# PLANT ASSEMBLY AND DARWIN'S FINCHES ON THE GALÁPAGOS ISLANDS: INTERPLAY OF ECOLOGICAL AND EVOLUTIONARY PROCESSES

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# ABSTRACT

Community ecology is a field characterized by a high degree of complexity, with multiple processes underlying patterns observed in nature and confounded by effects of historical contingency. There are only a few generalizations that can be made about the key processes driving assembly of species in communities, and they have been developed mostly from an ecological perspective, with emphasis on between species interactions and the interactions between species and the environment. However, in recent decades, there have been significant advances through the integration of evolutionary processes occurring at different temporal and spatial scales. In this thesis, I examine the joint effects of ecological and evolutionary processes in shaping community structure, using an emblematic insular system: plant communities and Darwin's finches on the Galápagos Islands. In Chapter 1, I examine the relative role of dispersal limitation, habitat filtering, and speciation in shaping the assembly of the Galápagos flora. Using an ecophylogenetic approach, I show that the Galápagos flora is a phylogenetic clustered subset of the continental source pools, suggesting that species assembly was influenced by strong filtering and adaptive radiation events. However, contrary to common expectations for oceanic islands such as the Galápagos archipelago, I found that environmental filtering was more important than dispersal limitation in determining the species composition of island assemblages. This result suggests that dispersal limitation might not be the primary determinant of the composition of insular floras as had been previously assumed. In Chapter 2, I investigate the eco-evolutionary feedbacks between Darwin's finches and plant communities. Based on feeding observations and the results of a four-year exclusion experiment conducted across two sites on Santa Cruz island, I show that the selective feeding behavior of Darwin's ground finches has a strong effect on the structure of seed banks—yet this effect is not consistently translated to concomitant shifts in above-ground vegetation. This decoupling of eco-evolutionary interactions between Darwin's finches and plant communities could be a product of several factors, including environmental fluctuations, trade-offs between multiple ecological processes influencing plant development, and stochastic population dynamics. In Chapter 3, I examine ecological and evolutionary factors shaping the reciprocal interactions between Darwin's ground finches and a focal plant species, *Tribulus cistoides*, upon which they feed, across seven islands of the archipelago over three years. I find evidence that finches likely affect seed survival of *T. cistoides* and impose phenotypic selection on *T. cistoides* fruit morphology. Both seed predation and phenotypic selection vary with climate fluctuations and finch species community composition. Additionally, I show that variation in a key morphological fruit trait—the number of spines—is associated with different species composition among islands. These results suggest that co-evolutionary dynamics, mediated by climatic fluctuations and finch community composition, link ground finches and *T. cistoides*. The body of work I present here highlights how our understanding of community structure can be enhanced by integrating evolutionary and ecological processes acting at different spatio-temporal scales.

# ABRÉGÉ

L'écologie des communautés est un domaine caractérisé par un degré élevé de complexité, avec de multiples processus sous-jacents aux modèles observés dans la nature et confondus par les effets de la contingence historique. Peu de généralisations peuvent être faites sur les processus clés conduisant à l'assemblage d'espèces dans les communautés, et elles ont été principalement développées d'un point de vue écologique, mettant l'accent sur les interactions interspécifiques et les interactions espèces-environnement. Cependant, au cours des dernières décennies, des progrès ont été accomplis grâce à l'intégration des processus évolutifs se produisant à différentes échelles temporelles et spatiales. Dans cette thèse, j'étudie les effets conjoints des processus écologiques et évolutifs sur la structure des communautés, en utilisant un système d'îles emblématique : les communautés végétales et les pinsons de Darwin des îles Galápagos. Dans le chapitre 1, j'examine le rôle relatif de la limitation de la dispersion, du filtrage de l'habitat et de la spéciation dans la formation de la flore des Galápagos. En utilisant une approche écophylogénétique, je montre que la flore des Galápagos est un sous-ensemble de groupes phylogénétiques de sources continentales, ce qui suggère que l'assemblage des espèces était influencé par de puissants événements de filtrage et de rayonnement adaptatif. Cependant, contrairement aux attentes ordinaires pour les îles océaniques, tel que l'archipel des Galápagos, j'ai constaté que le filtrage environnemental était plus important que la limitation de la dispersion pour déterminer la composition en espèces des assemblages d'îles. Ce résultat, combiné aux études précédentes montrant une forte prévalence de la dispersion sur de grandes distances parmi les plantes, suggère que la limitation de la dispersion pourrait ne pas être le principal déterminant de la composition des plantes insulaires, comme supposé précédemment. Dans le chapitre 2, j'étudie les réponses éco-évolutives entre les pinsons de Darwin et les communautés végétales. À l'aide d'observations sur leur façon de se nourrir et d'une expérience d'exclusion menée pendant quatre ans sur deux sites de l'île de Santa Cruz, je montre que le comportement alimentaire sélectif des pinsons de Darwin a un effet significatif sur la structure des banques de graines, mais cet effet ne se traduit pas systématiquement par un effet concomitant de changements dans la végétation. Ce découplage des interactions éco-évolutives entre les pinsons de Darwin et les communautés végétales peut être le résultat de plusieurs facteursde compromis entre les processus écologiques influençant le développement des plantes, et de dynamique stochastique des populations. Le chapitre 3 examine les facteurs écologiques et évolutifs qui déterminent les interactions réciproques entre les pinsons de Darwin et une espèce végétale clé, *Tribulus cistoides*, dont ils se nourrissent dans sept îles de l'archipel pendant trois ans. Je démontre que les pinsons affectent probablement la survie des graines de *T. cistoides* et exercent une sélection phénotypique sur la morphologie du fruit de *T. cistoides.* La prédation des graines et la sélection phénotypique varient avec les fluctuations climatiques et la composition de la communauté des espèces de pinsons. De plus, je montre que la variation d'un trait morphologique clé du fruit, à savoir le nombre d'épines, est associée à une composition spécifique différente entre les îles. Ces résultats suggèrent une dynamique de co-évolution, arbitrée par les fluctuations climatiques et la composition des espèces de la communauté des pinsons, reliant les pinsons et *T. cistoides.* L’ensemble de mes travaux met en évidence les moyens d’améliorer notre compréhension de la structure des communautés en intégrant des processus évolutifs et écologiques agissant à différentes échelles spatio-temporelles.

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# PREFACE

All manuscript chapters of this thesis (Chapter 2-4) constitute original contributions to scientific knowledge.

In Chapter 2, I examine the relative role of biogeographic, ecological, and evolutionary processes driving species composition of the Galápagos flora. I conclude that plant assemblages on the archipelago were shaped by strong filtering processes and speciation events, and suggest that habitat filtering might be a stronger driver of plant assemblages than dispersal limitations, even on isolated insular systems such as the Galápagos archipelago.

In Chapter 3, I examine feeding preferences of Darwin's ground finches and test their effect on seed banks and plant communities. I suggest that finches have a strong effects on the structure of seed banks, which might eventually influence finch evolution trajectories. However, the effect of these eco-evolutionary dynamics does not translate to above ground vegetation, which is driven by multiple ecological and stochastic factors.

In Chapter 4, I evaluate the reciprocal interactions between Darwin's ground finches and *Tribulus cistoides*. I find that finches have a strong effect on seed survival and are imposing phenotypic selection of fruit defense traits and suggest that these interactions are influenced by climatic fluctuations and spatial biotic heterogeneity.

# THESIS FORMAT

This thesis follows a manuscript-based format and includes: a general introduction (Chapter 1), three manuscript chapters (Chapter 2-4), a general conclusion (Chapter 5), and an appendix, which comprises supplementary material for all manuscript chapters. For all manuscript chapters, I am the lead author. Chapter 2 has been published previously and the publisher has granted permission for it to be reprinted here. Chapter 3 will be submitted for publication, and Chapter 4 was submitted for publication and is under revision. Each manuscript chapter is formatted according journal guidelines.

**Chapter 2:**

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# CONTRIBUTION OF AUTHORS

**Chapter 1**: Sofía Carvajal-Endara wrote the chapter with input from T. Jonathan Davies.

**Chapter 2:** Sofía Carvajal-Endara and T. Jonathan Davies designed the study with input from Andrew Hendry and Nancy C. Emery; Sofía Carvajal-Endara performed data analyses and wrote the first draft of the manuscript with input from Jonathan T. Davies; All co-authors reviewed the manuscript.

**Chapter 3:** Andrew P. Hendry, Luis F. de León, and Joost A.M. Raeymaekers designed and established the exclusion experiment; Luis F. De León, Joost A.M. Raeymaekers, Jeffrey Podos, Kiyoko M. Gotanda, Jaime A. Chaves, Diana M.T. Sharpe, and Sofía Carvajal-Endara collected data; Patricia Jaramillo assisted with plant identification; Sofía Carvajal-Endara, T. Jonathan Davies, and Andrew P. Hendry designed the study; Sofía Carvajal-Endara analyzed the data with input from T. Jonathan Davies and Andrew P. Hendry; Sofía Carvajal-Endara wrote the first draft with input from T. Jonathan Davies and Andrew P. Hendry.

**Chapter 4:** Sofía Carvajal-Endara and Marc T.J. Johnson designed the study with input from Nancy C. Emery and Andrew P. Hendry; Sofía Carvajal-Endara, Andrew P. Hendry, Nancy C. Emery, Corey P. Neu, Diego Carmona, Kiyoko M. Gotanda, and Marc T.J. Johnson collected data; Sofía Carvajal-Endara and Diego Carmona analyzed the data with input from Marc T.J. Johnson; Sofía Carvajal-Endara wrote the first draft with input from Marc T.J. Johnson; All co-authors reviewed the manuscript.

**Chapter 5:** Sofia Carvajal-Endara wrote the chapter with input from T. Jonathan Davies.

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# CHAPTER 1:

# Introduction

## Community assembly: the interplay between ecological and evolutionary processes

Although evolutionary biologists and ecologists recognize the overlap between their fields of research, the two fields have historically developed independently from each other (Levins 1968; Pimentel 1968; Antonovics 1976; Roughgarden 1979). In part, this disconnection stemmed from the assumption that ecological and evolutionary processes occur at different time scales (Slobodkin 1961): evolutionary biologists have mostly been concerned with how species change and diversify over large time scales, while ecologists have mostly focused on how organisms interact with their biotic and abiotic environments over short time scales. However, a better understanding of how ecological and evolutionary processes affect each other at various levels of organization (i.e. individuals, populations, communities, and ecosystems), and at different temporal and spatial scales has motivated a growing interest in unifying these two bodies of theory and in understanding when and where reciprocal feedbacks between ecology and evolution could play important roles in natural systems (Lavergne et al. 2010; Schoener 2011; Mittelbach and Schemske 2015).

The influence of ecology on evolutionary processes, such as adaptation, coevolution, and speciation, has been widely documented since the early development of evolutionary theories (Darwin 1859; Ford 1964). However, the imprint of evolution on ecological processes has received much less attention. In particular, within community ecology—a subdiscipline of ecology that focuses on species abundance, composition, and diversity within communities—most theoretical and empirical approaches have largely ignored evolutionary processes. As community ecology emerged into a distinct discipline, the processes that were considered the key determinants of community properties were the ones occurring over “ecological scales” of time, such as the interactions among species and local environmental conditions. Competitive interactions came to dominate much of ecological theory following the development of mathematical models by Lotka and Volterra in the 1920s and 1930s, and numerous theoretical and empirical studies at the time focused on testing the role of competition in shaping species coexistence (e.g. Gause 1934; Connell 1961; Miller 1967). Evidence from ecological studies at the time strongly supported the importance of competition and its associated patterns and processes, such as competitive exclusion—species ecologically similar tend to compete strongly for resources and are not able to coexist (Gause 1934)—and niche partitioning—closely related species are able to coexist by partitioning available resources (Lack 1944, Hutchinson 1957, 1959). These efforts led to the formulation of the general principle of limiting similarity that proposed there is a maximum level of ecological similarity that will allow species to coexist locally (MacArthur and Levins 1967). Importantly, while in some of these early ecological studies of species coexistence patterns the potential influence of evolutionary relatedness among species was acknowledged, it still was not directly incorporated into ecological models (but see Simberloff 1970).

While species interactions, such as competition and predation, proved to be important in structuring ecological communities (Cody and Diamond 1975; Connell 1983; Schoener 1983; Sih et al. 1985; Diamond and Case 1986), they were not sufficient to explain coexistence patterns in several systems (Abrams, 1977; Strong et al. 1984). Further, studies looking at species coexistence at larger spatial scales, suggested that local community structure might also be influenced by processes occurring at greater spatial and temporal scales than had traditionally been the focus of community ecology (Ricklefs 1987; Holt 1993). In a seminal work, MacArthur and Wilson (1967) proposed that that species diversity on islands was determined by the equilibrium between immigration of species from continents and local extinctions. Thus, smaller and more isolated islands would harbor fewer species than larger and connected islands. In a later contribution, MacArthur (1969) added speciation as a process increasing local diversity in communities. Influenced by this neutral, large-spatial scale perspective, community ecologists began to consider communities as the outcome of the interaction between local and regional processes where local extinction of species, driven mainly by antagonistic interactions (i.e. predation, diseases, and competition) and local environmental disturbances, is balanced by the immigration of species, which is determined by the generation and dispersal of new species from regional pools of potential colonists. The movement and establishment of species into local communities depends fundamentally on environmental and dispersal constraints, which are shaped by the strength of ecological conservatism among species. With this increasing appreciation of the importance of processes operating at larger scales, macroevolutionary dynamics were recognized as additional determinants of community structure (Ricklefs and Schluter 1993; Cornell and Lawton 1992).

The development of molecular tools and phylogenetic methods during the 1980s and 1990s facilitated the integration of species' evolutionary history into the study of community ecology (Emerson and Gillespie 2008; Cavender-Bares et al. 2009; Vamosi et al. 2009). A substantial number of studies included phylogenetic analyses to examine community structure, catalysed by the publication of Webb's (2002) seminal review paper, which promoted the development of phylogenetic community ecology as a promising area of research (Cadotte and Davies 2016). According to the theoretical underpinnings of this field of research, which connects trait evolution to phylogenetic patterns of relatedness in communities to infer assembly processes, if ecological traits are phylogenetically conserved and a community shows a pattern of phylogenetic overdispersion—species that co-occur in the community are more distantly related than expected by chance—competition is likely the more important process shaping the community via limiting similarity among coexisting species. On the other hand, if a community shows a pattern of phylogenetic clustering—species that co-occur in a community are more closely related than expected by chance—environmental filtering is more likely the predominant process shaping the community.

Despite the attractive simplicity of 'ecophylogenetic' theory, it was recognised that patterns of phylogenetic structure within communities could also be influenced by processes other than competitive interactions and environmental filtering (Carson and Root 2000; Helmus et al. 2013). For instance, other ecological interactions, including predation, parasitism, mutualism, and facilitation, could also shape community phylogenetic structure, although they have received much less attention. In addition, phylogenetic structure in communities can be influenced by regional evolutionary dynamics driven by specific modes of speciation (Mooers and Heard 2007; Schweiger et al. 2008; Davies et al. 2011), biogeographic history (Ricklefs 2004; Wiens and Donoghue 2004), and neutral processes such as local and regional dispersal

(Graham and Fine 2008; Kembel 2009). Disentangling the effect of these processes in community assembly and determining their relative importance at different temporal and spatial scales remains a central challenge for this growing area of research. Island biotas provide a particularly tractable system for extending phylogenetic approaches in community, since they can provide an explicit temporal and spatial context for the integration of ecological and evolutionary dynamics (Emerson and Gillespie 2008; Weigelt et al. 2015; Rominger et al. 2016).

### *Influence of contemporary evolution*

During the same time that approaches focused on understanding the interaction between macroevolutionary and ecological processes started to become widespread among community ecologists, alternative research frameworks looking at the influence of rapid evolution on community ecology also emerged. This was motivated by the growing realization that evolutionary changes within populations often occur over short-time scales (Reznick and Ghalambor 2001; Reznick et al. 2004), and directed significant interest towards the interactions between evolutionary and ecological processes that are acting at contemporary time scales, or eco-evolutionary dynamics, as defined by Hendry (2017). The study of these dynamics served to integrate within a common framework (1) the effect of ecological factors (biotic and abiotic) on the evolution of traits through selection: the eco-to-evo side, (2) the effect of phenotypic traits undergoing rapid evolution on ecological processes (within populations, communities, and ecosystems): the evo-to-eco side, and (3) the reciprocal feedbacks between these effects (Fussmann et al. 2007; Strauss 2014; Hendry 2017). Research based on this and complementary frameworks (e.g. community genetics, niche construction, geographic mosaic of coevolution) has grown considerably over the past two decades (Hendry 2017) with the development of theoretical models (e.g. Loeuille and Leibold, 2008; Vanoverbeke, 2016; McPeek 2017; Patel et al. 2018) and accumulation of empirical data (e.g. Yoshida et al. 2003; Bassar et al. 2010; Turcotte et al. 2012; Brunner et al. 2017), and has brought important new insights to the field of community ecology.

Community ecology has traditionally assumed that an explicit inclusion of within-species evolutionary processes is not required since the basic level of organization in most community ecology studies is the species level (Vellend 2016). However, recent studies on eco-evolutionary dynamics suggest that even though the effect of evolution might decrease at higher levels of organization (i.e. effects tend to be weaker at community and ecosystem levels than at population levels) (Bailey et al. 2009), the consequences of evolution within a focal species on community composition and ecosystem properties remain significant (Harmon et al. 2009; Bassar et al. 2010; Terhorst et al. 2014; Gómez et al. 2016). In addition, recent evidence suggests that the effect of variation within species could be as strong as the effect of variation among species on several community properties (Des Roches et al. 2018).

While there is mounting empirical data on eco-evolutionary dynamics to support the development of new conceptual models and methods that integrate evolutionary processes within species and community ecology, it has been claimed that most of this evidence comes from simplified experimental communities, such as those examined in laboratories or mesocosms established in the field (De Meester 2019; Hendry 2019). Because of this limitation, the relative importance of contemporary evolution on natural communities in relation to other ecological process, such as biotic interactions and environmental variation, still needs to be determined (Johnson and Stinchcombe 2007; De Meester 2019; Hendry 2019). Experiments developed under more natural conditions, in which multiple species are allowed to interact across heterogenous landscapes (i.e. along gradients in environmental factors or community composition), would help to fill this gap and provide a better understanding of the role of eco-evolutionary dynamics in natural systems (De Meester 2019; Hendry 2019; Ware et al. 2019).

In this thesis, I examine how the interaction of ecological and evolutionary processes influences community assembly. I focus on an emblematic insular system: plant communities and Darwin’s finches on the Galápagos Islands, and evaluate processes operating at two different spatio-temporal scales. First, at a larger scale, I consider the relative effect of biogeographic, ecological, and macroevolutionary processes on the Galápagos flora assembly. Second, at a smaller scale, I asses the importance of eco-evolutionary feedbacks between Darwin’s finches and plant communities.

# Study system: plant communities and Darwin's finches in the Galápagos archipelago

Insular systems, especially oceanic ones, are considered natural laboratories because they provide less complex biological scenarios than continents, where ecological and evolutionary processes can be studied across spatially discrete replicated units (i.e. islands within archipelagos) often over known time frames (Losos and Ricklefs 2009; Warren et al. 2015; Whittaker et al. 2017). They have served as models for development of key theories in biology that address processes shaping diversity gradients, including species diversification and trait evolution (Darwin 1859; Wallace 1881; Grant and Grant 1986; Losos et al. 1998; Schluter 2000), island biogeography (MacArthur and Wilson 1967; Whittaker et al. 2008; Losos and Ricklefs 2010), and species interactions (Diamond 1975; Case and Bolger 1991; Holt 1996). In addition, they harbor an important proportion of global species diversity, sometimes originating from outstanding species radiations.

Among insular systems, the Galápagos archipelago has particular significance in evolutionary biology due to its large influence on Darwin's work (Darwin 1839; 1841; 1845; 1859) and selection in natural populations (Grant 1986; Grant and Grant 2008; Grant and Grant 2014). This archipelago of volcanic origin is located approximately 1000km west of the Ecuadorian coast in South America; it comprises 14 main islands, which range from approximately 10 $km^2$ to $4700km^2$, and over 40 islets (Tye and Ortega 2011; Willis and Porter 1971). The Galápagos archipelago likely started to emerge 80-90 Ma ago, as the Nazca plate moved over a tectonic hotspot, originating groups of islands of similar age (Christie et al. 1992; Hoerlne et al. 2002). Among the present islands, the oldest are located to the southeast of the archipelago (~ 3.5 Ma of age), while the youngest (~ 0.4 Ma of age) are located towards the northwest (Geist 1996; Parent et al. 2008), yet the presence of drowned seamounts located east of the oldest existing islands suggest that the archipelago could have been colonized since at least 14 Ma ago (Werner at al. 1999).

Unlike other equatorial oceanic islands, the climate of the Galápagos islands is remarkably dry, with a distinct pattern of intra-annual seasonality that results from winds and surrounding ocean currents driven by the movement of the Inter-Tropical Convergence zone from north to south (Hamann 1979, Itow 2003; Sachs et al. 2009). From June to December, the islands experience a cool and dry season, and from January to May a warm and rainy season. The climate on the islands is modified by their topography: islands with higher elevation show different climatic zones (i.e. dry highlands, humid highlands, and dry lowlands), while islands with lower elevation are predominantly dry (Trueman and d'Ozouville 2010). In addition, the climate in the archipelago is strongly influenced by the El Niño Southern Oscillation (ENSO), which typically encompasses two irregular cyclic events (every three to six years): El Niño, the warm phase, which tends to produce intense rains and extend the warm season, followed by La Niña, the cold phase, which usually produces colder weather and severe droughts (Snell and Rea 1999; Dunbar et al. 1994; Riedinger et al. 2002). These climatic factors greatly impact vegetation patterns and animal population dynamics on the islands (Trueman and d'Ozouville 2010; Parent et al. 2008).

