp hardness, we first ran three independent principal component analyses to collapse the hardness measures and morphological measures into separate, multivariate axes: $PC1_{Global\ hardness}$ included hardness measures from all six positions on the mericarp, whereas $PC1_{Local\ hardness}$ included hardness measures from the three hardest positions on the mericarp (Appendix S2: Table S1) that we expect to be most directly involved in protecting seeds from finches predation. In this analysis, $PC1_{Size}$ was the first principal component generated from all six mericarp morphological traits (length, width, depth, upper spine size, longest spine, and spine position). We used a mixed-effects model to evaluate the relationship between hardness and morphology: $PC1_{Global\ hardness} = PC1_{Size} + \text{island} + \text{population(island)}$, with $PC1_{Size}$ as fixed effect, and island and population nested within island treated

as random effects. We repeated this model using $PC1_{Local\ hardness}$ as the response variable. Two additional models were fit, replacing $PC1_{Size}$ with the six individual morphological variables in the same model to simultaneously evaluate the independent contributions of each morphological trait variable to variation in $PC1_{Global\ hardness}$ and $PC1_{Local\ hardness}$. In each case, a model-averaging procedure was used. All data were standardized within populations to a mean of zero and standard deviation of one prior to analysis. R^2 values were computed for mixed-effect models using the function *r.squaredGLMM* from the R package *MuMIn* v. 1.15.6 (Barton 2016); we estimated R^2 values associated with fixed effects (R^2 marginal), and R^2 values associated with fixed and random effects (R^2 conditional).

Does T. cistoides fruit morphology differ among islands with contrasting finch community composition?—To evaluate if finch community composition (i.e., presence/absence of large-beaked finches) influences *T. cistoides* fruit morphology, we first fit a linear mixed-effects model for each of the following traits: width, length, upper spines size, and the $PC1_{size}$ separately, using the *lmer* function from the *lme4* v. 1.1-14 package (Bates et al. 2015). The data were fit to the following model: trait = finch community composition + year + finch community composition \times year + island + population (island) + error, whereby parentheses indicate nested terms. Finch community composition, year, and the interaction between these factors were included as fixed effects, while island and population nested within island were modelled as random effects. The models were also fit for each year separately to test the effect of finch community on mericarp traits in each year. Last, we analyzed presence/absence of lower spines as a response variable; for this analysis, we fit a logistic mixed-effects model using the function *glmer* implemented in the *lme4* v. 1.1-14 package (Bates et al. 2015).

RESULTS

Variation in seed predation by Darwin's finches

Seed predation by finches varied among populations, islands, and years, as well as with finch community composition. The proportion of seed predation per population differed among years ($\chi^2 = 208.60$, $P < 0.01$) and islands ($\chi^2 = 74.00$, $P < 0.01$). In 2016, a year following high precipitation, we found 39% less predation than in 2015 and 45% less predation than in 2017. In addition, higher annual precipitation, registered on Santa Cruz island, was associated with reduced seed predation the following year ($\chi^2 = 203.45$, $P < 0.01$). Among islands, mericarps on Isabela had 29% less predation than Santa Cruz and Floreana, and 39% less predation than San Cristóbal. The effect of finch community composition on the proportion of seed predation varied among years (finch community \times year: $\chi^2 = 40.34$, $P < 0.01$, Table 1 and Fig. 5).

Finch community composition did not influence the proportion of predation in 2015 ($Z = -1.20$, $P = 0.23$) or 2017 ($Z = -1.40$, $P = 0.16$). In contrast, in 2016, *T. cistoides* experienced 32% higher predation on islands where the large-beaked finches are present ($Z = 3.32$, $P < 0.01$), compared to islands where they are absent. These results excluded data from the three islands that were sampled only in 2016 (Española, Baltra, and Seymour Norte); yet similar results were obtained when all islands were included (Appendix S4: Table S1). The proportion of seeds eaten per mericarp also showed variation among years ($\chi^2 = 158.60$, $P < 0.001$), and finch community composition ($\chi^2 = 7.14$, $P = 0.008$; see Appendix S4: Table S2, Fig. S1). No effect of finch community composition was seen for the proportion of seeds eaten per mericarp in 2016 ($Z = 0.10$, $P = 0.809$). However, in 2015 and 2017, the proportion of seeds eaten per mericarp was 37% and 36% (respectively) lower on islands where the large-beaked finches were present compared to islands where they are absent. Overall, we found that, on islands where large-beaked finches were absent, predation rate per population decreased in the year following high precipitation, and the proportion of seeds eaten per mericarp increased in drier years.

Phenotypic selection on T. cistoides fruit morphology

Finches imposed phenotypic selection on mericarp morphology (Table 2). In samples from natural populations, smaller mericarps ($PC1_{Size}$: $\chi^2 = 21.47$, $P < 0.001$) with longer upper spines ($\chi^2 = 81.20$, $P < 0.001$) were more likely to escape predation by finches. The presence of lower spines also reduced predation, but the effect was marginally nonsignificant ($\chi^2 = 3.36$, $P = 0.067$). The pattern of selection on upper spine size and on the presence of lower spines depended on finch community composition (finch community \times upper spine size, $\chi^2 = 9.72$, $P < 0.002$; finch community \times lower spines, $\chi^2 = 6.25$, $P = 0.012$; Table 2). Longer upper spines and the presence of lower spines tended to provide greater protection to mericarps against seed predation on islands where large-beaked finch species were absent (Fig. 6a).

Selection on mericarp upper spine size and the presence of lower spines also varied among years (year \times upper spine size, $\chi^2 = 11.56$, $P = 0.003$; year \times lower spines, $\chi^2 = 9.83$, $P = 0.007$). Selection for longer upper spines was stronger in 2016 (Fig. 6b) than in 2015 and 2017, whereas selection on the presence of lower spines was strongest in 2015. Model-averaged coefficients are presented in Appendix S5: Table S1. Similar results were obtained when the proportion of seeds that survived predation per mericarp was used as the response variable (Appendix S5: Table S2), except that we found stronger evidence for selection on the presence of lower spines ($\chi^2 = 23.11$, $P < 0.001$) and selection on mericarp traits did not vary between years ($P > 0.5$).

In our short-term seed predation experiment in 2016, we recovered 32 of the 40 trays containing mericarps.

TABLE 1. Logistic mixed-effects models analyzing variation in the proportion of mericarps experiencing seed predation per population among islands and years.

Factor	Estimate	Z	χ^2	P
a				
Fixed effects				
Finch community			2.85	0.09
Year			208.60	<0.001
Finch community \times Year			40.34	<0.001
Random effect				
Island			74.00	<0.001
b				
Year 2015				
Fixed effect				
Finch community	-0.71 (0.59)	-1.20		0.23
Random effect				
Island			125.97	<0.001
Year 2016				
Fixed effect				
Finch community	0.39 (0.12)	3.32		<0.01
Random effect				
Island			0.00	0.50
Year 2017				
Fixed effect				
Finch community	-0.47 (0.34)	-1.40		0.16
Random effect				
Island			32.36	<0.001

Notes: The response variable was the proportion of mericarps that had at least one seed removed by finches in each population sample ($N = 100$ in most populations). Finch community composition was considered as a fixed binary factor, with 0 indicating the absence of the large-beaked finch species *Geospiza magnirostris* (only *G. fortis* present) and 1 indicating its presence. Estimate is a mean with SE in parentheses. In part a, the model included year, finch community composition, and the interaction between those factors as fixed effects. The effect of island was included as a random effect. In part b, separate models were fit for each year. The χ^2 and P values of fixed factors were estimated using type II Wald tests and random effects were estimated using likelihood-ratio tests with one degree of freedom. Effects significant at $P < 0.05$ are shown in boldface type. These models only include data from islands sampled in multiple years (see models including all islands in Appendix S4: Table S1).

From these trays, 18.3% of the mericarps showed evidence of predation by finches, 69.2% were uneaten, and 12.5% were not recovered. In our analysis, we included only the mericarps that were recovered. No relationship was found between number of upper spines and survival to finch predation ($\chi^2 = 1.26$, $P = 0.533$), but larger mericarps were more likely to escape predation ($PC1_{Size}$, $\chi^2 = 5.09$, $P = 0.024$), contrasting with the patterns we observed in natural populations.

Relationship between variation of fruit morphology and hardness

Morphological variation in mericarps was associated with variation in mericarp hardness. Mericarp hardness varied substantially among locations on the surface of mericarps ($F_{5, 235} = 15.301$, $P < 0.001$; Appendix S2: Table S2). We detected a negative relationship between overall mericarp hardness ($PC1_{Global\ hardness}$) and overall mericarp size ($PC1_{Size}$; $\beta = -0.437 \pm 0.102$, $\chi^2 = 16.876$, $P < 0.001$, $R^2_{conditional} = 0.397$, $R^2_{marginal} = 0.147$, $N = 102$; Fig. 7). We detected a similar negative relationship when only the hardest locations on the mericarp ($PC1_{Local\ hardness}$) were evaluated ($\beta_{length} = -0.239 \pm 0.107$, $P = 0.02$;

$\beta_{width} = -0.404 \pm 0.090$, $P < 0.0001$, $R^2_{conditional} = 0.335$, $R^2_{marginal} = 0.231$, $N = 102$; Fig. 7). When we replaced $PC1_{Size}$ with the six individual morphological variables, the best model identified a negative relationship between mericarp length and width and $PC1_{Global\ hardness}$ ($\beta_{length} = -0.300 \pm 0.096$, $P = 0.002$; $\beta_{width} = -0.435 \pm 0.084$, $P < 0.0001$; $R^2_{conditional} = 0.458$, $R^2_{marginal} = 0.334$; Fig. 7). Collectively, these analyses show that smaller *T. cistoides* mericarps tend to be harder than larger mericarps.