### *Plant communities*

Native flowering plants of the Galápagos Island comprise approximately 488 species from which ~50.4% are endemic to the archipelago (Jaramillo et al. 2017). Early assessments of the Galápagos flora indicated a close relationship with Neotropical flora, especially with the flora from the Andean region of South America (Hooker 1851; Porter 1976), suggesting colonization mainly occurred from closest areas of the continental mainland. It has been suggested that seeds arrived in the archipelago via transport by birds, oceanic currents, and wind (Porter 1983). Once established, an important fraction of species subsequently diversified. Among endemic species, it is estimated that 64.5% resulted from radiation events, with the rest a product of phyletic evolution (Tye and Francisco-Ortega 2011). There is still not enough information to estimate time frames for initial colonization or divergence events—however, the minimum divergence times estimated for endemic plants in the Galápagos currently ranges from 0.5 Ma in *Gossypium darwinii* (Small et al. 1998) to 2.5 Ma in *Tiquilia* (Moore et al. 2006).

Studies on plant diversity within the archipelago indicate that island size and isolation can explain variation in species richness among islands (Hamilton et al. 1964; Johnson and Raven, 1973). Yet other island properties, such as habitat diversity and age, could also have an important modifying influence (Connor and Simberloff, 1978; Van der Werff, 1983; Whittaker, 2008). One of the most prominent patterns of plant assembly on the archipelago is manifest in the steep climatic-altitudinal gradient within islands that defines island vegetation zones (Wiggins and Porter 1971). This strong vegetation structuring is a product of island elevation, ocean currents, and wind movement (Wiggins and Porter 1971; Trueman and d'Ozouville 2010). In general, on large islands with high elevations it is possible to identify five distinct climatic zones delineating plant diversity (i.e. from the lowlands to the highlands: littoral, dry, transition, humid, and high-altitude dry), whereas on islands with low elevation it is only possible to identify two broad vegetation types (i.e. littoral and dry) (Tye and Francisco-Ortega 2011).

The Galápagos flora is differentiated from the random species impoverishment that islands are also prone to undergo (Williamson, 1981) and has been characterized as a disharmonic plant assemblage (Darwin 1859; Porter, 1983). Disharmony usually refers to a distinctive taxonomic composition (i.e. with some groups overrepresented, and others poorly represented) in relation to the source pool (Carlquist, 1965; Williamson, 1981; Whittaker and Fernández-Palacios, 2007). A distinctive taxa composition on islands could result from biogeographic and ecological factors that impose filtering effects on species assembly (i.e. dispersal or environmental filtering), whereby only a subset of the species present in the species source pool (potential colonisers) are able to disperse and successfully establish on the islands (Carlquist, 1966, 1974; Williamson, 1981). Taxonomic disharmony could also be accentuated by evolutionary processes, such as the local speciation of those lineages that were able to successfully establish (Wilson, 1961; Grenslade, 1968, Gillespie 2007).

Across the Galápagos archipelago, a high proportion of weedy, long-distance dispersal species have been reported among the native flora (Darwin, 1839; Porter, 1983), suggesting that isolation from the mainland may have imposed a strong dispersal filter. However, recent reevaluations of dispersal syndromes (i.e. diaspore traits related to dispersal mechanisms) among native plants of the archipelago found that 36% of presumed colonizer species have unspecialized diaspore—diaspore with no traits associated to long-distance dispersal mechanisms such as dispersal by animals, ocean currents, or wind (Vargas et al. 2012). In addition, when the distributional extent of species across the islands was evaluated, species with unspecialized diaspore were found not to have more restricted distributions than species possessing traits associated with long-distance dispersal (Vargas et al. 2014). These findings question the assumed importance of dispersal limitation in driving plant assembly on the archipelago.

To date, the majority of studies on the Galápagos flora (as well as on other insular systems) have focused on geographic isolation and dispersal limitation as the predominant drivers of island community assembly. The relative importance of environmental filtering and evolutionary processes, such as speciation, in shaping plant assembly remains underexplored. The growing availability of ecological and evolutionary data (e.g. on species distributions, ecological traits, and phylogenetic relationships), as well as the recent development of phylogenetic community methods, provide new opportunities for examining these understudied factors, and for reevaluating the major forces shaping plant community structure.

### *Darwin's finches*

As documented for many remote locations, the Galápagos islands show an impoverished biota in relation to close neotropical continental regions. Among lineages that were able to colonize the archipelago, relatively few diversified on the islands; however those that did represent an important proportion of species diversity of the archipelago (Parent et al. 2008; Tye and Francisco-Ortega 2011). Among these lineages, Darwin's finches are best studied and represent a classic example of a rapid and young adaptive radiation (Grant and Grant 2008).

The 15 recognized species of Darwin's finches (14 from the Galápagos archipelago and one from Cocos Island) diverged from a common ancestor approximately 1.6-2 Ma (Petren et al. 2005) and through the course of the speciation process diversified in the shape and size of their beaks to adapt to different food resources (Grant 1999; Grant and Grant 2008). This rapid species radiation among finches was likely facilitated by the isolation of the archipelago, new ecological opportunities that favored local adaptation (e.g. climatic fluctuation; formation of new islands; glacial cycles), strong events of natural selection, competitive interactions, and interspecific gene flow (Grant and Grant 2006, 2008; Lamichhaney et al. 2015). A drying climate and a concomitant change in available food resources have been linked to the origin (100,000 to

300,000 years ago; Lamichhaney et al. 2015) of the two more recently diverged finch groups: the tree finches (which feed mostly on insects on trees) and the ground finches (which feed mostly on seeds on the ground) (Grant and Grant 2008). Further evidence for adaptive diversification comes from genetic studies, which have identified some regions of the genome under selection which are associated with craniofacial and beak development, involved in beak shape and size variation (blunt vs. pointed beak) among and within finch species (i.e. ALX1, HMGA2; Lamichhaney et al. 2015; 2016), and which could underlie observed intra- and interspecific differences in the use food resources.

The ecology of the adaptive evolution of finch beaks has been studied most closely within the ground finch group (genus *Geospiza*). Species of this group differ from each other in their body size and, most noticeably, in their beak size and shape (Grant and Grant 2008), with several studies showing variation in diet related to beak morphology, bite force, and food availability (Lack et al. 1947; Schluter and Grant 1984; Grant and Grant 1996; Herrel et al. 2005; De León et al. 2011; 2012). For example, Schluter and Grant (1984) showed that observed beak sizes among ground finches on each island closely matched their predictions based on distribution of seed sizes. In addition, feeding observations of sympatric species show that while finch diets can broadly overlap, when usually abundant shared items are scarce finches switch to feeding more on their preferred food sources—the diet to which they are best adapted (Grant and Grant 1996; De León et al. 2014). In the case of the large ground finch (*Geospiza magnirostris*), which has the largest beak, this is reflected in a switch towards larger and harder seeds; while the medium ground finch (*G. fortis*), which has an intermediate beak, eats more intermediate-sized seeds; the small ground finch (*G. fuliginosa*), which has a small and pointed beak, tends to eat smaller seeds; and the cactus finch (*G. scandes*), with a long and pointed beak, specializes on flowers and fruits from prickly pear cacti (*Opuntia*) (Lack 1947; Abbot et al. 1977; Grant and Grant 1996; De León et al. 2014). Severe changes in food source availability, are mediated by climatic events, such as El Niño or La Niña, can thus impose strong selection on beak morphology and drive rapid evolutionary response within finch populations (Grant and Grant 2008).

A long-term study of ground finches performed over 40 years on the island of Daphne Major illustrated the importance of abiotic environment to evolutionary dynamics, with evolutionary change in beak morphology within finch populations driven by environmental fluctuations (Grant and Grant 2002; Grant and Grant 2014). For instance, between 1976 and 1978 an intense drought caused a severe shortage of food, which led to a decline of approximately 85% in the *G. fortis* population. With the onset of drought, *G. fortis* individuals first depleted the small and soft seeds, which changed the distribution of seed size and hardness on the ground, which in turn caused a change in seed size selection; finches started to eat larger and harder seeds, such as *Tribulus cistoides,* that had not previously been common in their diet. As a consequence, the population underwent strong directional selection, favoring large birds with larger and deeper beaks (Boag and Grant 1981). Importantly, this long term study also showed that the strong directional selection on the evolution of beak morphology observed over short ecological timescales does not necessarily predict longer-term evolutionary dynamics. This is because selection on beak morphology varies in direction and magnitude through time according to environmental context, which is determined by largely unpredictable fluctuations in climate (Grant and Grant 2002).

Finches are selective feeders, preferentially feeding on seeds and fruit according to their size and hardness. It is this close coupling between diet and finch preferences that underlies the strong selection on finch beak morphology. It has additionally been suggested that this coupling might be reflected in important eco-evolutionary feedbacks between finches and their environment—i.e. the seed and plant communities upon which finches feed (Post and Palkovacs 2009; Hendry 2017). During dry periods, when the production and availability of seeds is reduced, selective consumption of seeds by finches could drive changes in seed size distributions, the feedback of which could affect finch evolutionary trajectories (as described above). Selective seed predation by finches could also change the species composition and structure of seed banks, which might scale up to impact the composition and structure of plant communities. It is also possible that seed predation by finches imposes selection on seed traits that could trigger co-evolutionary interactions between finches and the plants on which they feed—for example, harder seeds selecting for larger beaks that in turn drive evolution for increasing seed hardness. Such co-evolutionary interactions, which can be considered as a special case of eco-evolutionary dynamics (Post and Palkovacs 2009), can also result in arms race evolutionary dynamics. Grant (1981) suggested that *G. fortis* and *T. cistoides* might present one such example, with *G. fortis* imposing reciprocal selection on the fruit structures that protect the seeds of *T. cistoides,* particularly during dry periods, when other food sources are limited.

To date, there is no direct evidence of these eco-evolutionary feedbacks occurring between Galapagos finches and the plants on which they feed. Field observations suggest that finches can deplete seeds selectively, but it is not clear to what extend this affects seedbank communities, and whether potential changes in seed banks translate into shifts in plant communities. In addition, there has been very little work evaluating the importance of Darwin's finches as agents of selection of seed defense traits, with the exception of observations recorded by Grant in 1981, which were limited to one population of *T. cistoides* on Daphne Major Island.

In the following chapters, I address three key, but under-explored questions in the Galapagos finch-plant system, with the aim of improving our understanding of the processes driving community assembly and diversity in natural systems. First, I examine the relative roles of dispersal, habitat filtering, and speciation in shaping regional plant assemblies on the archipelago. Second, I test the importance of eco-evolutionary dynamics between Darwin's ground finches and plant communities at a local scale. Third, I evaluate the ecological and evolutionary signature of finch-plant reciprocal interactions among Darwin's ground finches and a focal plant species (*T. cistoides*) within a heterogenous landscape.

## Thesis organization

In Chapter 2, I use an ecophylogenetic approach to evaluate the relative importance of biogeographic, ecological, and macroevolutionary processes in shaping the Galápagos flora. First, I test whether the current Galápagos flora represents a nonrandom subset of the continental species pool, which would suggest Galápagos species underwent strong dispersal or habitat filtering. Second, I use information on the ecological dispersal traits and environmental niche preferences of potential colonisers and native species to test if colonization success is better explained by dispersal limitation or habitat filtering. Third, I examine the phylogenetic structure of island assemblages across the archipelago and test whether observed variation among islands is associated with island attributes and *in situ* diversification.

In Chapter 3, I use field observations and exclusion experiments to examine potential eco-evolutionary feedbacks between Darwin's finches and plant communities. First, I test whether finch feeding patterns are random or if they show preferences based on seed traits. Second, using information from exclusion experiments, I test the effect of seed predation by finches on the structure of seed banks and plant communities at two sites that present differences in finch beak size distributions. Third, I explore potential factors that could decouple eco-evolutionary interaction between finches and plants in the archipelago.

In Chapter 4, I explore the ecological and evolutionary signature of reciprocal interactions between Darwin's ground finches and *T. cistoides*. For this, I use seed predation information from 30 natural populations of *T. cistoides* sampled across seven islands over three years. First, I examine whether the intensity of seed predation and the strength of selection imposed on *T. cistoides* fruits vary within and across islands and over time. As different islands are characterized by different finch communities and the archipelago experienced important climatic fluctuations over the years of data collection, I thus expected to see significant differences in eco-evolutionary dynamics among locations and over years. Second, I test whether variation in fruit defense traits among islands is predictably associated with differences in finch community composition, which could suggest an adaptive response of fruit defenses to selection pressure imposed by finches.

Finally, in Chapter 5, I briefly summarize and discuss the contributions of this thesis to our knowledge of the study system and how these new findings advance our understanding of the effect of interactions between ecological and evolutionary processes on community assembly. I conclude by suggesting some directions for future research.

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# CHAPTER 2:

# Habitat filtering not dispersal limitation shapes oceanic island floras: species assembly of the Galápagos archipelago

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## Abstract

Remote locations such as oceanic islands typically harbor relatively few species, some of which go on to generate endemic radiations. Species colonizing these locations tend to be a non-random subset from source communities, which is thought to reflect dispersal limitation. However, non-random colonization could also result from habitat filtering, whereby only a few continental species can become established. We evaluate the imprints of these processes on the Galápagos flora by analyzing a comprehensive regional phylogeny for ~39,000 species alongside information on dispersal strategies and climatic suitability. Contrary to expectations, habitat filtering was more important than dispersal limitation in determining species composition. This finding may help explain why adaptive radiation is common on oceanic archipelagoes – because

colonizing species can be relatively poor dispersers with specific niche requirements. We therefore suggest that the standard assumption that plant communities in remote locations are primarily shaped by dispersal limitation deserves reconsideration.

## Introduction

Island systems have provided the inspiration for many key theories in ecology and evolution (Warren et al. 2015), including natural selection (Darwin 1859; Wallace 1869), community assembly (Diamond 1975), and island biogeography (MacArthur and Wilson 1967). In studies of island systems, particular emphasis has been placed on how biogeographic processes (e.g., immigration, extinction, speciation) and island characteristics (e.g. area, isolation, age) influence patterns of species diversity (e.g. Hamilton et al. 1963; Johnson and Raven 1973; Losos and Schluter 2000; Whittaker et al. 2008). However, ecological and evolutionary features of potential colonizers might additionally impact island community assembly (Lomolino 2000; Gillespie 2016). In this study, we attempt to disentangle the relative importance of dispersal, environmental filtering, and speciation in shaping the Galápagos flora.

The Galápagos flora has been characterized as a disharmonic species assemblage (Darwin 1859; Porter 1983). Disharmony, a prominent pattern among oceanic island biotas, refers to a distinct taxonomic composition relative to continental source regions; i.e. an overrepresentation of some groups and an underrepresentation of others (Gillespie et al. 2012). This pattern suggests the action of a strong dispersal filter, such that species composition is primarily determined by its isolation from the mainland (about 1000 km for the Galápagos). Most of the Galápagos flora was thought to have colonized the archipelago because they possessed traits that facilitated long-distance dispersal mechanisms (e.g. Hooker 1847; Carlquist 1967; Porter 1983). However, dispersal is only the first step in the colonization process. Evidence showing that an important proportion of native colonizers have no obvious mechanism for long-distance dispersal (Vargas et al. 2012), and that some species having long-distance dispersal mechanisms show relative restricted distributions within the archipelago (Vargas et al. 2014) suggest that factors other than dispersal potential can limit species establishment.

Environmental conditions might provide an additional filter to species establishment on oceanic islands (Carlquist 1965). For example, the Galápagos archipelago has desert and subtropical environments (Palmer and Pyle 1966), which could have favored establishment by some species over others (Porter 1983). Previous work has suggested that plant species composition on the Galápagos is correlated with island habitat diversity, particularly the availability of wet and dry environments, which are associated with island area and elevation (Hamilton et al. 1963; Johnson and Raven 1973; Hamann 1981; Van Der Werff 1983). However, few studies have directly evaluated the relative importance of dispersal versus environmental filtering in structuring insular plant assemblages. The Galápagos archipelago provides an excellent system to explore these relationships due to its oceanic origin, geographic isolation, and floristic similarity to adjacent continental biotas (Hooker 1847; Svenson 1946; Porter 1984).

Here, we evaluate the role of biogeographic factors in structuring the species composition of the Galápagos archipelago by examining the phylogenetic structure of plant assemblages. Phylogenetic approaches for ecological inference have most commonly been applied at local community level (Cavender-Bares et al. 2009; Mouquet et al. 2012), but they can also be applied to larger spatial scales, where they might capture the signature of historical biogeography and diversification (Davies and Buckley 2012, Emerson and Gillespie 2008; Baeten et al. 2015). While recent work by Vargas et al. (2014) and Nogales et al. (2016) has integrated evolutionary and ecological information to examine species dispersal on the Galápagos, our study is the first to directly test the relative importance of dispersal versus habitat filtering.

First, we analyzed the phylogenetic structure of the Galápagos flora relative to potential continental species pools. We might expect strong filtering to generate phylogenetic clustering (i.e. species more related than expected by chance), assuming key ecological traits show phylogenetic conservatism (Webb et al. 2002). Second, to disentangle the effect of dispersal versus habitat filtering, we examined the ecological characteristics of successful and unsuccessful colonizers, and tested whether species dispersal strategies versus environmental niche preferences better predict colonization success. Third, we assessed the processes driving phylogenetic structure across different islands within the archipelago. If habitat filtering is the primary determinant of species composition, we might expect greater phylogenetic overdispersion (species less related than expected by chance) on larger islands because they encompass multiple habitat types (Cavender-Bares et al. 2004), and greater phylogenetic turnover between islands that are most dissimilar in their abiotic environments rather than between islands that are more geographically distant.

We show that the native Galápagos flora is a phylogenetically clustered subset of the continental pool of potential colonizers. We also provide new evidence that indicates habitat filtering was more important than dispersal limitation in determining species composition on the archipelago and across individual islands within the archipelago. Last, we show that speciation influences the phylogenetic structure of plant assemblages by increasing phylogenetic clustering, on the archipelago, and increasing phylogenetic overdispersion on individual islands.

## Material and methods

### *Source areas and phylogenies*

To explore the processes shaping the Galápagos flora, we first identified the most likely geographic source pool from which native flowering plants could have originated. Using plant checklists, public databases, and literature (see Supplementary Information S1 in Appendix), we compiled a list of the 216 native, non-endemic species present in the archipelago and annotated their presence/absence in 15 surrounding regions including South America (mostly partitioned by country), Mesoamerica (Mexico and Central America), the West Indies, and North America. For each of the 15 putative source regions, we estimated: (1) a similarity index (SI) based on the proportion of the native, non-endemic, Galápagos species found in that region and (2) the probability that any given native, non-endemic, species found in the archipelago originated from that region ($p_i$), following Papadopulos and Baker 2011 (see Supplementary Information S1).

Next, we used the above floristic indices to define three potential regional species pools according to their likely contribution to the Galápagos flora: a large species pool (38,905 species) including Mesoamerica, Venezuela, Colombia, Ecuador, and Perú; a medium species pool (25,486 species) including Colombia, Ecuador and Perú; and a small species pool (6,465 species) restricted to the continental region of Ecuador (Fig. 2.1). Species names were standardized to The Plant List 1.1 <http://www.theplantlist.org/> using the taxonstand 1.7 R package (Cayuela et al. 2012). Unmatched names were rechecked using the Taxonomic Name Resolution Service <http://tnrs.iplantcollaborative.org> (Boyle et al. 2013). Higher taxonomic membership was corrected to the APG III (Angiosperm Phylogeny Group 2009).

Phylogenetic relationships were reconstructed based on the comprehensive species-level phylogeny of vascular plants generated by Zanne et al. (2014) and updated by Qian and Jin (2016). This phylogeny includes 30,193 angiosperm species and was used as a backbone onto which we placed additional species. From the species present in our species pools (38,905), 5,196 matched directly to those sampled by Zanne et al. (2014), and the remainder were added as polytomies at the root node for their genus membership using the merge tool implemented in the R package pez. 1.1 (Pearse et al. 2015). Species within genera that were not represented on the backbone tree (4,601 species) could not be included; we thus generated an additional tree placing taxa as polytomies at the root node for their families to favor species completeness.

### *Phylogenetic structure of the Galápagos flora*

We used the R-package picante 1.6 (Kembel et al. 2010) to calculate two commonly used indices of phylogenetic structure: Faith's (Faith 1992) phylogenetic diversity (PD) and the mean pairwise phylogenetic distances (MPD). To test the significance of the observed patterns and calculate standardized effect size of these metrics (SES.PD and SES.MPD) we compared observed PD and MPD values to null expectations generated by drawing species at random (999 runs) from each species pool (large, medium, and small). Positive SES values indicate phylogenetic overdispersion, whereas negative SES values indicate phylogenetic clustering. Here we place more emphasis on the metric of MPD because our interest was in measuring phylogenetic divergence rather than phylogenetic richness (Tucker et al. 2016), and the greater sensitivity of SES.PD to more terminal structure makes it better suited for exploring assembly processes working at finer temporal and spatial scales (Mazel et al. 2015). To examine the importance of speciation in driving archipelago phylogenetic structure, we recalculated each metric excluding species that were endemic to the Galápagos (156 species considered here) under the assumption that endemic species are more likely to be the products of *in situ* speciation.