Effect of finch community composition on fruit morphology

Mericarp morphology varied substantially among populations, islands, and years (Fig. 8; Appendix S6: Table S1). We found differences among islands in mericarp length ($\chi^2 = 11.9$, $P < 0.01$) and upper spine size ($\chi^2 = 5.08$, $P < 0.02$). For instance, mericarps from Isabela were shorter and had shorter upper spines than did mericarps from the other islands. Finch community composition was associated with the presence/absence of lower spines in mericarps ($\chi^2 = 17.98$, $P < 0.01$). The presence of the large-beaked finch species was associated

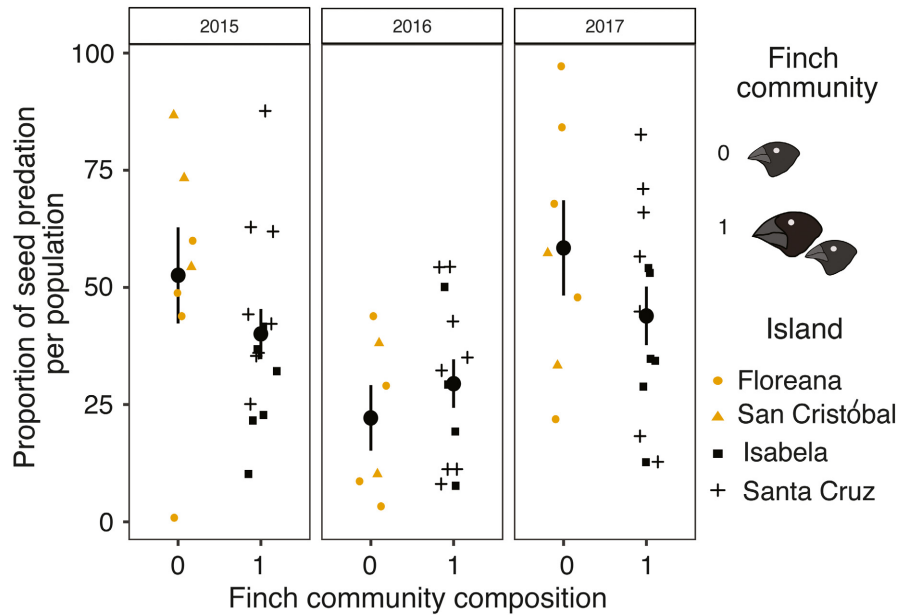


FIG. 5. Variation in the proportion of seed predation per population among islands, years, and with contrasting finch community composition (represented by different colors). The data correspond to the populations sampled on the four islands (represented by different shapes) that were visited repeatedly over three years of the study (2015–2017). The mean (dark circles) and the standard error (dark bar) of the proportion of mericarps with one or more seeds removed by finches in populations sampled from islands where the large-beaked finch species are absent (0), and present (1).

TABLE 2. Generalized mixed-effects model analyzing phenotypic selection on mericarp traits by finches.

Factor	χ^2	<i>P</i>
Fixed effects		
Finch community	1.44	0.229
Year	188.70	<0.001
PC1 _(Size)	21.47	<0.001
Upper spine size	81.20	<0.001
Lower spines	3.36	0.067
Finch community × Upper spine size	9.72	0.002
Finch community × Lower Spines	6.25	0.012
Finch community × Year	45.46	<0.001
Year × PC1 _(Size)	3.65	0.161
Year × Upper spine size	11.56	0.003
Year × Lower spines	9.83	0.007
Random effect		
Island	0.00	0.500
Population	462.80	<0.001
Island × PC1 _(Size)	0.00	0.500
Island × Upper spine size	0.00	0.500
Island × Lower spines	5.14	0.012

Notes: The response variable seed survival is binary, with 0 indicating mericarps with one or more seed removed by finches and 1 indicating complete mericarps with no seeds removed. Finch community composition was considered as a fixed binary factor, with 0 indicating the absence of the large-beaked finch species *Geospiza magnirostris* (only *G. fortis* present) and 1 indicating its presence. The χ^2 and *P* values of fixed factors were estimated using type II Wald tests and random effects were estimated using likelihood-ratio test with one degree of freedom. Effects significant at *P* < 0.05 are in boldface type.

with 67% more mericarps having lower spines. However, finch community composition was not associated with differences in mericarp width ($\chi^2 = 0.10$, *P* = 0.75), length ($\chi^2 = 0.24$, *P* = 0.62), or upper spine size ($\chi^2 = 0.0$, *P* = 0.44). The effect of finch community composition on fruit morphology also varied among years (mericarp width, $\chi^2 = 16.56$, *P* < 0.01; length, $\chi^2 = 41.60$, *P* = 0.03; upper spine size, $\chi^2 = 53.90$, *P* < 0.01; and lower spines, $\chi^2 = 47.03$, *P* < 0.01). When we examined the effect in each year, we found a significant effect of finch community composition on the presence of lower spines in 2017 ($\chi^2 = 11.13$, *P* < 0.01), but no effect of finch community composition on the other traits (mericarp width, length, and upper spine size). Divergence patterns of PC1_{size} were similar to those observed for mericarp width and length (see Appendix S6: Table S1).