Phylogenetic signal in colonization was estimated using the D statistic (Fritz and Purvis 2010), as implemented in the R package caper 0.5.2 (Orme et al. 2013), on the binary matrix of presences/absences in the Galápagos for each species pool. The D statistic allows us to test if the presence of flowering plants in the Galápagos is independent from phylogeny (D = 1), or if it follows the distribution expected under a Brownian motion model of evolution (D = 0). D values close to 0 would be expected if traits associated with colonization success (e.g. long-distance dispersal ability, vegetative propagation, long flowering periods) are tightly conserved on the phylogeny.

### *Dispersal and habitat filtering*

We evaluated the importance of dispersal and environmental filtering in determining the composition of the Galápagos flora by fitting a phylogenetic logistic regression (Ives and Garland 2010) with species presence/absence on the Galápagos archipelago as response, and species dispersal strategy and climatic suitability as predictors. For this analysis, we considered all species present in the medium regional pool, which we determined as the most likely source pool for Galápagos species based on our analyses of indices of floristic similarity and geographic distance.

We compiled information on species dispersal (see Appendix S2) and classified species as possessing or lacking a long-distance dispersal strategy. Species having zoochory (animal dispersal), anemochory (wind dispersal), or hydrochory (water dispersal) dispersal were classified as long-distance dispersers (except species that use insects as vectors). Species with unassisted dispersal, seeds that drop to the ground close to or beneath the parent plant, or seeds actively dispersed by the parent plant by explosive mechanism were classified as lacking a long-distance dispersal strategy (Willson 1993; Gómez and Espadaler 1998; Thomson et al. 2010). For species without a documented dispersal mechanism, we used descriptions of diaspore morphology from the literature to assign most likely strategy (Ridley, 1930; Van der Pijl 1982; Willson et al. 1990; Hughes et al. 1994, see details in Supplementary Information S2). In total, we were able to obtain dispersal information for 4339 species (data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.43b1t).

To estimate of climatic suitability of the Galápagos for potentially colonizing species, we quantified the distance between each species' continental climatic niche and the climatic space available on the Galápagos Islands. For this, we first compiled distribution data from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>) using the R package rgbif 0.9.3 (Chamberlain et al. 2016), then for each species' spatial location recorded within the putative source region (i.e. Colombia, Ecuador, and Perú) we extracted 19 climatic variables from WorldClim at a resolution of 30 arc-seconds (Hijmans et al. 2005, <http://www.worldclim.org>). Species with fewer than five localities were excluded from the analyses to avoid potential bias associated with small sample sizes, leaving a total of 11,934 included species. Species' continental climatic niches were summarized as the first three components of a principal component analysis on the 19 climatic variables. Next, we used the same WorldClim variables to characterize the climatic space of the Galápagos archipelago. We then calculated two climatic suitability metrics for each species. The first metric, niche dissimilarity (ND), was derived using the hypervolume package in R (Blonder et al. 2014), and represents the euclidean distance between each species' hypervolume centroid and the centroid for the climatic hypervolume represented by the Galápagos archipelago. The second metric, niche overlap (NO), was calculated in the nicheROVER 1.0 package (Swanson et al. 2015), and represents the probability that a randomly drawn point from a given species' climatic niche space falls within the Galápagos Islands climate space, using 1000 Monte Carlo draws.

We tested whether long-distance dispersal strategy and/or higher climatic suitability better explain species' presence on the Galápagos archipelago by fitting phylogenetic logistic regression models in the R package phylolm 2.3 (Ho and Ané 2014). The predictor variables were a binary categorization that scored each species for long-distance dispersal strategy (LDD), niche dissimilarity (ND), and niche overlap (NO). Because we were not able to obtain data on dispersal strategy and climatic suitability for all species, for model comparisons we fit models only using species that had data on both dispersal and climatic suitability (3,029 species). Model comparisons were performed using Akaike information criterion (AIC). Given the imbalance in our data set (162 species present and 2867 absent from the archipelago), we also evaluated statistical relationships across 1000 subsets of 162 species randomly drawn from the set of species absent from the archipelago. For each subset, we fit and compared three models: one with LDD as the predictor variable, the second with ND as the predictor variable and the third including both as predictor variables. In addition, we fit models separately for dispersal and climatic suitability including all species in the dataset, and used an alternative categorization of species' dispersal strategy based on the number of long-distance dispersal strategies to evaluate whether having multiple strategies was also a predictor of colonization success (Vander Wall and Longland 2004; Vargas et al. 2015).

### *Phylogenetic structure of islands within the archipelago*

To evaluate community composition on individual islands, we examined the association between phylogenetic structure, island geography, and climate. First, we pruned the regional phylogeny to just the species considered native to the archipelago (216 native non-endemics plus 156 endemics) for which we had data on distributions among islands (fourteen main islands) (Wiggins and Porter 1971; Jaramillo Díaz et al. 2015); this species set was considered to be the new regional source pool. Second, for each island assemblage we estimated SES.PD and SES.MPD (see above), using random draws from the regional species pool as our null. See Supplementary Information S3 for species list and geographical distributions.

Statistical relationships were assessed by fitting multivariate linear models with phylogenetic structure (SES.PD and SES.MPD) as the response variables and four key island characteristics as predictors: area (km$^2$), annual mean temperature (°C) and annual precipitation (mm), obtained from Weigelt et al. (2013), and island isolation (km), measured as the mean distance from each island to all the other main islands within the archipelago. Minimum distance between each pair of islands was obtained from Bisconti et al. (2001) and Hamilton and Rubinoff (1967). To evaluate the importance of speciation on phylogenetic structure, we (1) recalculated each SES metric excluding species that were endemic to the archipelago and compared results between the two analyses, and (2) included the degree of island endemism, calculated as the proportion of endemic species present on each island, as an additional predictor. Also, we fitted an additional model including the estimated minimum geologic age (million years) for each island, from Parent et al. (2008), to control for the effect of island ontogeny. All predictor variables were log transformed and standardized to a mean of 0 and a standard deviation to 1 prior to analysis. We did not detect significant multi-collinearity among predictors, as assessed by variance inflation factors (all VIFs < 10; Quinn and Keough, 2002). We thus generated the set of all possible additive models using the MuMIn 1.15.6 R package (Bartón 2016), and then calculated standardized coefficients for each predictor using model averaging with corrected $\Delta AIC_C < 4$ (Burnham and Anderson 2004).

Last, we calculated phylogenetic beta diversity (βMPD) among island assemblages using the R-package picante 1.6 (Kembel et al. 2010), and examined the association between βMPD and differences in island environment and geographic distance separating islands using partial Mantel tests in vegan 2.3-3 (Oksanen et al. 2015). Both mantel partial correlations were conditioned on area. Environmental differences among islands were calculated as euclidean distances of combined island annual mean temperature (ºC), annual precipitation (mm), minimum values of annual mean temperature range (ºC), and the coefficient of variation in monthly precipitation, from Weigelt et al. (2013).

# Results

## *Archipelago assembly from continental floras*

The Galápagos flora represents a highly phylogenetically clustered subset of the potential colonizers that are present in continental America. Species that are found on the archipelago are more closely related than expected by chance according to both phylogenetic structure metrics SES.PD and SES.MPD (Table 1, Fig. 2.2). Clustered patterns were consistent across all three putative continental source pools (small, medium and large). Stronger clustering was found using the largest source pool (SES.PD = -6.87; SES.MPD = -9.34, both $p$ <<0.05), but remained significant even when assuming the small pool of potential colonizers (SES.PD = -5.90; SES.MPD = -8.16, both $p$ <<0.05). Of the three species pools, the regions of Ecuador, Perú, Colombia, Venezuela plus Mesoamerica (large pool) showed the greatest similarity with the Galápagos flora (SI >> 0.70), whereas Ecuador, Perú plus Colombia (medium pool) had the highest probability of being the unique source of origin for species in the archipelago ($p_i = 0.17$, $p_i = 0.11$, and $p_i = 0.10$ respectively). However, more than 90% of the native non-endemic Galápagos angiosperms are found in the smallest and closest continental pool, the flora of Ecuador (Fig. 2.1, Supplementary Information S1).

Phylogenetic clustering was stronger when endemic species were included in the analysis (Table 2.1), revealing the importance of macroevolutionary processes, such as speciation, in shaping regional patterns of phylogenetic structure. Lower values of SES.MPD than SES.PD suggest that clustering occurs deep in the phylogeny, as SES.MPD is more sensitive to structure towards the root of the tree (Webb et al. 2002; Mazel et al. 2015). Similar patterns were observed using the reduced phylogeny with greater tip resolution (see methods above and Supplementary Information S4).

We found a highly significant phylogenetic signal in colonization, although D values (D = 0.87, 0.84, and 0.76 for the large, medium and small pools, respectively) were significantly greater than Brownian motion expectations ($D > 0$; $p < 0.001$). We suggest that this likely reflects a tendency for closely related species to share similar key traits related to dispersal and probability of establishment. Colonization success was correlated with species' climatic suitability (Table 2.2), with the top-ranked model by AIC including niche dissimilarity (ND) as the only predictor variable. Successful colonizers tend to have continental distributions encompassing climates that are similar to the Galápagos (e.g. niche dissimilarity [ND]: $z = -13.247$; $p < 0.001$). In contrast, long-distance dispersal (LDD) explained no additional variance ($\Delta AIC = 1.66$), and the model including only LDD had low support ($\Delta AIC = 215.86$). We found no association between having multiple dispersal strategies and colonization success (see Supplementary Information S5), and niche dissimilarity was always a better predictor of colonization success than the number of long-distance dispersal strategies. Repeating models across balanced subsets of data (equal number of species present and absent from the archipelago) produced broadly comparable results: models including both predictors (ND and LDD) did not show a better fit (AIC mean ± SD; 320.75 ± 16.44) to the data than the models including ND only (AIC = 319.76 ± 16.98). Models fit separately for dispersal strategy and climatic suitability including all species are included in Supplementary Information S5.

### *Phylogenetic structure of islands within the archipelago*

Island assemblages showed mixed patterns of phylogenetic structure (Fig. 2.3A). Among the fourteen islands, four showed significant phylogenetic structure, with Española (SES.MPD = -2.89, $p$ = 0.005), Floreana (SES.MPD = -1.81, $p$ = 0.032), and Pinzón (SES.MPD = -2.34, $p$ = 0.023) demonstrating phylogenetic clustering, and Santa Cruz demonstrating phylogenetic overdispersion (SES.MPD = 2.59, $p$ = 0.001). Equivalent results for SES.PD are reported in the supplemental material (Supplementary Information S6). When endemic species were excluded from the analysis, all islands showed an increased trend towards clustering (Fig. 2.3A).

Averaged multivariate models showed that SES.MPD is significantly associated with island area ($z$ = 0.583; $p$ = 0.022) and annual precipitation ($z$ = 0.569; $p$ = 0.030), and weakly associated with island annual mean temperature ($z$ = 0.522; $p$ = 0.056), but it is not correlated with island isolation ($z$ = -0464; $p$ = 0.094) or degree of endemism ($z$ = -0.409; $p$ = 0.224). Larger islands, with higher precipitation and mean annual temperature have assemblages that tend to be more phylogenetically overdispersed, whereas smaller islands, with lower annual precipitation and mean annual temperature tend to be more phylogenetically clustered (Table 2.3, Fig. 2.3B). Full models are presented in Supplementary Information S7. Including island ontogeny (age) did not appreciably alter the relationship between phylogenetic structure and the other predictor variables (Supplementary Information S7).

The analysis of phylogenetic turnover among islands revealed that geographically close islands were no more similar in phylogenetic composition than geographically distant islands (r = 0.12, $p$ = 0.25), but turnover was lower between islands with similar climates (r = 0.43 $p$ = 0.001).

## Discussion

The native flora of the Galápagos is a phylogenetically clustered subset of the regional continental species pool, with Ecuador, Perú, and Colombia being the likely source for most colonizing species. Contrary to standard expectations for oceanic islands, our results indicate that the Galápagos flora was shaped mainly by habitat filtering and not dispersal limitation. First, the match between a species' continental climate niche and the Galápagos climate was the single best predictor of colonization success. Second, plant phylogenetic structure on individual islands within the archipelago was better explained by island area and climate than by island isolation. Third, islands with plant communities that were phylogenetically similar shared similar climate conditions but were not close geographically. *In situ* speciation also shapes the phylogenetic structure of the archipelago by increasing clustering with respect to the continental pool, but it has the opposite effect on individual islands.

## *Archipelago assembly from continental floras*

We might expect species assemblages on islands to show, at a regional scale, strong phylogenetic clustering (Emerson and Gillespie 2008), and clustered patterns have been reported for angiosperm island assemblages with respect to the total pool of insular species (Weigelt et al. 2015). We find that this pattern also holds true for the Galápagos flora relative to the continental source pool. Our results indicate that the immediately adjacent landmasses of western South America were most likely the main source pool of colonizers for the Galápagos, matching previous work by Porter (1984). The relative contribution of the different continental floras might differ somewhat if we also consider the Galápagos endemic species, although it is more challenging to accurately infer the geographic histories of such species, and continental South America remains their most likely area of origin (Andrus et al. 2009, Tye and Francisco Ortega, 2011).

Phylogenetic clustering of species assemblages and a phylogenetic signal in colonization together suggest that assembly processes determining the composition of the Galápagos flora are influenced by species' traits that co-vary with phylogeny. This covariance could be driven by either dispersal or habitat filtering. If dispersal was more important, the presence of species on the archipelago should be best explained by their ability to disperse across long distances. If environmental filtering was more important, the presence of species should be best explained by climatic suitability. We found evidence for a role of both processes, but environmental filtering based on climate suitability was most important. Our results might seem unexpected for an oceanic archipelago 1000 km from the source pool, which should impose a strong dispersal filter (Nip-Van Der Voort et al. 1979; Kadmon and Pulliam 1993; Whittaker et al. 1997). However, we suggest that given the sufficient time, such as the approximately 14 million years in the case of the Galápagos archipelago (Werner et al. 1999), even poor dispersers could have an opportunity for colonization, but the lack of suitable habitats could be an insurmountable barrier to establishment. Indeed, the severe conditions for plant growth of the arid Galápagos environments likely prevented the establishment of immigrant species from adjacent continental habitats (Hamann 1981).

It remains possible that co-variation between dispersal strategy and climatic suitability reduced our ability to differentiate between these potential influences – and we do not dispute that overrepresentation of some species groups on islands is influenced by dispersal ability (see e.g. Heleno and Vargas 2015). However, our inference that high dispersal ability is not *essential* is consistent with observations that a substantial proportion of the Galápagos flora, and that of other oceanic islands, has no obvious mechanism for long-distance dispersal (Carlquist 1966a; Porter 1983; Vargas et al. 2012; Heleno and Vargas 2015). This pattern was previously ascribed, at least in part, to the loss of dispersal ability on islands (Carlquist 1966b, c, 1974; but see Patiño et al. 2015), yet some continental ancestors of island species also lack such mechanisms (Vargas et al. 2014). For these species, colonization seems to be achieved by chance assocation with dispersal vectors, such as the muddy feet of wading birds (Darwin 1859). Indeed, a new consensus is growing that long-distance dispersal events are often associated with non-standard dispersal mechanisms (Higgins et al. 2003; Nathan 2006), and that such mechanisms might be relatively common. Hence, dispersal might be less limiting than often assumed, at least over long time periods, whereas the importance of environmental matching between source pools and colonization sites may have been underestimated.

### *Island assembly within the archipelago*

Individual island assemblages also showed a general tendency for phylogenetic clustering consistent with predictions of strong filtering. However, this pattern was not universal, with some islands (e.g., Santa Cruz) instead showing evidence for overdispersion. The relative importance of different processes shaping species composition thus seems to vary among islands. In particular, phylogenetic clustering could be driven by island isolation, speciation, and/or strong environmental filtering by a habitat type on phylogenetically conserved traits (Webb et al. 2002; Emerson and Gillespie 2008); whereas phylogenetic overdispersion could result from competitive exclusion of closely related species, filtering across multiple habitats on an island, and/or environmental filtering for a single habitat type when key traits are convergent in the phylogeny (Webb et al. 2002; Cavender-Bares et al. 2004).

We found that phylogenetic overdispersion was more common on islands that were larger, warmer, and wetter. We suggest that this pattern is unlikely to arise via competitive interactions, which should be stronger on *smaller* islands with less habitat heterogeneity (Cardillo et al. 2008; Emerson and Gillespie 2008). Instead, we suggest that larger islands show phylogenetic overdispersion as a result of environmental filtering, because larger islands harbor multiple habitats (Van Der Werff 1983; Hamann 1984; Kohn and Walsh 1994; Parent and Crespi 2006) that should favor the establishment of different clades with different niche requirements. In contrast, if dispersal were the primary process shaping island phylogenetic structure, we would expect more isolated islands to show greater phylogenetic clustering (assuming phylogenetic conservatism of dispersal traits). However, we found no association between phylogenetic structure and island isolation. In addition, phylogenetic turnover among islands was correlated with climate differences rather than geographic distances between them, providing further support that habitat filtering is more important than dispersal in structuring species assemblages.

### *Speciation and phylogenetic structure*

Oceanic archipelagoes provide many classic examples of rapid evolution and adaptive radiation, such as silverswords in Hawaii, Darwin’s finches in Galápagos, and anoles in the Greater Antilles. We expected that such speciation for plants in Galápagos would increase phylogenetic clustering (Vamosi et al. 2009). As predicted, the inclusion of endemics, some of which form *in situ* radiations, elevated clustering across the archipelago. However, the inclusion of endemics tended to reduce rather than enhance clustering on individual islands. We suggest this trend may reflect the restricted distributions of endemic species across the archipelago (Vargas et al. 2014) and speciation via anagenesis (Stuessy et al. 2006). A high frequency of speciation by anagenesis, as may be indicated by the low proportion of congeneric endemic species on individual islands (about ~30% of endemics in our analysis are found as single members of their genus), might simultaneously drive phylogenetic clustering of the archipelago flora and phylogenetic overdispersion within individual islands because sister taxa may rarely co-occur on the same island.

### *Concluding remarks*

The patterns we report were robust across our sensitivity analyses; however, we acknowledge several limitations that could be improved in future work. For example, it is likely we did not sample the complete continental species pool, and our phylogenetic tree lacked resolution at the species level; although this is not expected to impact our conclusions (Swenson 2009), it limits our ability to detect processes acting at finer spatial and temporal scales. In addition, the WorldClim data used for our habitat analysis can be less precise in regions with few climatic stations, such as tropical mountainous regions (Soria-Auza et al. 2010). However, our ability to detect a climate signal despite these limitations suggests that environmental filtering is likely strong. Finally, the Galápagos flora has likely been influenced by multiple processes that we did not consider, including volcanic activity, changes in sea levels, and island subsidence (Ali and Aitchison 2014, Geist et al. 2014; Trianthis et al. 2016). We explored island ontogeny, which might capture some of this complex history. Although this factor was additionally significant, it did not change our conclusions regarding the effect of dispersal and habitat filtering.

In conclusion, we show that the native Galápagos flora is a phylogenetically clustered subset of species from the adjacent mainland, with Ecuador, Perú, and Colombia being the most important species sources. Contrary to expectations, we found that habitat filtering rather than dispersal limitation was likely the predominant process structuring plant species composition. We suggest that the importance of filtering by environment may have been underestimated in previous studies of species assembly on oceanic islands, where dispersal filtering is traditionally assumed to be the dominant driver. In particular, while dispersal limitation might be most important in early stages of colonization, other processes (e.g., habitat filtering, speciation, competition) should later dominate as more species arrive from the regional pool and habitats become occupied (Silvertown 2004; Emerson and Gillespie 2008). We note that our results might help explain why adaptive radiation is common on oceanic archipelagos as they indicate that some colonizing species are not necessarily good dispersers but might have specific niche requirements, facilitating reproductive isolation.

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**Table 2.1.** Phylogenetic clustering of the Galápagos archipelago estimated using three potential source pools (small, medium and large). Standard effect sizes of phylogenetic diversity (SES.PD) and mean pairwise distances (SES.MPD) calculated from 999 random draws from the phylogeny. Negative values indicate phylogenetic clustering. Significant patterns relative to the null model are marked with an asterisk (*).

| **Species pool** | | **SES.PD** | **SES.MPD** |
|---|---|---|---|
| **Small** | Native species | -5.90* | -8.16* |
| | Native species, non-endemics | -3.99* | -3.54* |
| **Medium** | Native species | -6.72* | -8.52* |
| | Native species, non-endemics | -4.49* | -3.79* |
| **Large** | Native species | -6.87* | -9.34* |
| | Native species, non-endemics | -4.75* | -6.19* |

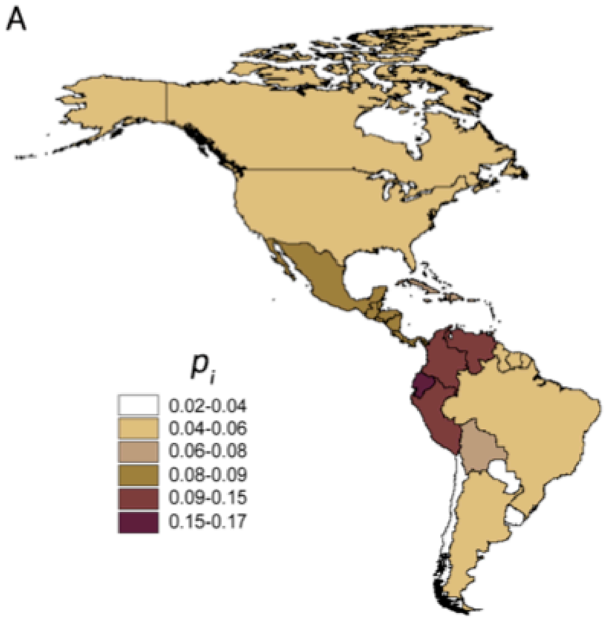
**Table 2.2** Phylogenetic logistic regression of species colonization success on the Galápagos archipelago. The response variable was presence/absence of species in the archipelago (P/A, 0 = absence, 1 = present). Species dispersal strategy was coded as a binary variable representing species' long-distance dispersal strategy (LDD, 0 = absent, 1 = present). For species climatic suitability, we used two variables (see methods): niche dissimilarity (ND, lower values indicate higher similarity) and niche overlap (NO, higher values indicate greater overlap). 100 bootstrap replicates were used to estimate confidence intervals (CI).

| **Parameter** | **Coefficient** | **z value** | **95% CI** | ***P* values** | **AIC** |
|---|---|---|---|---|---|
| Model: P/A ~ ND | | | | | 929.165 |
| ND | -3.508 | -13.247 | (-3.922 – -3.069) | $p < 0.001$ | |
| Model: P/A ~ ND + LDD | | | | | 930.823 |
| ND | -3.069 | -11.464 | (-3.644 – -2.611) | $p < 0.001$ | |
| LDD | 0.596 | 1.589 | (-0.140 – 1.381) | $p = 0.112$ | |
| Model: P/A ~ NO | | | | | 983.761 |
| NO | 0.553 | 11.719 | (0.398 – 0.640) | $p < 0.001$ | |
| Model: P/A ~ NO + LDD | | | | | 985.910 |
| NO | 0.552 | 11.783 | (0.297 – 0.640) | $p < 0.001$ | |
| LDD | -0.037 | -0.126 | (-0.704 – 0.460) | $p = 0.900$ | |
| Model: P/A ~ LDD | | | | | 1145.028 |
| LDD | -0.772 | -3.312 | (-1.172 – -0.371) | $p < 0.001$ | |

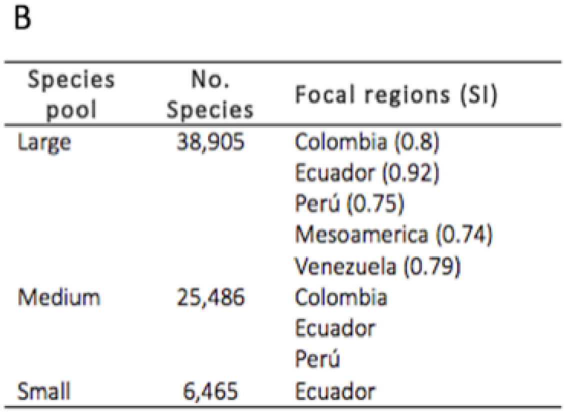
**Table 2.3** Multiple linear regression evaluating drivers of island phylogenetic structure (SES.MPD). Standardized coefficients were estimated by averaging the parameters from the top $AIC_C$ models ($\Delta$ $AIC_C < 4$). Predictor variables included area ($km^2$), annual mean temperature (°C) and annual precipitation (mm), island isolation (km), and endemism (calculated as the proportion of endemic species present on each island). Variables were log transformed and standardized to a mean of 0 and standard deviation of 1 prior to analysis. Confidence intervals are shown in parentheses (CI).

| **Predictor variable** | **Coefficient (z)** | **Adjusted Standard error** | **95% CI** | ***P* values** |
|---|---|---|---|---|
| Area | 0.583 | 0.254 | (0.086 – 1.080) | $p = 0.022$ |
| Temperature | 0.522 | 0.273 | (-0.013 – 1.057) | $p = 0.056$ |
| Precipitation | 0.569 | 0.263 | (0.055 – 1.084) | $p = 0.030$ |
| Isolation | -0.464 | 0.277 | (-1.008 – 0.080) | $p = 0.094$ |
| Endemism | -0.409 | 0.337 | (-1.069 – 0.250) | $p = 0.224$ |

**Figure 2.1** Potential species source pools for the Galápagos flora. **A.** Map showing focal regions shaded by, $p_i$, the probability of each area of being the unique source of origin of any native Galápagos species (see Supplementary Information S1). **B.** Size (number of species) and focal regions of selected species pools. Similarity index (SI) measured as the proportion of native, non-endemic, angiosperms from the Galápagos present in each region.



B



| Species pool | No. Species | Focal regions (SI) |
|---|---|---|
| Large | 38,905 | Colombia (0.8)<br>Ecuador (0.92)<br>Perú (0.75)<br>Mesoamerica (0.74)<br>Venezuela (0.79) |
| Medium | 25,486 | Colombia<br>Ecuador<br>Perú |
| Small | 6,465 | Ecuador |

**Figure 2.2** Phylogenetic structure of the Galápagos flora. Phylogeny of species within the medium size pool (Colombia, Ecuador, and Perú); red bars indicate species native to the Galápagos Islands, and gray bars non-native species. Native species to the archipelago are more closely related than expected by chance according to the standard effect sizes of phylogenetic diversity (SES.PD) and mean pairwise distances (SES.MPD) (SES.PD = -6.72, $p$ = 0.001; SES.MPD = -8.52, $p$ = 0.001).

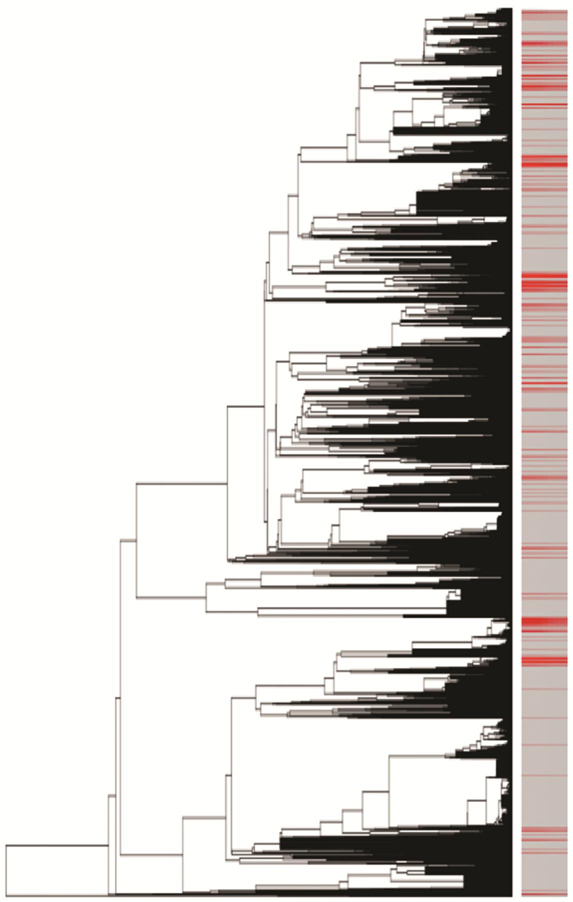
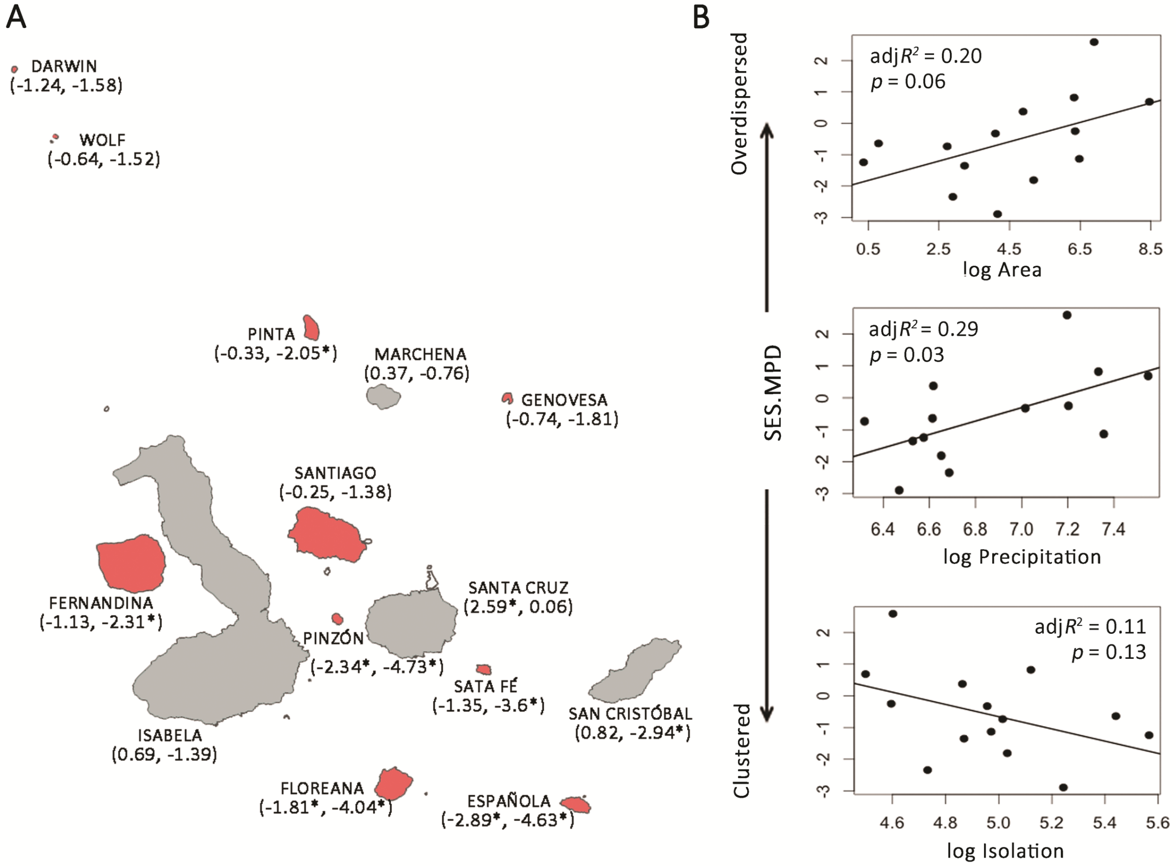


**Figure 2.3** Island phylogenetic structure. **A.** Map of the 14 main Galápagos islands colored by their phylogenetic structure. Red indicates phylogenetic clustering and grey indicates phylogenetic overdispersion with respect to the species pool for the archipelago. In parentheses, standard effect sizes of mean pairwise distances (SES.MPD) for species on each island, with and without including endemic species respectively. Positive values correspond to overdispersed assemblages, whereas negative values correspond to clustered assemblages, significant SES.MPD values indicated by an asterisk (*). **B.** Biplots showing the single effect of island area [$km^2$], annual precipitation [mm], and isolation [km] on SES.MPD. However, multivariate linear models showed significant and independent effects of area (z = 0.583; $p$ = 0.022), and annual precipitation (z = 0.569; $p$ = 0.030), but not isolation (z = -0.464; $p$ = 0.094).



# CONNECTING STATEMENT 1

In Chapter 2, I examined the effects of ecological and evolutionary processes occurring at a large spatio-temporal scales. For this, I used an ecophylogenetic approach to infer which processes were most important in shaping the regional flora of the Galápagos. This approach confirmed that native flowering plants represent a phylogenetically clustered subset of potential colonisers, which is likely a product of strong ecological filtering. This clustered pattern increased when endemic species were included, suggesting that speciation also plays an important role in structuring the Galápagos flora. Filtering could be associated with the geographical isolation of the archipelago from the continental source pool and/or the distinctive environmental conditions of the archipelago. I differentiated between these two drivers using phylogenetic and ecological information on both the species native to the Galápagos islands and on the potential continental colonizer species. Traditionally, it has been assumed that the assembly of oceanic island floras is shaped predominantly by dispersal limitation; however, I suggest here that, in the case of the Galápagos flora, habitat filtering might have had a stronger effect.

In Chapters 3 and 4, I focus on how interactions between ecological and evolutionary processes occurring at finer spatio-temporal scales (eco-evolutionary dynamics) affect community assembly. For this, I explore the interactions between Darwin's finches and plant communities of the archipelago. Although previous work has shown that seed availability is a key driver of beak evolution within ground finch communities, the potential reciprocal effects on the ecology and evolution of seed plant communities have not been studied. In Chapter 3, I examine the effect of seed predation by Darwin's ground finches on seed banks and emergent above-ground vegetation. For this, I use information from feeding observations of Darwin's ground finches across five years and from a four year exclusion experiment at two sites on Santa Cruz Island.

# CHAPTER 3:

# Eco-evolutionary coupling and decoupling between Darwin's finches and plants of the Galápagos Islands

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# Abstract

Species can evolve rapidly in response to changing ecological conditions and, in turn, species' evolutionary responses might influence their environment. However, there is still a lack of empirical evidence on the importance and persistence of such coupling in natural systems. We examine the interplay between Darwin's finches and plants of the Galápagos Islands, a classic system for studies of contemporary evolution in finches, with seed availability shown to impose selection on finch beak depth. We not only show that finches are selective seed predators, but also that seed predation strongly modifies seed bank structure. However, this tight eco-evolutionary coupling between finches and the seeds upon which they prey, does not translate into predictable and consistent change at the scale of emergent plant communities. Our results suggest environmental fluctuations, trade-offs between ecological process, and stochastic or neutral community processes, might act to decouple eco-evolutionary dynamics.

# Main

Much excitement has recently attended the potential for short-term ("contemporary" or "rapid") evolution to modify ecological dynamics at the population, community, or ecosystem levels. Support for the likely importance of such "eco-evolutionary dynamics" comes mainly from theoretical models and from empirical studies in simplified ecological settings, such as the laboratory or mesocosms (e.g., Yoshida et al. 2003; Johnson and Agrawal 2005; Harmon et al. 2009; Palkovacs and Post 2009; Bassar et al. 2010; Pantel, et al. 2015; Gómez et al. 2016). Although these studies often reveal strong ecological effects of intra-specific variation and its evolution (Hendry 2017; Des Roches et al. 2018), the simplified testing arenas leave uncertain the extent to which observed outcomes might extrapolate to more complex natural environments (Hendry 2019). In particular, it has been suggested that the high (non-evolutionary) variation in biotic and abiotic variables in complex natural communities might swamp any effects on contemporary evolution on those communities (De Meester et al. 2019; Hendry 2019). In this near vacuum of relevant information, studies of eco-evolutionary dynamics in natural systems are needed (Ezard, Côté, and Pelletier 2009; Turcotte et al. 2011; Farkas et al. 2013). We sought to reduce this severe inferential gap through examining the coupling and decoupling of eco-evolutionary feedbacks between Darwin's finches and plants in the Galápagos.

The finch-plant system of the Galápagos is exemplary for studying eco-evolutionary feedbacks in natural systems (Post and Palkovacs 2009; Hendry 2017). From an eco-to-evo perspective, variation in plant communities is known to have shaped the adaptive radiation of finches (Grant and Grant 2008), and abiotic variables that alter plant reproduction continue to drive the contemporary evolution of finch beaks (Grant and Grant 2014). In particular, seed size and hardness exert selection on beak size and shape in the granivorous ground finches (Geospiza spp.), with deeper beaks more adept at processing larger and harder seeds (Lack 1983; Grant 1986; De León et al. 2014). Given that seed traits influence beak evolution (eco-to-evo), a logical evo-to-eco extension is that the distribution of finch beak sizes should modify the distribution of seed traits, which could in turn alter species composition in recruitment limited plant communities. We here investigate this expectation through a series of observations and experiments conducted on natural finch populations.

To evaluate how Darwin's finches might influence plant communities, we first quantified the feeding patterns of finches at two sites on Santa Cruz Island. The two sites have different ground finch beak size distributions, and thus we would expect differential impacts of plant communities. We then measured seed traits and quantified plant phylogenetic structure so as to extend our predictions to possible effects on the functional and phylogenetic diversity of the seed bank. We experimentally tested these expectations by establishing and monitoring, over four years, a series of replicate finch exclosures at the two sites. Finally, we explored whether the observed finch-driven shifts in seed bank structure translated into parallel shifts in above ground vegetation of annual and short-lived plant communities.

## *Finch-plant interactions and seed traits*

Feeding observations of the four ground finch species (*Geospiza magnirostris*, *Geospiza fortis*, *Geospiza scandens*, *Geospiza fuliginosa*) over five years at two sites (El Garrapatero –EG, Academy Bay – AB; see Supplementary Figure 1), demonstrated strong non-random consumption of seeds. The ecological networks describing finch-plant associations (Fig. 3.1A) suggested that network interactions during most of the observational period (between 2003-2006) were less even, and hence more specialized, than expected by chance (evenness' index = 0.49 ± 0.11; $P < 0.01$; specialization index = 0.39 ± 0.09; $P < 0.001$). However, in 2007, a year in which the wet season started with high rainfall (see Supplementary Figure 2 ), finches fed on fewer plant species, and the distribution of finch-plant associations was no different from that expected by chance (evenness' index = 0.67 ± 0.04; $P > 0.05$; specialization index = 0.3 ± 0.08; $P > 0.05$). A similar temporal trend was found in the distribution of species interaction strengths, with these strengths being inter-correlated between the years 2003 to 2006, but uncorrelated with estimates from 2007 (see Supplementary Table 1). Thus, although finch-plant interactions are generally conserved across years, they can change substantially in some years, most likely in response to external environmental drivers (here rainfall), consistent with earlier observations of temporal fluctuation in seed predation patterns (Boag and Grant 1984a; Grant and Grant 2002).

Selectivity of seed predation by finches generated associations between finch predation and seed morphology. Seeds from plant species consumed by finches at both sites tended to be softer than seeds from plant species not consumed by finches ($t = -3.27$, $P = 0.003$ and $t = -2.12$, $P = 0.041$, from t-tests for EG and AB respectively), and at EG they were also longer ($t = 2.03$, $P = 0.048$) and wider ($t = 2.47$, $P = 0.017$) (Fig. 3.1B). Because these seed traits are phylogenetically conserved (Fig. 3.1C), seed predation by finches should covary with plant phylogenetic relationships. Contrasting the phylogenetic distribution of seed predation with a null model of no phylogenetic structure, we found that seeds from species escaping finch predation (concentrated within the orders Solanales, Fabales, Malvales, and Sapindales; Fig. 3.1C) are more phylogenetically clustered than expected by chance at EG (SES.MNTD = -2.458, $P = 0.008$); but not at AB (SES.MNTD = -0.699, $P = 0.246$). Thus, seed banks under strong seed predation by finches are predicted to have harder seeds and, at EG, smaller seeds and reduced phylogenetic diversity.

### *Effect of finches on seed banks*

We tested these *a priori* predictions on seed bank attributes – and searched *post hoc* for additional suggestive patterns – in a finch exclusion experiment over 5 years (year of experiment set up - baseline, and after one, two, and four years). We measured the signals of finch predation by comparing the seed bank between paired (finch exclosures versus immediately-adjacent controls, which were exposed to seed predation by finches) plots at the two study sites (EG and AB). The local finch communities differ somewhat between these sites, with El Garrapatero having more small-beaked species (*G. fuliginosa*) and fewer large-beaked species (large *G. fortis* and *G. magnirostris*) (Fig. 3.2A).

Finch predation had strong effects on seed banks. First, finches reduced the abundance of seeds at both sites: control plots with finches had a lower abundance of intact seeds (seeds not opened/consumed by finches) and a higher proportion of cracked seeds (seeds opened/consumed by finches) than did exclosure plots without finches (Fig. 3.2B). Second, finch predation shifted the species composition of the seed banks at EG (F = 1.635, *P* = 0.001 from partial constrained analysis of principal coordinates; Supplementary Figure 5). For instance, the relative abundance of seeds from *Heliotropium angiospermum* and *Blainvillea rhomboidea,* two abundant species on which finches are known to feed, was higher within exclosure plots (321.2% and 87.4%, respectively), whereas the relative abundance of seeds from *Evolvulus convolvuloides,* a species not eaten by finches, was higher (97.5%) in the control plots. At AB, some locally abundant species commonly eaten by finches, such as *Scutia spicata* (38.5%), whereas the relative abundance of seeds from *Ipomoea sp,* a species not eaten by finches, was higher (69.1%) in the control plots, although species composition of the seed bank was not significantly different between exclosure and control plots (F = 1.00, *P* = 0.073; Supplementary Figure 5).

Third, finch predation altered the taxonomic and phylogenetic diversity of seed banks. Taxonomic diversity, measured via the Shannon diversity index, was lower in control plots exposed to seed predation at both sites (Table 3.1A), and this pattern was consistent across years (Table 3.1; Fig. 3.2C). By contrast, the effects of seed predation on phylogenetic diversity, estimated using the mean nearest taxon distance (MNTD), differed between sites (Table 3.1; Fig. 3.2D). At EG, finches increased phylogenetic clustering of the seed bank (Table 3.1A), matching our expectations from feeding observations (above); whereas at AB, finches reduced phylogenetic clustering of seed banks (Table 3.1A). However, patterns varied across years, and we observed a switch in the finch effect on phylogenetic clustering at EG in the last year (2014) of the experiment (Fig. 3.2D).