DISCUSSION

Seed predation by Darwin’s finches was found to influence ecological and evolutionary processes associated with *T. cistoides*. Several findings address our initial questions. First, Darwin’s finches were an important source of mortality for *T. cistoides* seeds, with the intensity of seed predation varying over time and space in partial association with finch community composition. Second, finches imposed phenotypic selection on *T. cistoides* fruit traits whereby seeds within smaller and

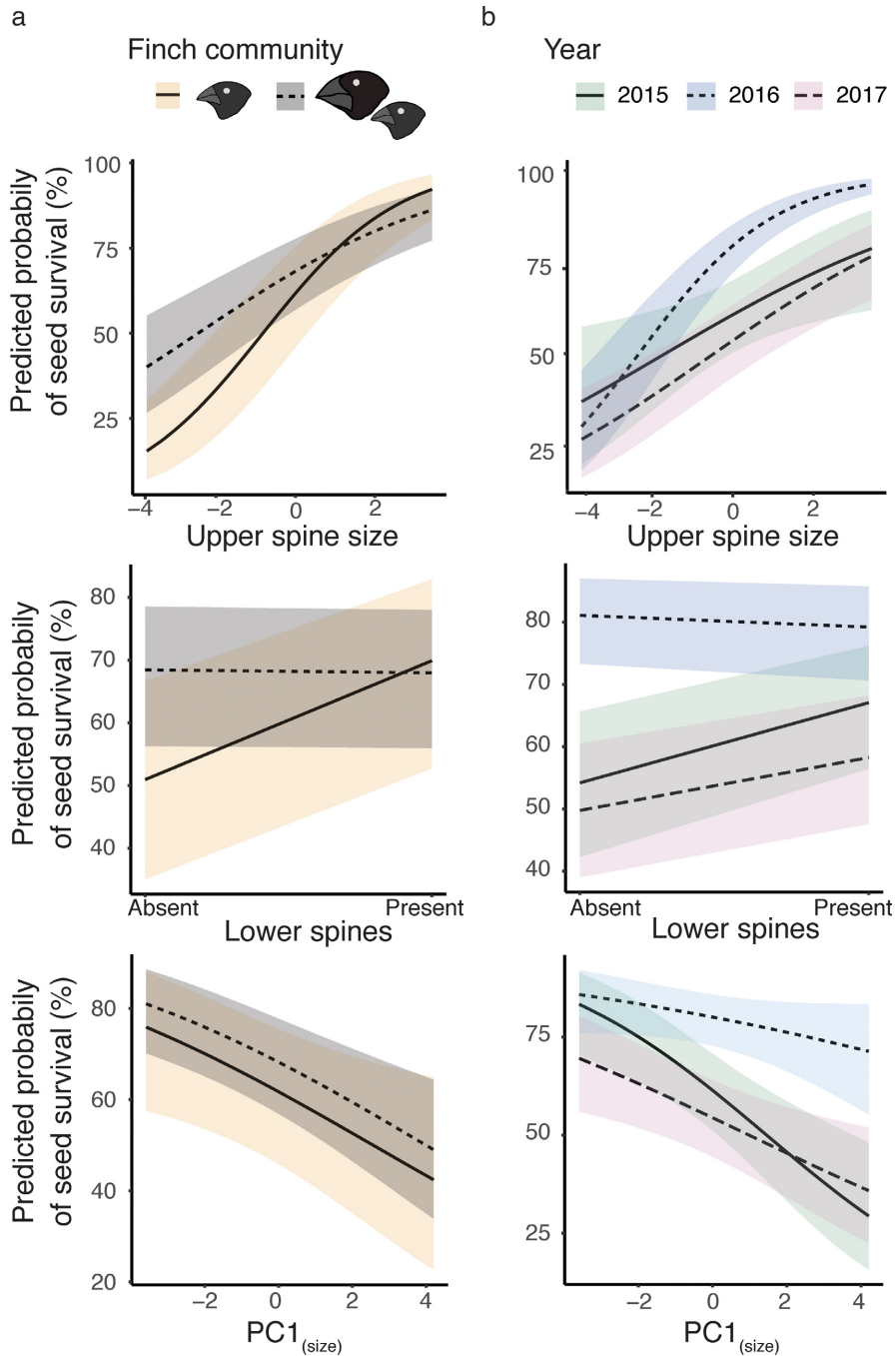


FIG. 6. Predicted seed survival probability for each mericarp trait estimated from logistic linear mixed-effects models in relation to (a) finch community composition and (b) year. The response variable used was binary, with 0 indicating mericarps with one or more seeds removed by finches, and 1 indicating complete mericarps with no seeds removed. Finch community composition was considered as a fixed binary factor, with 0 indicating the absence of the large-beaked finch species *Geospiza magnirostris* (only *G. fortis* present) and 1 indicating its presence. Shaded areas show 95% confidence intervals.

harder mericarps, and with longer or more numerous spines, often exhibited higher survival from finch predation. The details of this finch-associated selection on defense traits varied over time in accordance with variation in precipitation and changes in finch community

composition among islands, indicating that geographic variation in coevolutionary dynamics (sensu Thompson 2005) could be a source of phenotypic diversification in fruit morphology. Third, one of the traits examined, the presence of lower spines, exhibited divergence among