Fourth, finch predation shifted seed trait distributions within seed banks: at both sites, seeds were shorter in control than they were in exclosure plots (Fig. 3.2E). This pattern was generally consistent over the years of the experiment, but again at EG the opposite pattern was found in the last year (2014) of the experiment (Fig. 3.2E). Finally, a visual comparison of the distribution of seed traits between exclosure and control plots suggests a weak effect of predation on seed hardness, which is more evident at AB than at EG (Fig. 3.2F), but no obvious effect on the distribution of seed width (Supplementary Figure 6).

Collectively, our results show that finches have predictable effects on the seed banks. By selectively reducing seed abundance, finch predation alters seed species composition, and reduces taxonomic diversity of seeds. In addition, some site-specific predictions of the effect of finch predation were supported, including a reduction in phylogenetic diversity at EG, and a differential effect on seed traits consistent with the distribution of beak size of local finch communities. For example, at AB, where the distribution of finch beak sizes is shifted larger relative to EG, seeds also tend to be larger (Fig. 3.2E), and the strength of finch preferences for larger seeds greater, even when comparing the same suite of plant species (Supplementary Figure 7).

## *Effect of finches on above ground vegetation*

Despite finding strong evidence that seed predation by finches restructured the seed banks, shifts in seed species composition and diversity within seed banks did not consistently map onto changes in emergent above ground vegetation (annual and short-lived species). Exclosure plots did not differ significantly from control plots in either plant taxonomic or functional diversity (Table 3.1B; Fig. 3.3A). However, at AB, where data visualisation (Fig. 3.2E and 3.2F) suggests finch preferences on seed traits may be stronger, we found some evidence that finch predation had an effect on plant species composition ($F = 1.919$, $P = 0.048$ from partial constrained analysis of principal coordinates; Supplementary Figure 5), and plant phylogenetic diversity (Table 3.1B) which would be consistent with shifts in seed phylogenetic diversity (Fig. 3.2D). In contrast, at site EG, where finches may be less selective seed predators, we found no evidence of an effect of finches on plant species composition (F = 1.377, *P* = 0.117; Supplementary Figure 5) or phylogenetic diversity (Table 3.1B).

Analysis of "sham-controls" which were covered by a metal mesh but had open sides to allow finch access, provided assurance that observed difference were not simply the result of a "cage-effect" on vegetation growth. We found no effect on plant species composition (F = 1.225, *P* = 0.226) or phylogenetic diversity (t = 0.422, *P* = 0.674) at AB.

We have shown that, although seed predation can reshape seed bank phylogenetic, functional and taxonomic structure, there is only a weak relationship between selective seed predation by finches and above ground vegetation, suggesting a decoupling of finch-plant eco-evolutionary interactions. The lack of a direct relationship (i.e., decoupling) between the predation-driven shifts in seed bank structure and the emergent plant community could have several explanations – our data can illuminate two of these. First, an inter-specific trade-off might exist between defense against seed predation and success in germination, such that seeds that escape predation have lower germination success. Such a trade-off is suggested in general by evidence that small seeds, which we show are often less favoured by finches (Fig. 3.2E), have lower survival as seedlings and adults (Moles and Westoby 2004; Moles, Westoby, and Eriksson 2006). We also find some evidence for the trade-off within our experiment: at EG (but not AB), the plant species that experienced lower seed predation had lower establishment success (Supplementary Figure 8) – and, as we describe above, the disconnect between finch effects on seed banks and plant community structure was also most apparent at this site.

Second, plant recruitment might not be seed limited, leading to a lack of a correlation between seed abundance and adult plant abundance. It is already well established that additional factors, such as space (i.e., microsite availability), seedling survival, and other more stochastic processes (e.g., secondary seed dispersal, delayed germination, specific density dependent interactions, climate variation) can limit recruitment (Muller-Landau et al. 2002; Clark et al. 2007; Crawley 2014). If such processes dominate, effects of finches at the plant life stage on which they forage then could be erased, or highly modified, by different processes acting between that plant stage and the next. Indeed, we found a positive relationship between seed abundance and plant cover for only 28% of annual and short-lived species, suggesting seed survival may be an important driver of plant recruitment for only a minority of species in our plots.

## *Coupling and Decoupling in Eco-Evolutionary Dynamics*

Various authors have argued that contemporary evolution should modify many ecological processes at the community level (Hairston et al. 2005; Fussmann et al. 2007; Urban et al. 2008; Bailey et al. 2009; Schoener 2011; Fussmann and Gonzalez 2013; Hendry 2017) whereas other – and sometimes the same – authors have alternatively argued that such eco-evolutionary dynamics might be weak, perhaps even undetectable, in natural populations (Ellner et al. 2011; De Meester et al. 2019; Hendry 2019). Our goal was to use an exemplary model system – Darwin's finches and the plants on which they feed – to consider these two perspectives. Previous work has established that seed availability shapes finch beak evolution. We confirm that Darwin's ground finches are selective seed predators, differentially consuming seeds in association with species-level differences in seed/fruit size and hardness. Also, we confirm that this selectivity strongly impacts seed bank structure (i.e., altering seed abundance, species composition, diversity, and seed trait distribution). This coupling between finch beak evolution and the ecological processes shaping seed bank structure highlights the role of eco-evolutionary dynamics in structuring natural systems. However, we also found that finch-driven shifts in seed banks do not directly translate into changes in above ground vegetation. Empirically-supported explanations for this transition from coupling to decoupling include trade-offs in plant defense versus recruitment and also stochastic effects on population dynamics.

Overall, our results suggest that eco-evolutionary dynamics can be strong in nature but– at the same time – might not generate strong feedbacks. That is, changes in plant communities shape finch beak evolution and finch beak evolution shapes plant communities – but these causes versus effects of finch evolution are not tightly connected in a feedback loop. More studies are needed to determine if these findings hold for other finch-plant communities, for other herbivore-plant communities, for other predator-prey communities, or for other eco-evolutionary contexts.

Our study indicates the importance of conducting eco-evolutionary experiments in natural systems, despite the time and effort they require.

# Methods

## 1. Outline

To address the effect of finch predation on seed banks and above ground vegetation, we examined finch-plant interactions and performed a finch exclusion experiment in nature. First, using feeding observations, we built bipartite networks to describe finch-plant associations. Second, we examined seed traits and phylogenetic structure to characterise finch preferences. Third, we used a finch exclusion experiment to test the hypothesis that finch seed preferences restructure seed banks. Fourth, we evaluated whether shifts in the seed bank translated into changes in the emergent plant community composition.

## 2. Data

### (a) *Feeding observations*

We examined finch-plant interactions through feeding observations on four species of ground finch (*G. magnirostris*, *G. fortis*, *G. fuliginosa*, *G. scandens*) at two sites (El Garrapatero – EG, Academy Bay – AB) located in dry lowland forest on Santa Cruz Island (see map in Supplementary Figure 1). The approximately 7054 independent point-in-time feeding observations were performed during the wet season (January - March) over five consecutive years (2003 - 2007) as detailed in De León et al. (2014).

### *(b) Vegetation surveys*

Vegetation surveys were performed during the wet season over three years (2005 - 2007) across 50 randomly-positioned 1-m$^2$ plots. Once per year per plot, we quantified the number of potential plant food items (fruits, seeds, and buds) per plant species (see De León et al. 2014). Most plant items were identified to species level or genus level except in the case of graminoids, which were treated as a single category "Grass".

### *(c) Seed and plant traits*

We quantified seed traits from intact seeds collected from standing vegetation or from the seed bank at the two study sites (EG and AB). Seed length (longest dimension in mm), width (intermediate dimension in mm), and depth (shortest dimension in mm) were measured, using a digital caliper (Neiko 01407A, 0.01mm), for 20 seeds per species collected from 10 individual plants (or fewer in those rare cases where 10 plants could not be found). Seed mass was measured on a digital balance (Adam Equipment HCB 123, 0.001g) to the nearest mg. For a few species (*Tribulus cistoides, Boheravia tuberosa, Sida ciliaris, and Sida spinosa*), finches have to crack a hard or fibrous fruit structure to obtain the seeds; in these cases, the length, width, depth, and mass measurements were taken from these outer fruit structures rather than the seeds themselves. For species known to be present at our sites, but for which seeds could not be found, we used specimens stored in the Herbarium collection of the Charles Darwin Research Station (CDRS) or, in a few cases, we had to extract the relevant data from the literature (Wiggins and Porter 1971). Seed hardness was obtained for 44 species using a Kistler Force Transducer attached to a Kistler charge amplifier (details in De León et al. 2014). Seed trait information, collection data, and data sources are provided in Supporting information (Supplementary Data 1).

Additional plant traits were obtained primarily from individual plants at the two study sites (EG and AB). For each species, we sampled 10 individuals and measured plant height (m), specific leaf area (SLA in mm$^2$mg$^{-1}$), and leaf dry mass (LDM in mg). We also recorded growth form (tree, shrub, wine, herb, or grass), fruit type (dry or fleshy), and life cycle (annual/short lived, perennial, or both). For species not found during our sampling, trait data were recorded from specimens stored in the CDRS Herbarium collection or extracted from the literature (Wiggins and Porter 1971). Plant trait data, and data sources are provided in Supporting information (Supplementary Data 2).

### *(d) Phylogenetic reconstruction*

We estimated plant phylogenetic relationships using two DNA barcoding genes (*rbcL ~800pb* and *matK ~550pb:* CBOL Plant Working Group 2009). For 58 species, we extracted and amplified DNA directly from individuals sampled within our plots. Sequencing followed standard procedures in laboratories associated with the Barcode of Life Database (BOLD) project (Sequences accession numbers provided in Supplementary Table 2). For an additional 22 species, sequences were downloaded from GenBank (Benson et al. 2017). Sequences for congeneric close relatives were used for a 7 species for which sequence data were not available (Supplementary Table 2). Sequences were aligned using MAFFT version 7. (Katoh and Standley 2013) and then manually edited using Geneious version 5.4 (Drummond et al. 2011).

Phylogenetic reconstruction was performed on an alignment of 1372 base pairs in BEAST version 2.4.5 (Bouckaert et al. 2014) and assuming a TVM + I + G model of sequence evolution, selected based on AIC criteria estimated for each gene region using jModelTest version 2.1.10 (Darriba et al. 2012). The topology of the phylogeny was constrained using the APG III phylogeny for plant orders (Group Angiosperm Phylogeny 2009). Branch lengths were made proportional to time assuming an uncorrelated lognormal relaxed molecular clock model (Drummond et al. 2006) and dated with three time-calibration points based on fossil information [44.3 mya for the crown of Solanales (Collison, Boulter, and Holmes 1993), 65 mya for the crown Sapindales (Knobloch and Mai 1986), and 83.5 mya for the crown of Caryophyllales (Collison, Boulter, and Holmes 1993)] and a calibrated Yule model as the tree prior. Fossil calibrations were assigned a log-normal prior distribution, with the age of the fossil as the minimum and 97.5 % of the distribution as the maximum constraint. Analyses were performed across four chains, running $10^7$ generations and sampling every $10^3$ generations. We used Tracer version 1.6 (Rambaut et al*.,* 2014) to examine posterior estimates, credible intervals, and the effective sample sizes, and to visually assess convergence. We estimated the maximum clade credibility tree using TreeAnnotator version 2.4.5 (Rambaut and Drummond, 2013), and used this topology for all downstream analyses.

### *(e) Exclusion experiment*

Effects of seed predation by finches were examined using exclusion experiments in two sites, EG and AB. Although both sites are in dry lowland forest, they differ in plant community composition, and finches at the two sites differ in beak size and shape distributions (Hendry et al. 2006; De León et al. 2010; Fig. 3.2A). At each site (EG and AB), we established 20 paired plots of 1 $m^2$, one plot in each pair was covered by a metal mesh that excluded finches "exclosure plot", whereas the other provided a control that was open to the finches "control plot" (for a picture see Supplementary Figure 9). Starting in 2011, we also placed five paired "sham-control" plots at each site, which were covered by a metal mesh but had open sides to allow finch access (see Supplementary Figure 9).

We performed annual surveys of the plots during the wet season (January-March) from 2010 (baseline – immediately after establishment) to 2014, except in 2013 due to logistical constraints. In each survey, we recorded – for each plant species – the percentage of coverage above ground, and the number of flowers, fruits, seeds, and buds. Plants were identified to species (when possible) or genus; except graminoids, which were pooled. Within each plot, we also quantified the number of seeds (intact and cracked) on the ground within a 10 $cm^2$ subplot, with a different subplot sampled each year. Seeds were counted and identified in the field, and also in the laboratory from a soil sample (~ 25g), which parallels the procedure for the previously conducted "vegetation surveys" described above.

### *(f) Finch capture and beak measurements*

Morphological data were collected from four species of ground finches (*G. fuliginosa*, *G. fortis*, *G. magnirostris*, *G. scandens*) between 2010 and 2014. Birds were captured using mistnets, and each was banded with a unique combination of three colored plastic leg bands and a numbered metal leg band. Each individual was then inspected visually assigned to species – a procedure that is usually very accurate and consistent (Foster et al. 2008). Each individual was also classified when possible as a juvenile, male, or female (based on plumage, beak color, and the presence of a brood patch; (Grant 1999)). Each bird was then measured (following Boag and Grant 1984b) for beak length (anterior edge of nares to anterior tip of upper mandible), beak depth (at the nares), and beak width (at the base of the lower mandible).

## 3. Statistical analyses

Unless indicated otherwise, we used R programming language, version 3.4.2 (R Development Core Team 2008) to analyse and plot the data. Adobe Illustrator was used to format and assemble the data plots into figures.

### *(a) Bipartite network analyses*

To characterise finch-plant interactions we constructed quantitative bipartite networks from finch feeding observations at EG and AB (see methods section 2a), using the bipartite R package, version 2.08 (Dormann, Gruber, and Fründ 2008; Dormann et al. 2009; Dormann 2011). In these networks, feeding observations are represented as links between finches and plants at each site. Network topology was described using four indices: (1) Connectance, the linkage density (interaction density) divided by number of species in the network (Tylianakis et al. 2007); (2) Interaction evenness, estimated as Shannon's evenness for the web entries and used to identify potential skewness in the distribution of interaction frequencies, with values close to 1 indicating more even interactions. (3) Specialization (H2'), a metric of species discrimination, with values close to 1 indicating specialization and values close to 0 indicating absence of specialization. Significance was evaluated by comparing observed values to 999 random webs keeping the connectance of the original network constant (Vázquez et al. 2007). In addition, we calculated the interaction strength for each plant species in the network, the sum of dependencies of each plant as in Bascompte et al. (2006) (i.e. the number of finch species with which they are interacting) to measure the relevance of each plant species in the network. Interaction networks were constructed for each year of feeding observations (2003-2007).

### *(b) Feeding preference*

We explored finch seed preferences by comparing seed traits between eaten and uneaten seeds. Mean species values of seed traits: length, width, and hardness were contrasted using independent t-tests. Trait values were fourth root transformed to improve normality. In addition, we fit a multivariate generalized linear model using the *glm* function and family = poisson. As the response variable we used the number of observed seeds eaten per species, and as predictor variables we included species mean trait values (length, width, and hardness), previously standardized (mean = zero and standard deviation = one), and species availability, quantified as the mean of food items per species during the vegetation surveys (see section b).

Phylogenetic signal in seed traits was quantified using the K statistic (Blomberg, Garland, and Ives 2003) on log-transformed trait values (length, width, depth, mass, and hardness) in the R package picante, version 1.7 (Kembel et al. 2010). K values close to 0 indicate a random or convergent pattern of evolution. K values close to 1 indicate a Brownian motion pattern of evolution. Significance was evaluated by comparing observed K to values obtained under null models where taxa labels were shuffled across the tips of the phylogeny (Kembel et al. 2010).

To examine phylogenetic structure in finch seed predation preferences, we pooled feeding observations across years, and then pruned the regional plant phylogeny to just the subset of species at each site (EG and AB). We quantified phylogenetic structure using the mean nearest taxon distance (MNTD) between species falling in each category (eaten vs uneaten), weighting estimates by the frequency of observed seed predation events per plant species. Significance was assessed by comparing observed MNTD to null expectations generated by drawing species at random (999 runs) from the local pool of species present in each study site and calculated standard effect sizes (SES; see Kembel et al. 2010). Positive SES values indicate phylogenetic overdispersion (species are less related than expected by chance), whereas negative

SES values indicate phylogenetic clustering (species are more related than expected by chance). Analyses were conducted using the R package picante, version 1.7 (Kembel et al. 2010).

### *(c) Exclusion experiments*

To quantify the effects of finch predation on seed banks (seeds on the ground or in the soil), we compared measures of seed abundance, species composition and diversity, and the distribution of seed traits between paired experimental exclosure and control plots.

Differences in seed abundance were first explored using a linear mixed-effects model in lme4, version 1.1-13 (Bates et al. 2014), with number of intact (uneaten) seeds, square root transformed, as the response. We included three fixed categorical predictors: treatment (exclosure vs control), year since establishment (1, 2, and 4), and site (EG and AB), and the interaction between treatment and site. We included paired plot id as a random effect nested within each year to account for the paired design of the experiment. Second, we refit this model, but with the proportion of cracked seeds (seeds consumed by finches) as the response and assuming a binomial error structure.

Shifts in seed composition were analysed using a partial constrained analysis of principal coordinates (partial CAP) on the Jaccard dissimilarity matrix of community composition with the *capscale* function in the R package vegan, version 2.5-3 (Oksanen et al. 2018). Treatment (exclosure vs control) was set as the constraint, and plot id was included as the condition (the variable that is partialled out before the constraint). Significance of factors and axis (CAPs) was estimated using a permutational anova.

Shifts in seed diversity were analysed using the Shannon diversity index (a metric of taxonomic diversity) and the standardized abundance weighted mean nearest taxon distance (SES.MNTD, a metric of phylogenetic diversity, described above) calculated in the R packages vegan and picante, respectively. Linear mixed-effects models were then fit with treatment, year, site, and the interaction between treatment and site as fixed effects, and plot id (nested within year) as a random effect.

Shifts in seed traits were explored using community weighted means of the seed length, width, and hardness for each plot and linear mixed-effects models, with fixed and random effects as described above in this section. To improve normality, mean weighted seed width and hardness were transformed to their quadratic roots, and mean weighted seed length was log (base 10) transformed.

To test whether the effect of seed predation on seed banks translates to shifts in above ground vegetation, we repeated the statistical analyses described above for seeds, but using plant percent cover of annual and short-lived species rather than seed abundance, and a different suite of plant functional traits. For these analyses, functional diversity was estimated from (mean values per species): plant height, specific leaf area, leaf dry mass, and fruit type. For each plot, we calculated Gower distances among plant traits using the R package cluster, version 2.0.6 (Maechler et al. 2017), and calculated the standard effect size of the mean pairwise distance (SES.MPD), as a metric of functional diversity. Traits were standardized to a mean 0 and a standard deviation of 1 prior to analysis.

Finally, because the effect of seed predation on emergent plant communities might be moderated by the other processes affecting plant recruitment, such as germination and seedling establishment, we further examined the relationship between seed predation and plant recruitment. First, we evaluated the sign and strength of the relationship between finch seed preference measured during the experiment and the change in plant coverage in exclosure plots. To account for the additional effect of seed size and seed abundance on recruitment, we used a structural equation model approach to include these terms as direct and indirect effects. For this analysis, we aggregated the coverage of some congeneric species, and excluded some species that were identified in the above ground vegetation but not as seeds, so as to match taxa in both sets of plant data. Structural equation model estimates and path regression coefficients were obtained using the R package lavaan, version 0.6-3 (Rosseel 2012).

We fit a model for both sites (EG and AB). The model included an estimate of species relative establishment success (relative change on plant coverage in plots without finches; a mean value per species across plots and years) as the response variable, with finch seed preference (relative difference of number of seeds found in control and exclosure plots; a mean value per species across plots and years), and the two covariates: seed size (seed length mm; mean per species) and seed abundance (number of seeds and fruits on standing vegetation within plots; mean per species across plots and years) as predictor variables. In addition, we included the indirect effect of seed abundance and size on the change in plant coverage through finch seed preference (see path diagram in Supplementary Figure 8). We performed this analysis using annual or short-lived species.

Second, we evaluated whether recruitment of the species in our study plots was seed limited by using multiple regressions between plant coverage and seed abundance per species in plots without finches. In this analysis, we included only annual and short-lived species that were frequently found in our studied our plots (present in more that 10 plots).