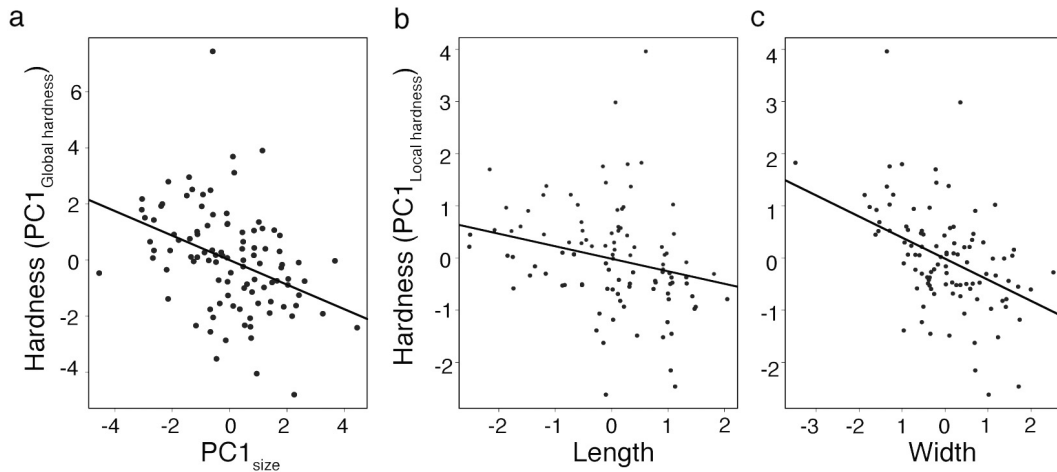


FIG. 7. Relationships between mericarp morphology and hardness. (a) Relationship between the global hardness estimate ($PC1_{Global\ hardness}$) and a multivariate measure of mericarp size ($PC1_{Size}$). Relationship between an estimate of hardness based on the three hardest locations on the mericarp ($PC1_{Local\ hardness}$) and (b) mericarp length and (c) mericarp width. Regression lines are based on intercepts and slopes estimated from linear mixed models including island and population nested within island as random effects (see *Statistical analyses*).

islands consistent with differences in finch community composition. Overall, our results are consistent with the interpretation that finches impose phenotypic selection on fruit morphological traits, and that these traits act as plant defenses in an ongoing coevolutionary arms race between Darwin's finches and *T. cistoides*.

Patterns of temporal and spatial variation in seed predation by Darwin's finches

We documented temporal and spatial variation in predation on *T. cistoides* by finches, with predation rates being higher in 2015 and 2017 than in 2016. Temporal variation in seed predation is common in plants (e.g. Hulme 1994, Kolb et al. 2007), typically being attributed to temporal variation in biotic and abiotic factors (Hulme and Benkman 2002). On the Galápagos Islands, temporal variation is strongly influenced by cycles in precipitation, especially those attributable to the El Niño Southern Oscillation cycle. This variation in precipitation drives plant productivity in the arid zone (Porter 1979) where *T. cistoides* occurs. The abundance of preferred foods of Darwin's finches (seeds, fruits, and insects) increases with higher precipitation (Grant and Boag 1980, Boag and Grant 1984, Price 1985, Gibbs and Grant 1987), which influences predation patterns of less-preferred seeds (Grant 1986, De León et al. 2014, Grant and Grant 2014). Indeed, it has been shown that finches generally avoid *T. cistoides* in wet seasons and in particularly wet years (Boag and Grant 1981, Grant 1981). In accordance with these previous studies, our results suggest seed predation of *T. cistoides* is mediated by variation in precipitation. We found that the lowest predation rate on *T. cistoides* occurred in 2016, which followed a year with high precipitation associated with an El Niño (wet) event;

whereas the highest predation rate occurred in 2017, following a year with low precipitation associated with a La Niña (dry) event. However, we caution against over-interpretation of this finding because our observations correspond to a period of only 3 yr. In addition, temporal variation in finch predation on *T. cistoides* was not uniform across islands, suggesting that features particular to each island might also shape the intensity of seed predation; however, variation in precipitation within and among islands could not be included in our analysis, given that direct measurements of precipitation were only available from one population on Santa Cruz island. One intriguing possibility is that higher survival of *T. cistoides* seeds associated with years of high precipitation could be reinforced by a masting breeding strategy of *T. cistoides*. Although masting is a well-known mechanism in many tree species to increase survival of seeds by satiating predators (Janzen 1971, Silvertown 1980), this strategy has not been evaluated in *T. cistoides*.