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**Table 3.1** Effect of seed predation by Darwin's ground finches on plant communities. Linear mixed-effects models analyzing the effect of seed predation by Darwin's ground finches on the diversity of seed banks (A) and above ground vegetation (B) in an exclusion experiment at two study sites (EG and AB) on Santa Cruz Island. Three fixed categorical effect were included: treatment (exclosure vs control), year since establishment (1, 2, and 4), and site (EG and AB), and the interaction between treatment and site, and paired plot id was included as a random effect nested within each year to account for the paired design of the experiment. Effects significant at $P < 0.05$ are in bold. Since interactions between treatment and site were significant for phylogenetic diversity, independent models for each site were performed including treatment, year, and interaction between treatment and year as fixed effects.

| **A. Effect on seed bank diversity** | | | | | **B. Effect on above ground vegetation diversity** | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Fixed effect* | *Estimate* | *Std. Error* | *t* | *P* | *Fixed effect* | *Estimate* | *Std. Error* | *t* | *P* |
| Taxonomic diversity (Shannon index) | | | | | Taxonomic diversity (Shannon index) | | | | |
| Treatment | -0.267 | 0.072 | -3.703 | **< 0.001** | Treatment | -0.007 | 0.057 | -0.132 | 0.895 |
| Site | 0.702 | 0.100 | 6.995 | **< 0.001** | Site | 0.512 | 0.091 | 5.610 | **< 0.001** |
| Year | 0.012 | 0.035 | 0.336 | 0.737 | Year | -0.316 | 0.033 | -9.444 | **< 0.001** |
| Treatment x Site | 0.031 | 0.107 | 0.286 | 0.776 | Treatment x Site | 0.028 | 0.085 | 0.326 | 0.745 |
| Phylogenetic diversity (SES.MNTD) | | | | | Phylogenetic diversity (SES.MNTD) | | | | |
| Treatment | 0.454 | 0.300 | 1.439 | 0.1549 | Treatment | 0.217 | 0.127 | 1.638 | 0.105 |
| Site | 0.641 | 0.296 | 2.151 | **0.033** | Site | 0.147 | 0.200 | 0.733 | 0.465 |
| Year | -0.227 | 0.090 | -2.503 | **0.015** | Year | 0.058 | 0.096 | 0.515 | 0.607 |
| Treatment x Site | -0.985 | 0.388 | -2.509 | **0.014** | Treatment x Site | -0.543 | 0.186 | -2.872 | **0.005** |
| Site EG | | | | | Site EG | | | | |
| Treatment | -1.524 | 0.559 | -2.809 | **0.007** | Treatment | -0.502 | 0.157 | -1.212 | 0.233 |
| Year | -0.606 | 0.169 | -3.588 | **< 0.001** | Year | -0.037 | 0.114 | -0.181 | 0.857 |
| Treatment x Year | 0.458 | 0.227 | 2.095 | **0.043** | Treatment x Year | 0.102 | 0.076 | 0.467 | 0.644 |
| Site AB | | | | | Site AB | | | | |
| Treatment | 0.714 | 0.343 | 2.105 | **0.058** | Treatment | 0.507 | 0.232 | 2.184 | **0.033** |
| Year | 0.158 | 0.131 | 1.140 | 0.260 | Year | -0.003 | 0.121 | -0.029 | 0.857 |
| Treatment x Year | -0.234 | 0.144 | -1.693 | 0.103 | Treatment x Year | -0.097 | 0.091 | -1.081 | 0.616 |

**Figure 3.1** Finch-plant interactions in Galápagos dry lowland forest. (**A)** Finch-plant interactions represented as bipartite networks for each year (2003-2007) at site EG. Upper level boxes represent finch species *G. fortis* (blue), *G. fuliginosa* (red), *G. magnirostris* (yellow), and *G. scandens* (black). Lower level boxes represent plant species. Grey lines indicate the frequency of interactions. Note that in 2003 there were no feeding observation for *G. magnirostris* at this site (see bipartite networks for AB in Supplementary Figure 3) (**B)** Length and hardness distribution of eaten (in gray) and uneaten (in red) seeds at EG. The size of the gray circles (eaten seeds) represents the number of feeding observations. A multivariate generalized linear model showed seed hardness, seed length, and seed availability were significant predictors of seed predation ($\beta_{\text{hardness}} = -0.661 \pm 0.046$, $P_{\text{hardness}} < 0.001$; $\beta_{\text{length}} = 0.534 \pm 0.028$, $P_{\text{length}} < 0.001$; $\beta_{\text{availability}} = 0.300 \pm 0.096$, $P_{\text{availability}} = 0.002$; pseudo $R^2 = 0.137$). Distribution of seed traits (length and hardness) at AB are shown in Supplementary Figure 4. (**C**) Phylogenetic distribution of eaten (gray branches) and uneaten (red branches) seeds found at EG and AB. Seed length is represented by the size of red circles. Plant species that are more closely related tend to have more similar seeds with respect to length (K = 0.35; $P = 0.001$), width (K = 0.56; $P = 0.002$), depth (K = 0.52; $P < 0.001$), mass (K = 0.45, $P = 0.001$), and hardness (K = 0.68; $P = 0.001$). Finch photos provided by Luis F. De León.

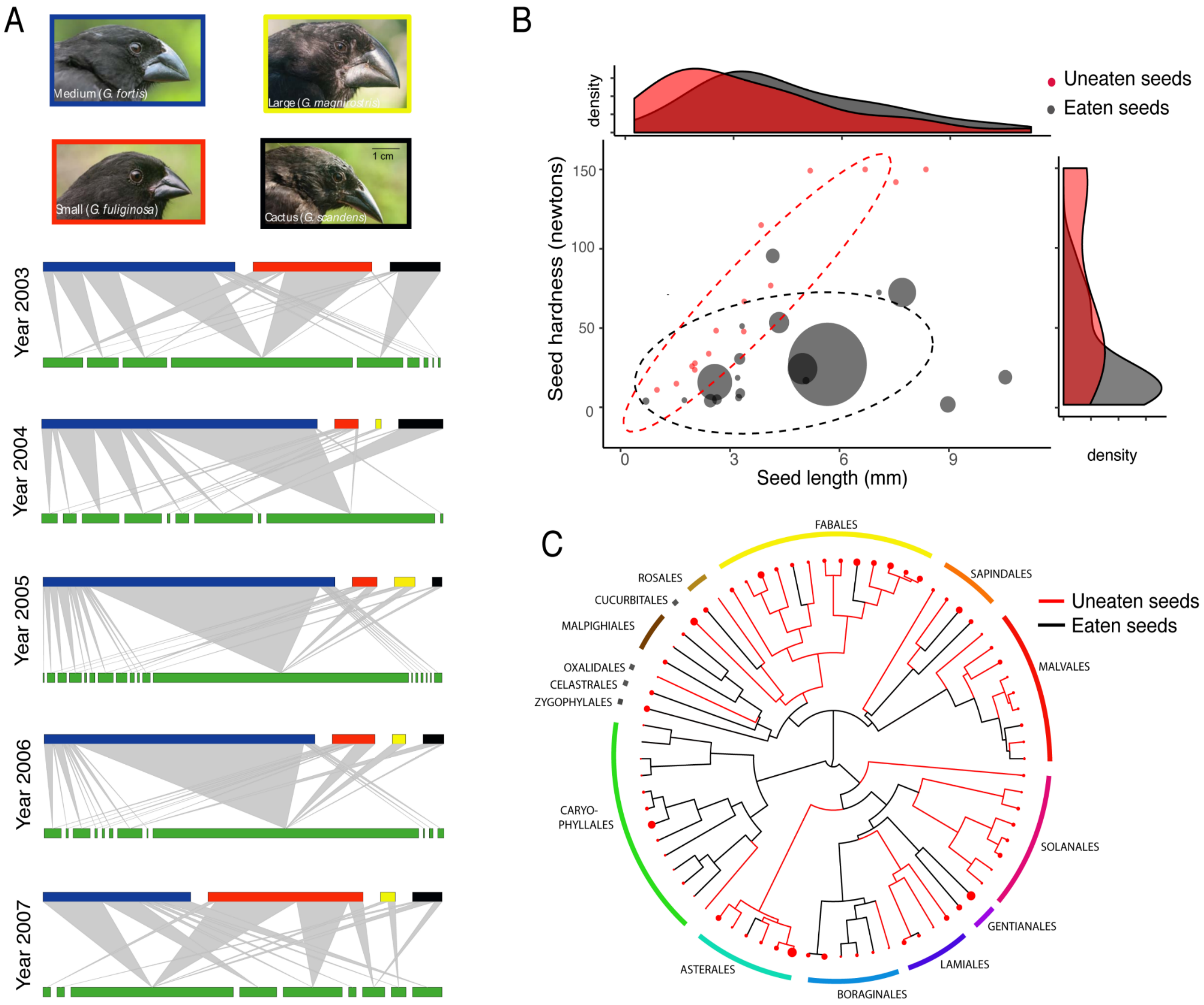

A
Medium (G. fortis)
Large (G. magnirostris)
Small (G. fuliginosa)
Cactus (G. scandens)
1 cm
Year 2003
Year 2004
Year 2005
Year 2006
Year 2007
B
density
Uneaten seeds
Eaten seeds
Seed hardness (newtons)
150
100
50
0
0
3
6
9
Seed length (mm)
density
C
FABALES
SAPINDALES
ROSALES
CUCURBITALES
MALPIGHIALES
OXALIDALES
CELASTRALES
ZYGOPHYLALES
MALVALES
CARYO-
PHYLLALES
SOLANALES
GENTIANALES
LAMIALES
ASTERALES
BORAGINALES
Uneaten seeds
Eaten seeds

**Figure 3.2** Effect of seed predation by Darwin's finches on seed banks in an exclusion experiment at two study sites (EG and AB) on Santa Cruz Island. **(A)** Beak shape distributions at the two sites. Principal component analysis (PCA) was performed on beak dimensions (beak length, beak depth, beak width) for the four species combined. A density plot was used to visualize the distribution of the first (PC1) principal component. **(B)** Abundance of intact and cracked seeds within control (exposed to finch predation) and exclosure (without finches) plots over the four years of the experiment. Data points above the diagonal dashed line indicate there were more intact seeds in exclosure plots and the ones below it indicate there were more cracked seeds on control plots. A linear mixed effects model showed control plots had a lower abundance of intact seeds than exclosure plots ($t = -4.41$, $P < 0.001$), and a logistic mixed-effects model showed control plots had a higher proportion of cracked seeds than exclosure plots ($Z = 9.083$, $p < 0.001$). **(C)** Difference in taxonomic diversity (Shannon index) of seeds between exclosure and control plots. Data points below horizontal dashed line indicate a decrease in diversity **(D)** Difference in phylogenetic diversity (Standard effect size of mean nearest taxon distance – SES.MNTD) of seeds between exclosure and control plots. (**E**) Distribution of mean weighted seed length (log) and **(F)** seed hardness (quadratic root) in exclosure and control plots. Linear mixed-effects models showed control plots had shorter ($t = -2.395$, $P = 0.019$) and a trend towards harder ($t = 1.822$, $P = 0.072$) seeds than exclosure plots.

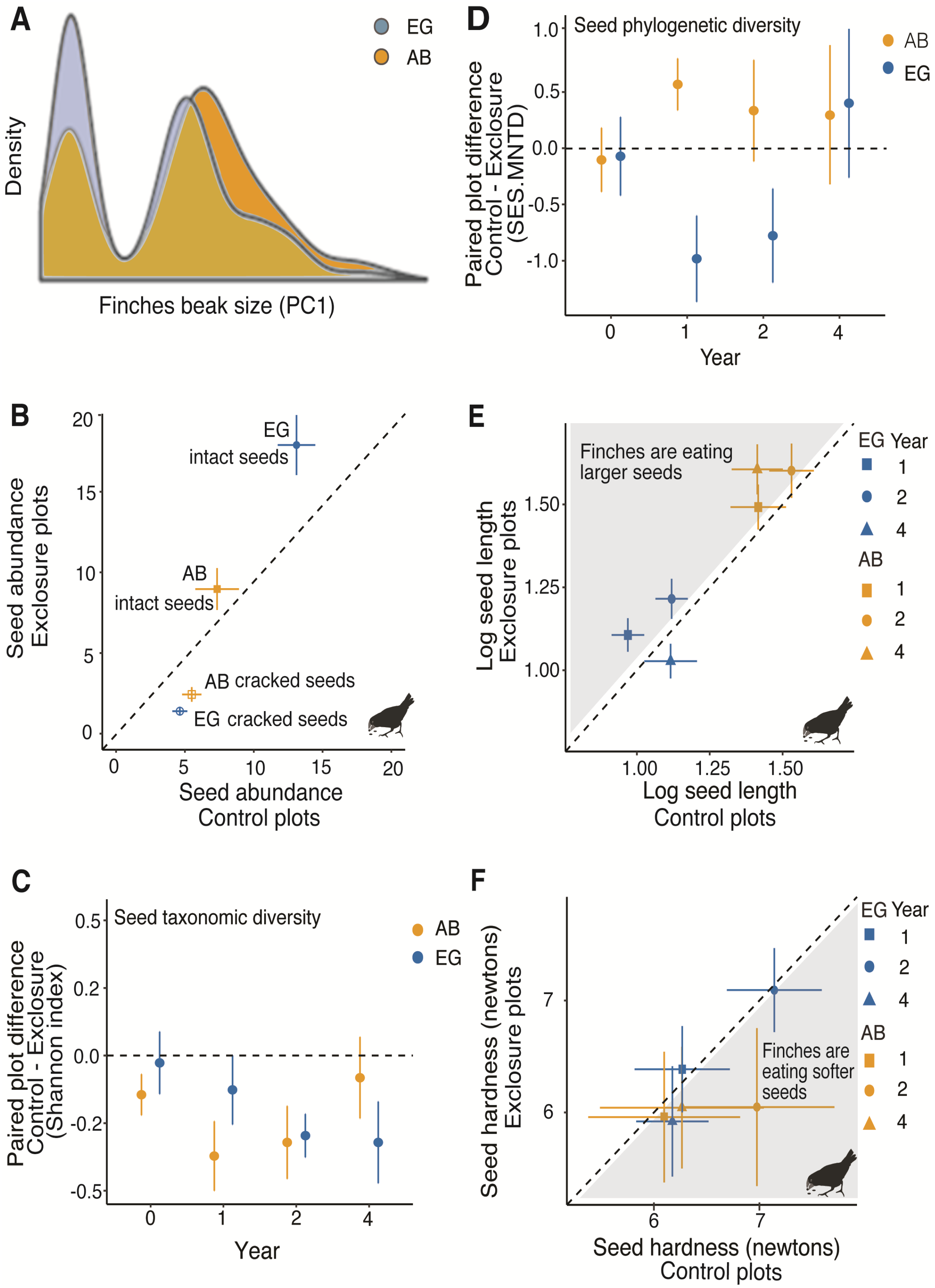
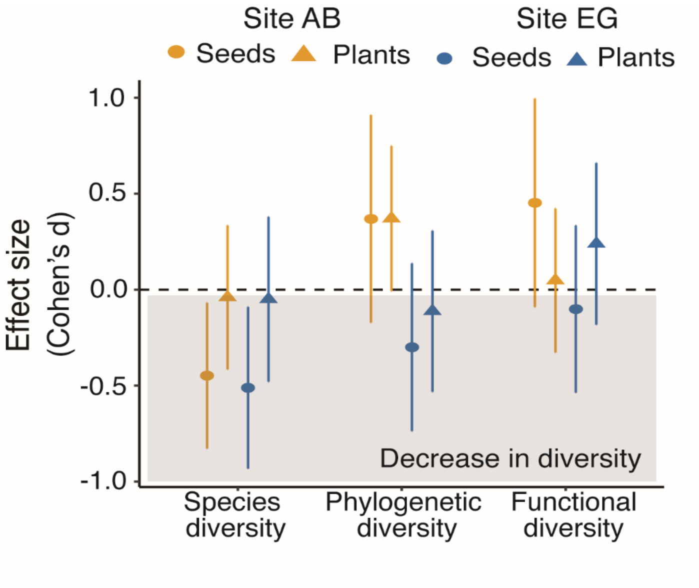

A
EG
AB
Density
Finches beak size (PC1)
D
Seed phylogenetic diversity
AB
EG
Paired plot difference
Control - Exclosure
(SES.MNTD)
1.0
0.5
0.0
-0.5
-1.0
0
1
2
4
Year
B
EG
intact seeds
AB
intact seeds
AB cracked seeds
EG cracked seeds
Seed abundance
Exclosure plots
20
15
10
5
0
0
5
10
15
20
Seed abundance
Control plots
E
Finches are eating
larger seeds
EG Year
1
2
4
AB
1
2
4
Log seed length
Exclosure plots
1.50
1.25
1.00
1.00
1.25
1.50
Log seed length
Control plots
C
Seed taxonomic diversity
AB
EG
Paired plot difference
Control - Exclosure
(Shannon index)
0.5
0.2
0.0
-0.2
-0.5
0
1
2
4
Year
F
EG Year
1
2
4
AB
1
2
4
Finches are
eating softer
seeds
Seed hardness (newtons)
Exclosure plots
7
6
6
7
Seed hardness (newtons)
Control plots

**Figure 3.3** Effect size of seed predation by finches on seed bank and plant community diversity. Cohen's d estimates (midpoint), represented with circles for seeds and triangles for plants (annual and short-lived species). The bars represent 95 percent confidence interval. Linear mixed-effects models showed no significant difference between exclosure and control in either plant taxonomic (t = -0.132; *P* = 0.895) or functional diversity (t = -0.650; *P* = 0.518).



# CONNECTING STATEMENT 2

In Chapter 3, I tested the effect seed predation by Darwin's finches on the ecological structure of plant communities. Information from feeding observations shows that finches are selective seed predators, preferentially feeding on seeds according to their size and hardness. Using a finch exclusion experiment, I illustrated the strong effect of finch predation on seed community structure. This finding suggests that eco-evolutionary feedbacks might play an important role in structuring plant-finch dynamics. Thus, finches could potentially influence the evolutionary trajectory of their beaks by changing the structure of seed communities through selective seed predation. However, I also showed that a decoupling of these eco-evolutionary feedbacks as shifts in the composition of seed banks is not consistently translated to equivalent changes in above ground plant communities. The potential for decoupling of eco-evolutionary interactions in this system requires additional studies on the fitness trade-offs occurring at different plant life-stages, and on the importance of environmental fluctuations and stochastic events on plant community structure.

In Chapter 4, I further examine the role of eco-evolutionary dynamics on community structure, focusing on the co-evolutionary interactions between Darwin's finches and the plants upon which they feed. Previous studies have shown that phenotypic differences in the fruit of *Tribulus cistoides* impose selection on finch beak morphology. However, the reciprocal interaction—the effect of finch predation on *T. cistoides*—has received much less attention. To fill this gap, I here examine the effect of seed predation by Darwin's finches on the ecology and evolution of *T. cistoides* seed morphology across islands with different finch community compositions.

# CHAPTER 4:

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

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This chapter is under review in *Ecological monographs*

# 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 are a potent agent of selection that drives rapid evolutionary change in finch beak morphology. Although the effects of these interaction 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*. Our research questions sought to understand whether the intensity of seed predation and the strength of natural selection by finches on fruit defense traits varied 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 tested 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 three years. Our study revealed three key results. First, Darwin's finches strongly influence *T. cistoides* seed survival, whereby seed predation varied with differences in finch community composition among islands and in response to inter-annual fluctuations in precipitation. Second, finches imposed 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 explained variation in phenotypic selection on fruit defense traits. Third, variation in the number of spines on fruits among islands was 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 the strength of this coevolution varies in space and time.

# Introduction

Antagonistic interactions play a major role in the evolutionary diversification of traits that mediate species interactions (Thompson 1999, Vamosi 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 favours traits that better protect plants against herbivores and predators can lead to rapid 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 rapid evolutionary changes in the 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 the size and shape of a finch's beak (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 likely 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 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 in the Galápagos Islands is expected to be mediated by both climate and the strength of species interactions (Grant and Grant 2014). For instance, the effects of seed predation by finches during periods with high precipitation might be negligible owing to the high production of seeds by many plant species. However, during extended droughts, when seed production is reduced, selective seed predation by finches could influence the abundance, distribution, and evolution of seed defense traits in the plant species consumed. 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; Grant and Grant 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. 4.1). Grant (1981) showed that, within a *T. cistoides* population in 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 thus 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 in 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 medium-sized *G. fortis*, such as Santa Cruz and Isabela (Fig. 4.2a), 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: Q1. Does seed predation by finches vary among populations, islands, finch community composition, and years? Q2. Do finches impose selection on *T. cistoides* fruit morphology, and does selection vary among populations, islands, years, and with finch community composition? Q3. Does *T. cistoides* fruit morphology differ among islands with contrasting finch community composition (i.e., the presence/absence of large-beaked finches)? 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 three years, and performed a seed predation experiment in one population of 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 interpret the importance of these results for understanding the potential coevolution and eco-evolutionary interactions between Darwin's finches and the plants whose seeds they consume.

# Methods

## 1. 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. 4.2a), and that harbor at least one of the three finch species that consume T. cistoides seeds: Geospiza 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 that 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* produces fruits called schizocarps (Fig. 4.1a), which contain five individual segments referred to as mericarps that typically separate from one another as the fruit dries (Fig. 4.1b) (Wiggins and Porter 1971). Each *T. cistoides* mericarp is a hard fibrous structure that includes up to seven seeds contained within individual compartments. 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. 4.1b).

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. 4.1c, 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. 4.1d), often one compartment at a time (Video S1). Mericarps opened by finches are easily distinguished from mericarps depredated by insects, which make smaller circular “drill” holes. Mericarps opened by finches are also distinguishable from mericarps from which seeds germinated, which present empty seed compartments still partially enclosed by the mericarp wall, without the rough damage characteristic of seed predation by finches.

## 2. Population sampling and experimental design

To explore impacts of seed predation by finches, we sampled nearly 7000 mericarps from 30 T. cistoides populations across seven islands of the archipelago over three years (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. 4.2a). The medium-beaked species, Geospiza fortis, is present on all sampled islands except Española (Fig. 4.2a). Sampling was performed between the months of February and March, corresponding to the end of the dry season and beginning of the wet season, 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. 4.2b).

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 sampled populations (island, geographic coordinates, years of sampling) is provided in Supplementary Information S1: Table S1. From each population, we collected approximately 100 mericarps chosen haphazardly across the area, for a total of 6,943 mericarps across all islands, populations, and years. For each mericarp, we used digital calipers to measure mericarp length (mm), width (mm), and the distance between the tips of the upper spines (upper spine size, mm) located towards the distal end of the mericarp, and noted the presence or absence of lower spines and the number of seeds removed by finches (Fig. 4.3a). 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(length) + log(width) + log(length) x log(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 Supplementary Information 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 4 to 5 mericarps. In total, we thereby 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, 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 Supplementary Information 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 days.

Finally, to evaluate the relationship between mericarp morphology, anatomy, and hardness, we used 102 mericarps collected in 2017 from three populations on Isabela Island and seven populations on Santa Cruz Island (Supplementary Information S1: Table S1). For each mericarp, we measured hardness (0-100 value on a Shore D scale; Pampush 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. 4.3b), we measured hardness at six locations on each mericarp (see detailed information in Supplementary Information S2: Figure S1). In addition, on each mericarp we measured six morphological traits (length, width, depth, upper spine size, longest spine length, and spine position; Fig. 4.3a).

## 3. Statistical analyses

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

### *(a) 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 x finch community composition + island + error. Year, finch community composition, and the interaction between both factors 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). 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 x 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).

### *(b) 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 (Supplementary Information 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 (as above) number of seeds per mericarp. Each of these response variables were considered in separate models, with mericarp traits treated as fixed effects.

Mericarp length, width, and upper spine size were log-transformed to improve normality and standardized to a mean of zero and a standard deviation of one. 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 captured variation in both dimensions (correlation with mericarp width $r = 0.85$ and length $r = 0.85$). The third trait was a binary response variable corresponding to the presence (1) or absence (0) of lower spines. In addition, to test whether 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 = $PC1_{Size}$ + upper spine size + presence of lower spines + year + finch community + year x $PC1_{Size}$ + year x upper spine size + year x presence of lower spines + finch community x $PC1_{Size}$ + finch community x upper spine size + finch community x presence of lower spines + island + population(island) + island x $PC1_{Size}$ + island x upper spine size + island x presence of lower spine + error.

Using the functions *dredge* from the R package MuMIn v. 1.15. 6. (Barton 2016) and *glmer*, we compared the models resulting from all combinations of the fixed effects. The best-fitting models were selected based on the lowest 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. The 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, and 2 according to the number of large spines remaining on the mericarp), presence/absence of lower spines, and $PC1_{Size}$ (i.e., mericarp size, see above) 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, as above.

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 (Supplementary Information 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: $PC1_{Global\ hardness} = PC1_{Size}$ + island + 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 selection procedure was used as described above. All data were standardized within populations to mean = 0, and standard deviation = 1, 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 to fixed effects ($R^2$ marginal), and $R^2$ values associated to fixed and random effects ($R^2$ conditional).

### *(c) 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 variation, we fit a linear mixed effects model for each mericarp trait (width, length, upper spines 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 x year + island + population(island) + error, whereby parentheses indicate nested terms. Finch community composition, year, and the interaction between these factors were fixed effects, 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. When analyzing presence/absence of lower spines as a response variable, we fit a logistic mixed-effects model using the function *glmer* implemented in the lme4 v. 1.1-14 package (Bates et al. 2015) as described above.

## Results

### Variation in seed predation by Darwin's finches

Seed predation by finches varied among population, 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. 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 x year: $\chi^2 = 40.34$, $P < 0.01$, Table 4.1 and Fig. 4.4). Finch community composition did not influence the proportion of predation in 2015 ($Z = -1.20$, $P = 0.23$) or 2017 ($Z = -1.40$, $P = 0.16$). By 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 (Supplementary Information 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 Supplementary Information S4: Table S2 and Supplementary Information S4: Fig. S1). No effect of finch community composition was seen on 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 4.2). 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 non-significant ($\chi^2 = 3.36$, $P = 0.067$). The pattern of selection on upper spine size and on the presence of lower spines depended on finch community composition (finch community x upper spine size: $\chi^2 = 9.72$, $P < 0.002$; finch community x lower spines: $\chi^2 = 6.25$, $P = 0.012$; Table 4.2). 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. 4.5a).

Selection on mericarp upper spine size and the presence of lower spines also varied among years (year x upper spine size: $\chi^2 = 11.56$, $P = 0.003$; year x lower spines: $\chi^2 = 9.83$, $P = 0.007$). Selection for longer upper spines was stronger in 2016 (Fig. 4.5b) than in 2015 and 2017, whereas selection on the presence of lower spines was strongest in 2015. Averaged-model coefficients are presented in Supplementary Information S5: Table S1. Similar results were obtained when the proportion of seeds that survived predation per mericarp was used as the response variable (Supplementary Information S5: Table S2), except that there was 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. 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 (see above).

### *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 ($F_{5, 235} = 15.301$, $P < 0.001$; Supplementary Information S2: Table S2). We detected a negative relationship between overall mericarp hardness ($PC1_{Global\ hardness}$) and overall mericarp size ($PC1_{Size}$) ($\beta = -0.437 \pm 0.102$, $\chi2 = 16.876$, $P < 0.001$, $R^2_{conditional} = 0.397$, $R^2_{marginal} = 0.147$, N=102; Fig. 4.6). 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. 4.6). 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. 4.6). 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. 4.7; Supplementary Information 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 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).

## Discussion

Seed predation by Darwin's finches was found to influence ecological and evolutionary processes associated with *T. cistoides.* Several specific results are most relevant to answering 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 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 islands consistent with differences in finch community composition. Overall, our results support the conclusion 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). In 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, and it is therefore likely to influence the abundance of preferred foods of Darwin's finches. Indeed, previous work has shown that finches generally avoid *T. cistoides* in wet seasons and in particularly wet years (Grant 1981; Boag and Grant 1981), when *T. cistoides* fruits are most abundant. 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, temporal variation in finch predation on *T. cistoides* was not uniform across islands, suggesting that features particular to each island also shape the intensity of seed predation.

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* 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 interaction between spatial 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 longer upper spines and the presence of lower spines, and that were smaller, were more likely to survive predation. 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 (Abbot et al. 1977). However, we showed 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 on fruit morphology varied over time and space, as has been seen in other systems (Siepielski et al. 2009; Bell 2010; Siepielski et al. 2013; Thompson 2017). 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 days), whereas the observational data captures data from many populations over multiple years. Our experimental results, therefore, further emphasise the conditional nature of finch seed predation, and how selection varies in 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; but selection on *T. cistoides* fruit morphology has further implications in the Galápagos Islands (Fig. 4.8). *Tribulus cistoides* mericarps impose selection on the size and shape of the beak of *G. fortis* (Boag et al. 1981; Boag and Grant 1984; Grant and Grant 1999), which drives episodic bouts of rapid evolutionary change (Grant and Grant 2002, 2006). During dry periods, when small and soft seeds species 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* towards smaller beaks (Grant and Grant 2006).

Therefore, the interaction between *G. fortis* and *T. cistoides* seems to be 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.

## *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 of 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* is a relatively recent invasive species brought by humans (Porter 1967; Grant 1981). If so, it is possible that *T. cistoides* has not yet had enough time – in combination with the above factors (e.g., founder effects, gene flow, opposing selection forces) – to strongly locally adapt to finch community composition.

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. Divergence among populations and islands in many of these traits further supports the idea that these traits are genetically based. However, we acknowledge that some of this variation in mericarp traits could be due to phenotypic plasticity. Future common garden experiments and genomic analyses would add to our understanding of the evolution of morphological defenses in *T. cistoides*. Thus, we can see a number of questions to be addressed in future work. 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; Boag and Grant 1984; Grant and Grant 2006). We can now 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* invest 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. However, 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 they eat. A long history of research, which includes Charles Darwin (1859), David Lack (1947), Peter and Rosemary 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.

## Acknowledgments

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**Table 4.1** Logistic mixed-effects models analyzing variation in the proportion of seed predation per population among islands and years. 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. (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. (b) Separate models were fit for each year.

**a**

| | | $\chi^2$ | ***P*** |
|---|---|---|---|
| *Fixed effects* | Finch community | 2.85 | 0.09 |
| | Year | 208.60 | **< 0.001** |
| | Finch community x Year | 40.34 | **< 0.001** |
| *Random effect* | Island | 74.00 | **< 0.001** |

**b**

| | | **Estimate (Std. Error)** | ***Z*** | $\chi^2$ | ***P*** |
|---|---|---|---|---|---|
| **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** |

*Note:* $\chi^2$ 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 bold. These models only include data from islands sampled in multiple years (see models including all islands in Supplementary Information 4: Table S1).

**Table 4.2** Generalized mixed-effects model analyzing phenotypic selection on mericarp traits by finches**.** 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.

| | | $\chi^2$ | ***P*** |
|---|---|---|---|
| *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 x Upper spine size | 9.72 | **0.002** |
| | Finch community x Lower Spines | 6.25 | **0.012** |
| | Finch community x Year | 45.46 | **< 0.001** |
| | Year x $PC1_{(Size)}$ | 3.65 | 0.161 |
| | Year x Upper spine size | 11.56 | **0.003** |
| | Year x Lower spines | 9.83 | **0.007** |
| *Random effect* | Island | 0.00 | 0.500 |
| | Population | 462.80 | **< 0.001** |
| | Island x $PC1_{(Size)}$ | 0.00 | 0.500 |
| | Island x Upper spine size | 0.00 | 0.500 |
| | Island x Lower spines | 5.14 | **0.012** |

*Note:* $\chi^2$ 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 bold.

**Figure 4.1** *Tribulus cistoides* fruits and *Geospiza fortis.* (a) *T. cistoides* fruits (schizocarps) attached to a maternal plant. (b) two sets of mericarps showing variation in size and number of spines. (c) *G. fortis* (medium ground finch) holding a *T. cistoides* mericarp. (d) Mericarps found on the ground close to *T. cistoides* plants, showing empty compartments where seeds were removed by finches. Photo credits: Andrew P. Hendry (a, b, and d) and Kiyoko M. Gotanda (c).

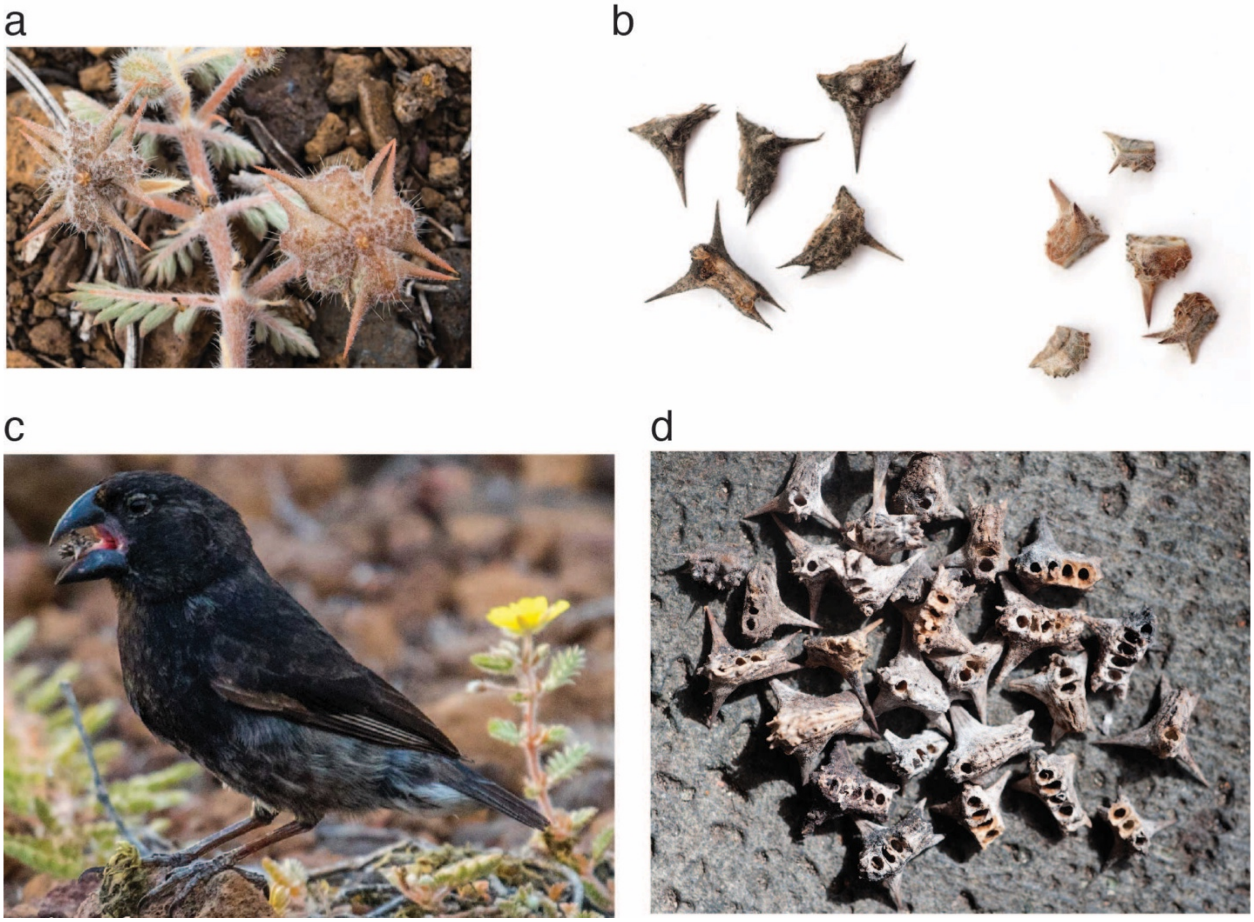


**Figure 4.2** Study system. (a) Map showing the seven islands of the Galápagos archipelago where *Tribulus cistoides* fruits were sampled. Black and dark gray identify the islands where large-beaked ground finches are present: the large ground finch (*Geospiza magnirostris*) is present on Isabela and Santa Cruz and the large cactus finch (*G. conirostris*) is found on Española. Light gray 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. (b) Variation in monthly precipitation (mm) from 2014 to 2017 in the Santa Cruz island, according to data provided by the Charles Darwin Research Station (CDRS 2017).

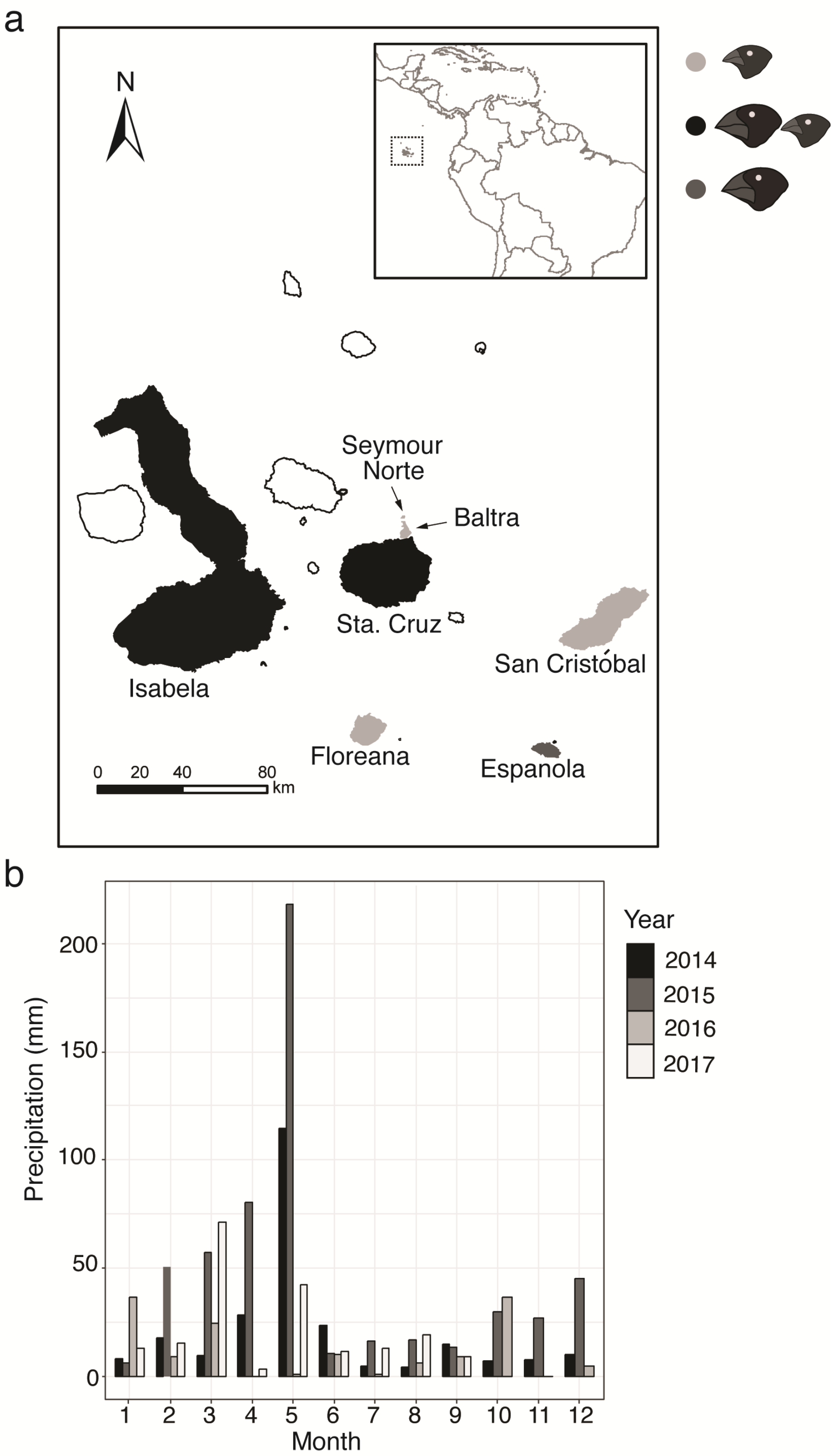

a
N
Seymour Norte
Baltra
Sta. Cruz
San Cristóbal
Isabela
Floreana
Espanola
0
20
40
80
km
b
Year
2014
2015
2016
2017
Precipitation (mm)
0
50
100
150
200
1
2
3
4
5
6
7
8
9
10
11
12
Month

**Figure 4.3** *Tribulus cistoides* fruit traits. (a) Mericarp traits and morphological measurements. (b) Micro-computed tomography (μCT) image showing mericarp wall variation over its surface.

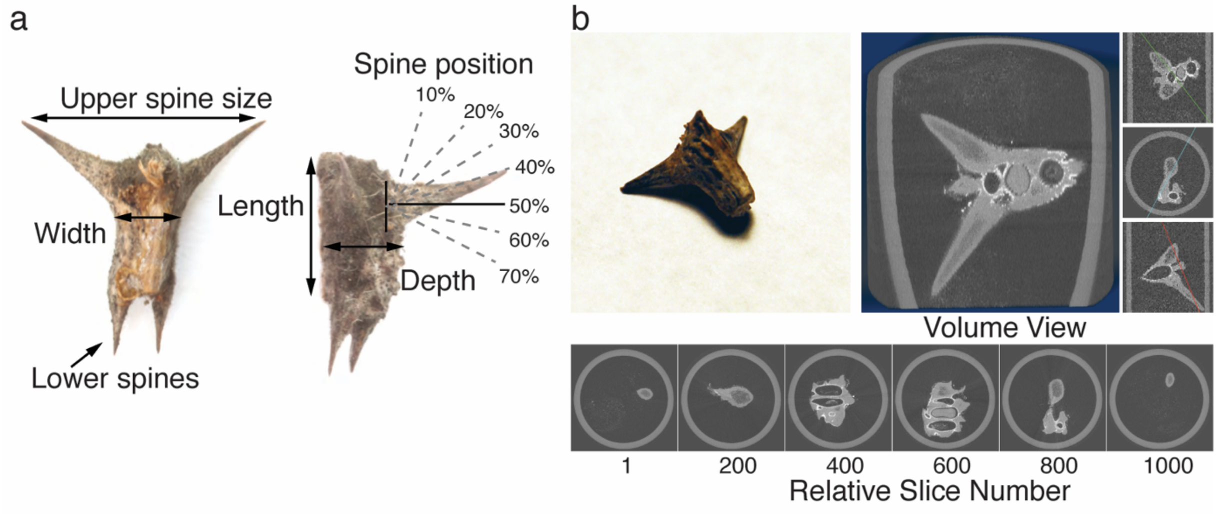


**Figure 4.4** Variation in the proportion of seed predation per population among islands, years, and with contrasting finch community composition. The data correspond to the populations sampled on the four islands (represented by different shapes) that were visited repeatedly over three years of the 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).