The observed spatial variation in seed predation is likely also driven by a combination of biotic and abiotic factors. For example, we expected the highest rates of *T. cistoides* seed predation on islands with the large-beaked finch species *G. magnirostris* and *G. conirostris*. Our results were partially consistent with this expectation. In 2016, when predation rates on *T. cistoides* were typically low, islands with large-beaked finch species indeed showed higher predation, but no effect of community composition was evident in other years. The smallest finch species that feeds on *T. cistoides* is *G. fortis* (Grant 1981), but this finch prefers other food sources that are available following El Niño years. By contrast, large finches have less difficulty feeding on *T. cistoides* and they continue to feed on mericarps even following El Niño events. Thus, variation in seed predation can only be understood by looking at the

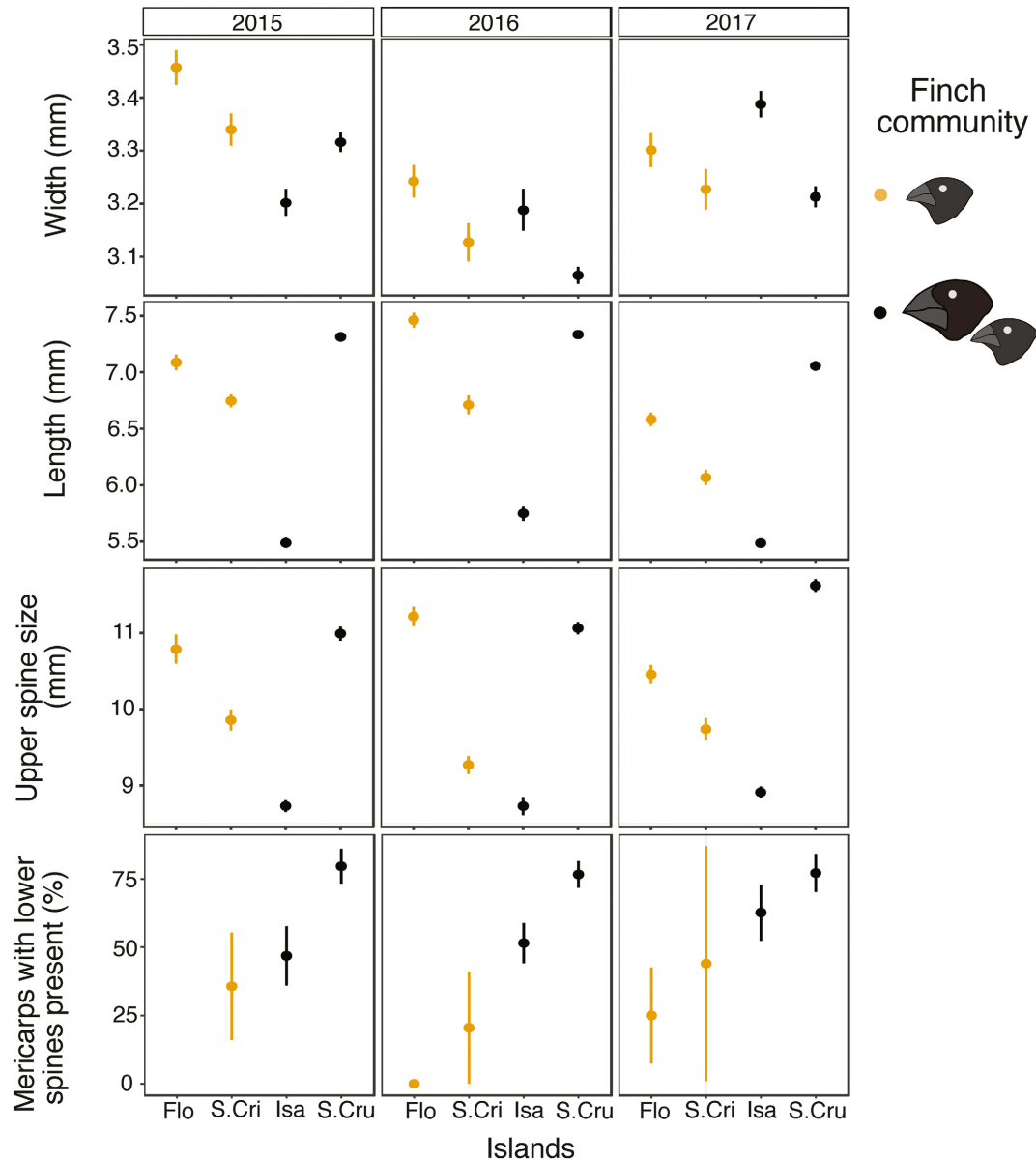


FIG. 8. Variation in *Tribulus cistoides* mericarp morphology. Means (circle) and standard error (bars) of each mericarp trait for the four islands that were sampled from 2015 to 2017: Floreana (Flo), San Cristóbal (S.Cri), Isabela (Isa), and Santa Cruz (S.Cru). Islands where large-beaked finch species are absent (only *G. fortis* present) are indicated in orange and islands where this species (i.e., *Geospiza magnirostris*) is present are indicated in black.

interaction between finch community composition and temporal variation in climate.

Selection by Darwin's finches on fruit traits of T. cistoides

Darwin's finches were found to impose phenotypic selection on *T. cistoides* fruit defense traits. Mericarps sampled from natural populations that had lower spines, longer upper spines, and that were smaller, were more likely to survive predation. Finches might prefer larger mericarps because larger mericarps have

more seeds and thus represent a greater reward. Interestingly, we also found that mericarp size was inversely associated with mericarp hardness, which contributes to defense against ground finches (Boag and Grant 1981, Price et al. 1984). The ability of seeds or fruits to escape predation is generally thought to be greater for larger seeds (or fruits), for which leverage becomes more difficult, and harder for seeds (or fruits), which require more bite force to crack open (Abbott et al. 1977). However, we showed that smaller mericarps were harder than larger mericarps, which suggests that small mericarps could be as

(or perhaps more) difficult to open than large mericarps. Since finches commonly use specialized twisting motions to open mericarps (Grant 1981; Video S1), instead of just a direct biting effort, smaller mericarps also could require more precision and handling ability.

The strength of selection varied over time and space, as has been seen in other systems (Thompson 2005, Siepielski et al. 2009, 2013, Bell 2010). As with the observed temporal variation in seed predation, variation in selection on *T. cistoides* appeared to follow climatic cycles, although we do not yet know the causal links between precipitation and specific forms of selection. Furthermore, selection for longer upper spines and the presence of lower spines was stronger on islands where the large-beaked finch species were absent, perhaps because the largest beaked finch species (i.e., *G. conirostris* and *G. magnirostris*) are less deterred by *T. cistoides* defense traits. Stated in another way, the largest species might have little difficulty opening even the most strongly defended *T. cistoides* mericarps. Once again, it is the interaction between finch community composition and climate that appears to determine spatial and temporal variation in finch–*T. cistoides* interactions.

Results from the short-term seed predation experiment did not match our observations from natural populations. In the experiment, smaller mericarps were more likely to be preyed on and no association was evident between the presence of spines and mericarp predation.

These divergent results are perhaps not surprising since the experiment was conducted in only a single location and over a relatively short period of time (30 d), whereas the observational data capture data from many populations over multiple years. Our experimental results, therefore, further emphasize the conditional nature of finch seed predation, and how selection varies through time.

Evidence for phenotypic selection by Darwin's finches on *T. cistoides* fruits suggests a potential ongoing coevolutionary arms race between Darwin's finches and *T. cistoides*. Our results thus add to previous studies in other systems showing that seed predators impose selection on fruit morphology (e.g., Coffey et al. 1999, Gómez 2004); however, selection on *T. cistoides* fruit morphology has cascading implications in the Galápagos Islands (Fig. 9). *Tribulus cistoides* mericarps impose selection on the size and shape of the beak of *G. fortis* (Boag and Grant 1981, Boag and Grant 1984, Grant and Grant 1999), which drives episodic bouts of evolutionary change (Grant and Grant 2002, 2006). During dry periods, when small and soft seeds are scarce, larger beaked birds of *G. fortis* that are able to crack *T. cistoides* mericarps are favored when *G. magnirostris* are absent. However, when *G. magnirostris* are present, they compete with *G. fortis* for *T. cistoides* fruits, and cause an adaptive shift in *G. fortis* toward smaller beaks (Grant and Grant 2006). Therefore, the interaction between *G. fortis* and *T. cistoides* seems to be

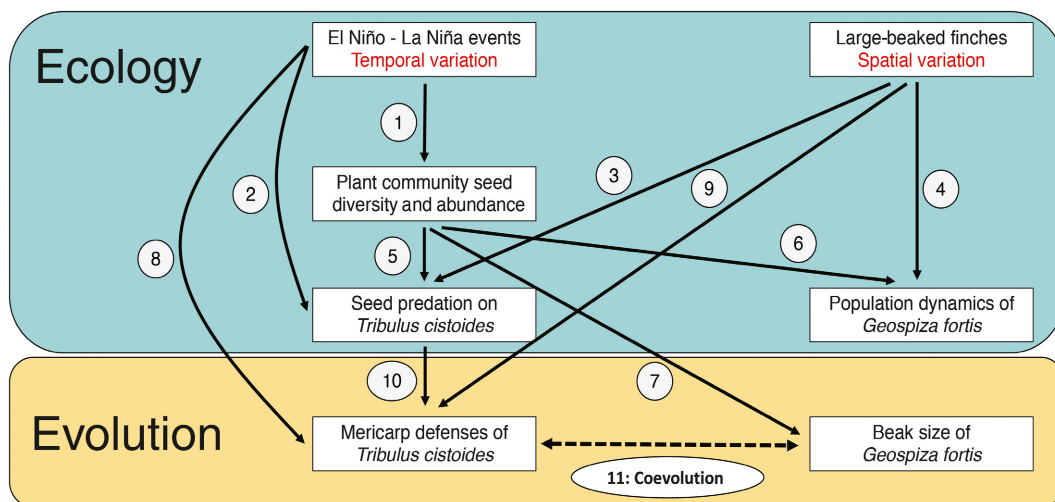


FIG. 9. Ecological and evolutionary processes influencing interactions between *Tribulus cistoides* and Darwin's finches. (1) Dry periods reduce seed diversity and abundance; (2) predation increases the year following La Niña years (low precipitation); (3) presence of large-beaked finches increases seed predation the year following El Niño years (high precipitation); (4) large-beaked finches compete with *Geospiza fortis*; (5) decreased seed diversity/abundance leads to greater predation on *T. cistoides*; (6) decreased seed diversity/abundance reduces *G. fortis* population size; (7) decreased seed diversity/abundance selects for larger beaks of *G. fortis* when large-beaked bird species are absent, and smaller beaks when they are present; (8) selection for longer upper spines increases following El Niño years, whereas selection for the presence of lower spines and decreased size increase following La Niña years; (9) absence of large-beaked finch species leads to stronger selection for longer upper spines and for the presence of lower spines; (10) seed predation selects for longer upper spines and smaller mericarps (11); hypothesized coevolutionary arms race between *T. cistoides* and *G. fortis*. Interactions might also operate between the evolutionary processes and population dynamics within species (arrows not shown).

driven by reciprocal evolutionary changes that are mediated by temporal variation in La Niña/El Niño precipitation cycles and spatial (or temporal) variation in finch community composition. To further test this hypothesis, future research should focus on testing whether an adaptive evolutionary response of *T. cistoides* fruits to finch predation modifies selection patterns imposed on finches' beaks and affects their evolutionary trajectory.

Relationship between finch community and T. cistoides fruit morphology

Spatial variation in natural selection imposed by Darwin's finches has likely already caused adaptive divergence among island populations of *T. cistoides*. For example, the absence of lower spines in mericarps was associated with islands where the large-beaked finch species were absent. However, other traits examined (mericarp length, width, and upper spine size) were not consistently associated with finch community composition. The mismatch between selection pressure and patterns of variation of defense traits might have several causes. For instance, some defense traits might have low heritability, or opposing selective pressures, such as from dispersal and germination, which could mask the effects of seed predation on evolution (Primack 1987, Alcántara and Rey 2003, Agrawal et al. 2013). In addition, fluctuating selection in space and time, as in the case of mericarp defense traits, coupled with gene flow, population bottlenecks, and founder events could constrain the translation of selection effect into morphological change, as predicted by the geographic mosaic of coevolution (Thompson 2005). Finally, it has been suggested that *T. cistoides* was introduced into the archipelago by humans (Porter 1967, Grant 1981), sometime after 1535, when the islands were discovered by Spanish explorers (Grant and Grant 2014). If true, it is possible that *T. cistoides* has not yet had sufficient time, in combination with the above factors (e.g., founder effects, gene flow, opposing selection forces), to locally adapt to finch community composition. However, the history of *T. cistoides* on the archipelago remains unresolved.

The evolutionary response of fruit morphology in *T. cistoides* to selection imposed by ground finches depends on several factors for which we still lack detailed information, such as heritability of fruit traits. Galápagos National Park restrictions prevented us from conducting common garden quantitative genetics experiments on *T. cistoides*; nonetheless, we detected variation among individual plants for almost all measured mericarp traits. These results are consistent with the expectation that variation in these traits is at least partially controlled by genetic variation. Future common garden experiments and genomic analyses would add to our understanding of the evolution of morphological defenses in *T. cistoides*. Key questions that could be addressed in future work include: What is the genetic structure and demographic history of *T. cistoides*

populations across the archipelago? Do trade-offs exist between natural selection imposed by finches and other potential drivers of selection on *T. cistoides* fruit morphology, such as dispersal, germination, and establishment? And, finally, is *T. cistoides* native to the islands or was this plant species introduced recently to the islands, possibly by humans?

CONCLUDING REMARKS

We report evidence that Darwin's finches select *T. cistoides* fruits based on defense traits, and that the variation in selection patterns can be explained, in part, by finch community structure and variation in climate. Previous work has suggested that predation on *T. cistoides* mericarps is an important agent of natural selection on finch beaks (Boag and Grant 1981, 1984, Grant and Grant 2006). We here suggest that a reciprocal process of natural selection by finches on mericarp morphology is also likely and, hence, that finches and *T. cistoides* are coevolving in an arms race. To inhibit finch predation, *T. cistoides* invests in physical defense structures, such as spines and mericarp hardness. In turn, the higher levels of defense in mericarps select for finches that are able to remove the seeds more efficiently. The specific process of reciprocal natural selection that leads to reciprocal adaptation has yet to be directly documented, but the individual component interactions make this scenario highly likely. In addition, considerable temporal variation in selection on mericarp defenses as well as finch beak morphology (Grant and Grant 2002), indicates that climatic conditions and spatial variation in finch communities mediate the ecological strength and evolutionary outcomes of this finch–plant interaction.

Our work expands the understanding of ecological and evolutionary interactions between Darwin's finches and the plants whose seeds they eat. A long history of research, which includes Charles Darwin (1859), David Lack (1947), Grant and Grant (2014), and many other past and present researchers, has built a foundation for understanding the interplay between ecology and evolution from studying Darwin's finches. We hope that our study supports and inspires new avenues of research into these interactions.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1392/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qq4715f>