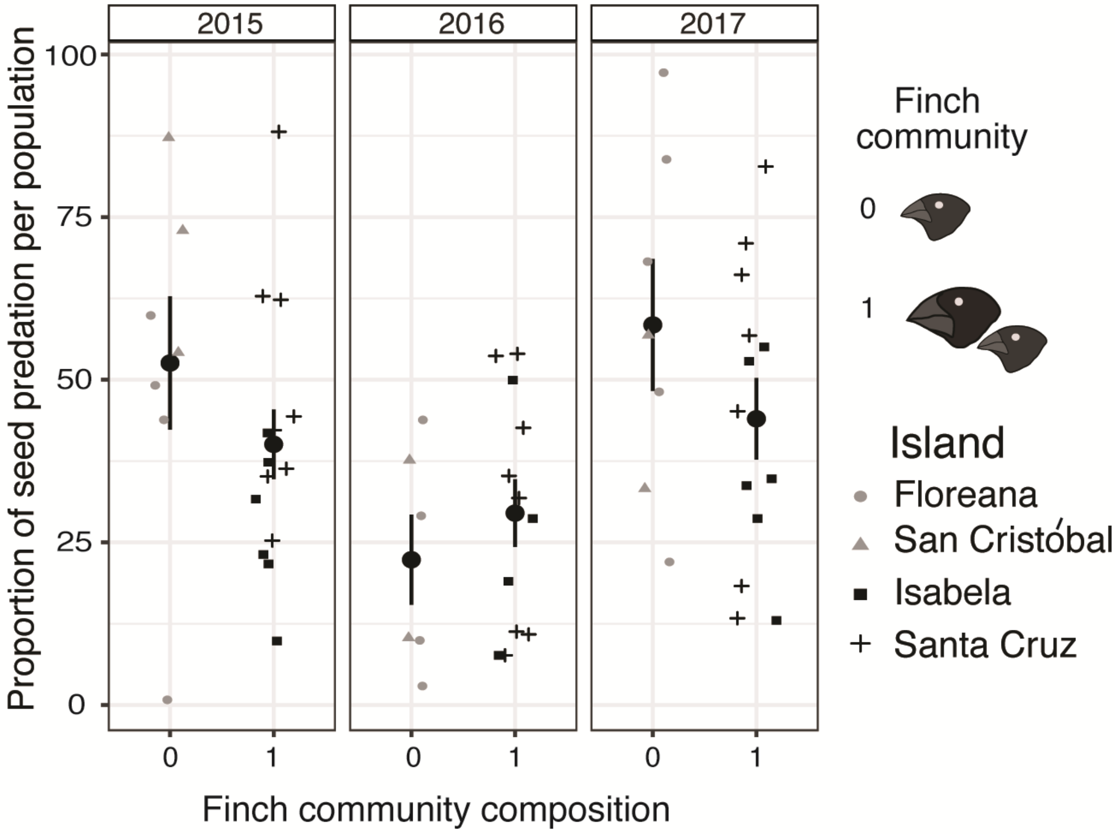


**Figure 4.5** Predicted seed survival probability for each mericarp trait estimated from logistic linear mixed-effects models. Variation in relation to finch community composition (a) and year (b). The response variable used was binary, with 0 indicating mericarps with one or more seeds removed by finches, 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.

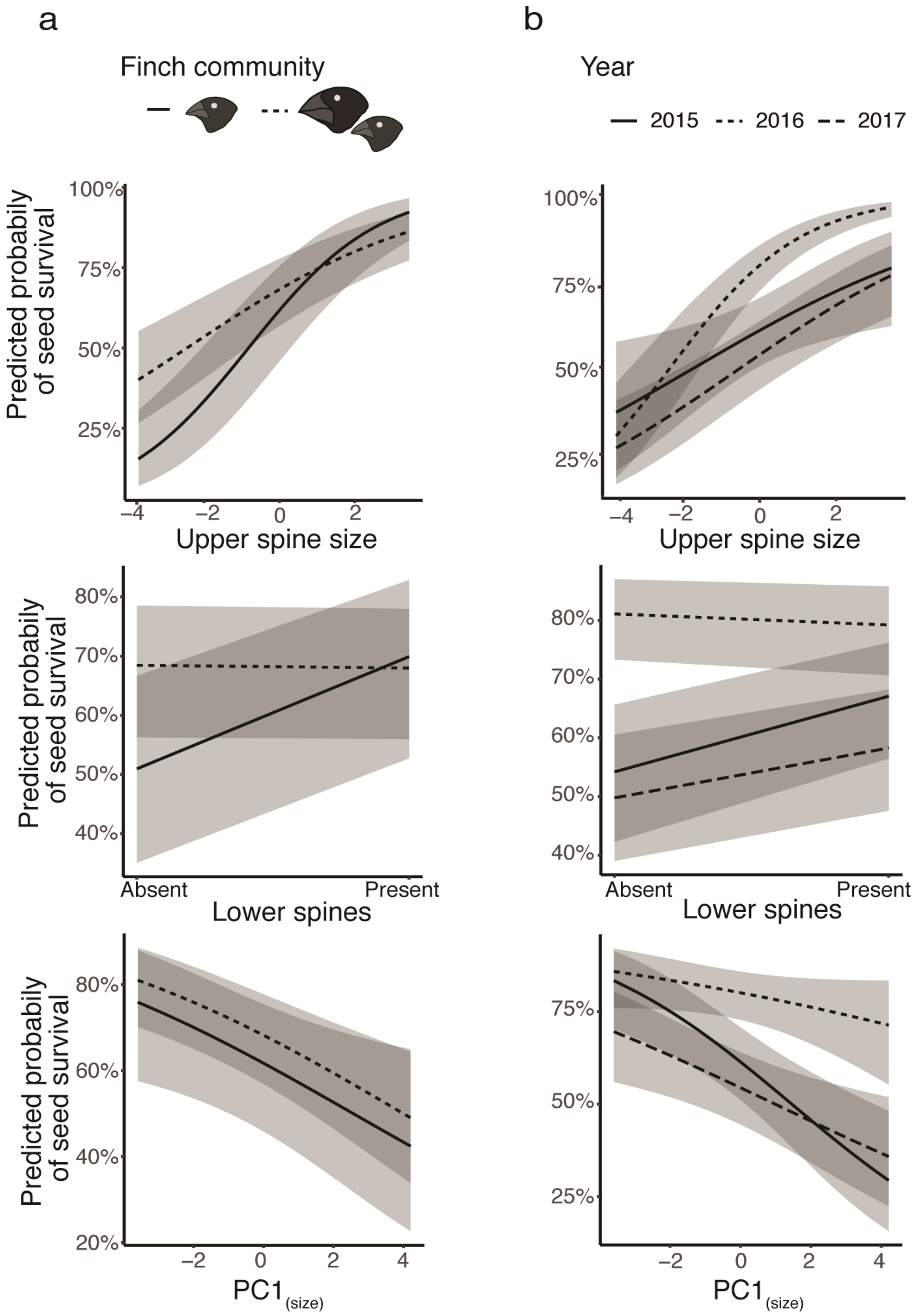

a
Finch community
b
Year
2015
2016
2017
Predicted probabily of seed survival
100%
75%
50%
25%
−4
−2
0
2
Upper spine size
80%
70%
60%
50%
40%
Absent
Present
Lower spines
20%
4
PC1 (size)

**Figure 4.6** 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 mericarp length (b) and mericarp width (c).

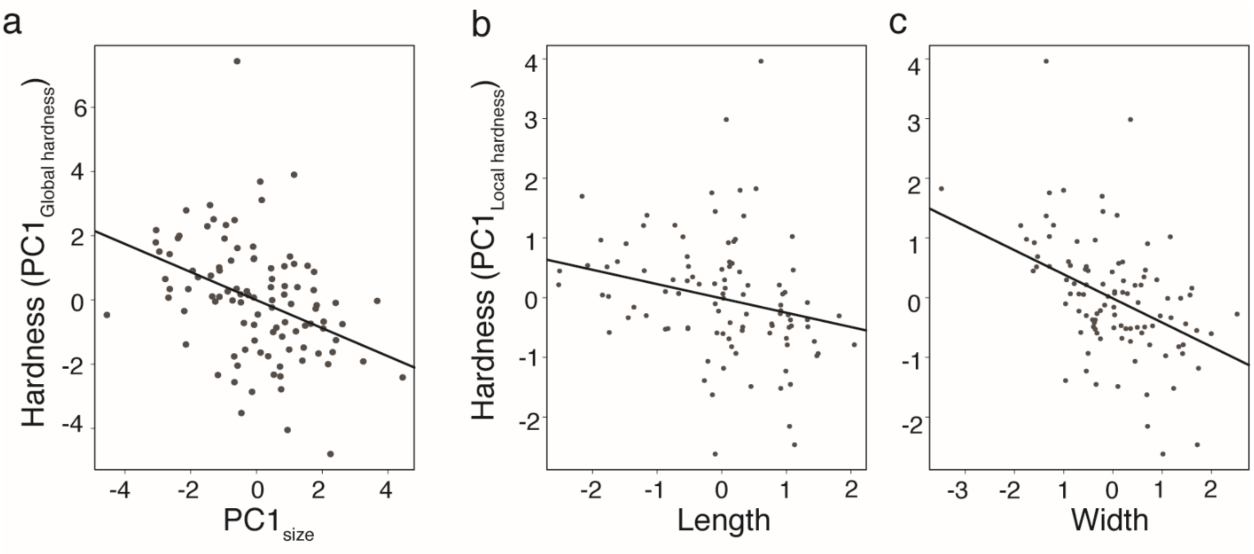


**Figure 4.7** Variation in *Tribulus cistoides* mericarp morphology. Means (circle) and standard error (bars) of each mericarp trait for the four islands that were sampled from 2015 to 2017: Floreana (Flo), San Cristóbal (S.Cri), Isabela (Isa), and Santa Cruz (S.Cru). Islands where large-beaked finch species are absent (only *G. fortis* present) are indicated in grey and islands where this species (i.e. *Geospiza magnirostris*) is present are indicated in black.

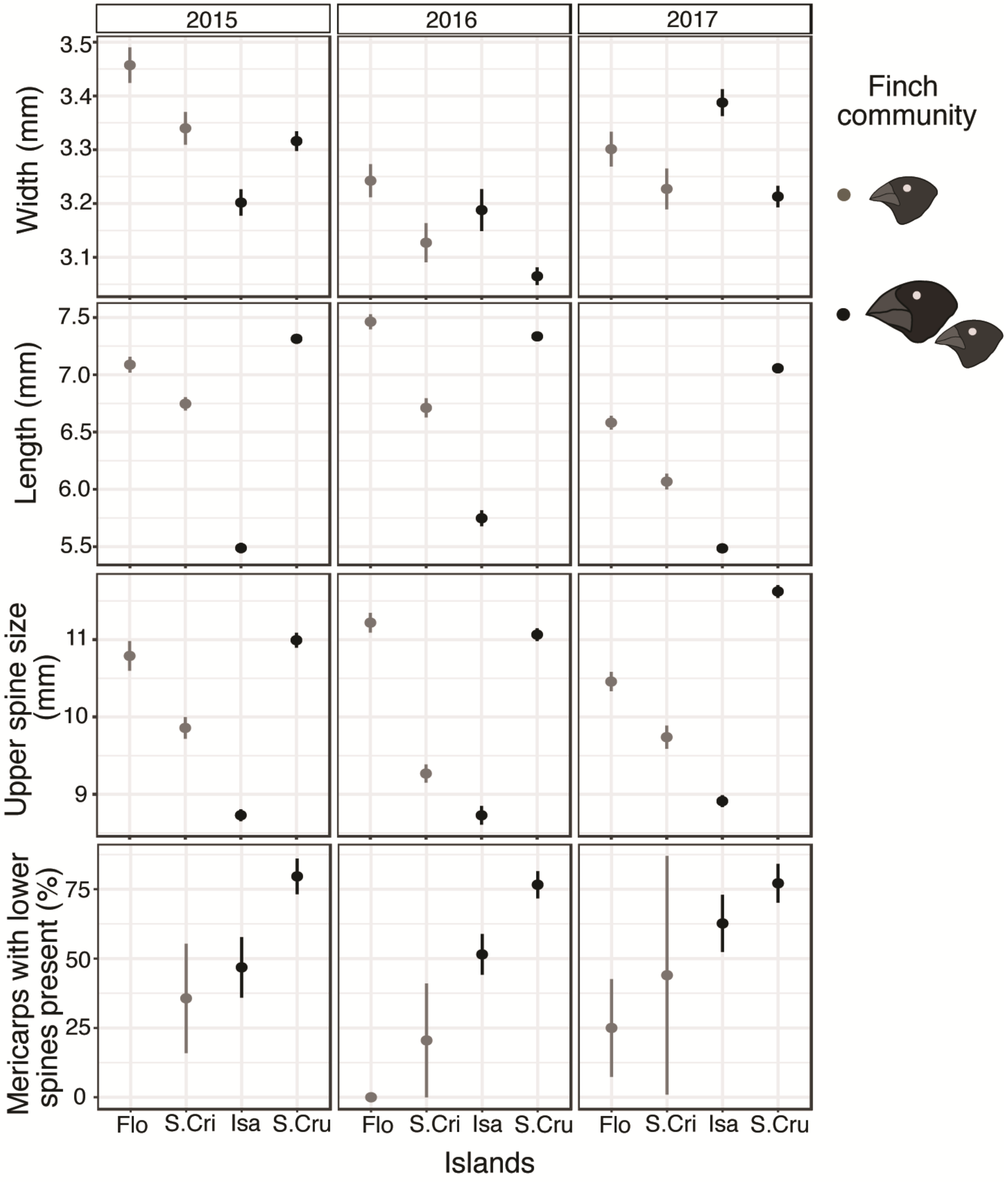
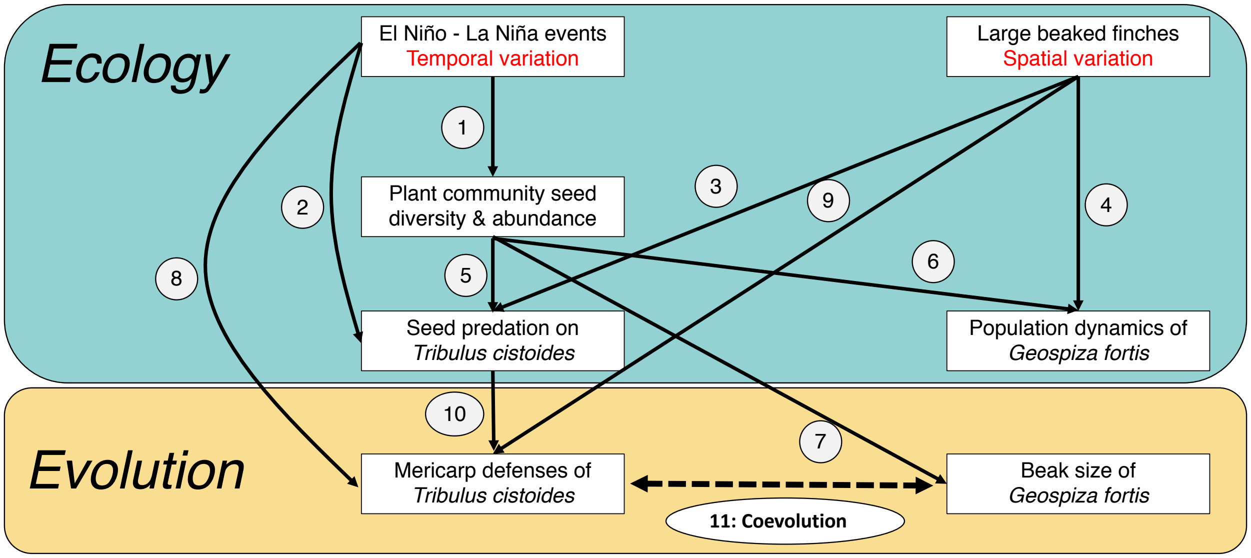


**Figure 4.8** Ecological and evolutionary processes influencing interactions between *Tribulus cistoides* and Darwin's finches. (1) Dry periods reduce seed diversity and abundance; (2) Predation increases the year following La Niña years (low precipitation); (3) Presence of large-beaked finches increases 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* populations size; (7) Decreased seed diversity/abundance selects for larger beaks of *G. fortis* when large-beaked bird species are absent; 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*. Eco-evolutionary feedbacks might also operate between the evolutionary and population dynamics within species (arrows not shown).



# CHAPTER 5:

# Conclusion

In this chapter, I review the main contributions of this thesis to our current understanding of how the interplay between ecology and evolution can influence the structure of species assemblages and to our current knowledge of plant communities and Darwin's finches in the Galápagos Islands. I also consider some questions that remain unaddressed and suggest future research directions that can build from this body of work. I focus first on processes occurring at large saptio-temporal scales, as discussed in Chapter 1, and then consider processes operating at contemporary spatio-temporal scales (Chapters 2 and 3).

## Large spatio-temporal scales

In the second chapter of this thesis, I examined the effect of macroecological and macroevolutionary processes on the assembly of flowering plants on the Galápagos archipelago. The phylogenetic structure of the native Galápagos flora showed strong phylogenetic clustering in relation to expectations generated from drawing species at random from the pool of potential continental colonisers. This pattern coincides with general characterizations of disharmonic insular biotas (Whittaker and Fernández-Palacios, 2007), and likely reflects strong ecological selective pressures imposed during colonization and establishment that disproportionately favored a subset of species with particular traits. In addition, in the case of the Galápagos flora, this regional clustering was enhanced by *in situ* speciation events that have significantly contributed to endemic species diversity (~64.5 %; Tye and Francisco-Ortega 2011).

### *Dispersal limitation vs habitat filtering*

Species assembly on insular biotas is traditionally thought to be driven primarily by island isolation and area. Among potential colonisers, species with traits associated with long-distance dispersal ability are considered those most likely to colonise isolated locations, such as oceanic islands. However, as presented in Chapter 2, I found evidence suggesting that habitat filtering had a stronger effect than dispersal limitation in shaping the Galápagos flora. Colonization success on the archipelago was better explained by species climatic suitability than by species dispersal ability. In addition, the phylogenetic structure of species assemblages on individual islands and the variation in phylogenetic structure among islands were also better explained by island climate than by island isolation. The adaptive loss of dispersal ability in insular species (Carlquist 1966) could potentially have been a confounding influence; however, there is no evidence supporting such a trend among species of the Galápagos flora (Vargas et al. 2012; Vargas et al. 2014). Furthermore, evidence indicating that plant long-distance dispersal can frequently occur by non-standard means (Nathan 2006) suggests that species without long-distance dispersal traits might be less geographically restricted than expected by isolation. The body of work presented here suggests that the relative importance of habitat filtering on species assembly of insular floras should be reconsidered. Over long periods of time, even poor dispersers might be able to arrive at remote locations, yet they may be unable to overcome unsuitable climatic conditions while attempting to establish.

## *Speciation*

Matching expectations, I found that speciation also had an important effect on the phylogenetic structure of species' assemblages, but that the effect varied with the scale of analysis. Endemic species, which are more likely to be a product if *in situ* speciation, increased the clustering of the Galápagos flora in relation to the potential pool of colonisers from the continent; and there is evidence to suggest that several taxa, once established on the archipelago, underwent subsequent adaptive radiation (e.g. *Scalesia*, *Opuntia, Alternanthera, Mollugo*). However, endemic species reduced the strength of clustering within individual island assemblages when evaluated against expectations derived from resampling the flora of the entire Galápagos archipelago. Although this pattern needs to be further examined, I suggest it likely reflects the restricted distribution of endemic species (Vargas et al. 2014), and the important proportion of endemic taxa that probably resulted from anagenetic evolution (i.e. a single endemic taxon produced after a colonization event) (Stuessy et al. 2006)—such anagenic speciation events do not result in clustering of close relatives.

Observation of the phylogenetic structure of the Galápagos flora raises additional questions that might remain unanswered until more information on species phylogenetic relationships and species ecology becomes available. Several interesting questions remain unanswered, including: to what extent have the Galápagos flora and diversification within this island system influenced the species diversity of regional source pools? In this study, I assumed that colonization occurred in only one direction, from the continent to the archipelago; however, recent evidence suggesting cases of "reverse colonization" from islands to continents (Bellemain and Ricklefs 2008) deserves further attention. It is also important to better understand the dynamics of species' evolution on the islands and which factors trigger and constrain radiation vs anagenesis within colonizing lineages. In addition, it would be valuable to obtain a deeper understanding of the constraints that determine the distribution of endemic species within and among islands. At smaller temporal and spatial scales, the effect of biotic interactions and local climate might co-dominate, whilst at larger scales biotic interactions may become less constraining (Cavender-Bares et a. 2009; Vamosi et al. 2009). With an increasing number of introduced species establishing on the archipelago over recent decades (Tye 2001), addressing such questions is increasingly pressing and will be important for managing and conserving this unique ecosystem.

## Contemporary spatio-temporal scales

In the third and fourth chapters of this thesis, I addressed the role of eco-evolutionary interactions occurring at contemporary time scales in natural communities. I used Darwin's ground finches and the plants upon which they feed as my study system. Given the established strong effect of seed availability on the evolution finch beaks, there has been speculation that reciprocal ecological and evolutionary feedbacks might shape finch-plant dynamics (Post and

Palkovacs 2009). I show some evidence for the existence of such feedbacks, but their importance within this system is mediated by multiple additional, and in some cases unpredictable, factors.

### *Coupling and decoupling of eco-evolutionary interactions in nature*

In Chapter 3, from observations of ground finch behavior, I show significant selectivity in ground finch dietary choices. However, as is also documented in previous studies (Grant and Grant 1986), in wet conditions finches rely less on plant food items, and thus both the strength of interactions and selectivity on plant food items decrease. I also show that seeds which escape predation by finches tend to be clustered on the plant phylogeny; I suggest this likely reflects shared evolved traits that influence finch preferences. This is supported by seed trait comparisons between eaten and uneaten seeds: finches tend to eat softer seeds, and in one site, larger seeds. It is also possible that finch preferences are influenced by secondary compounds acting as chemical defenses against seed predation (Agrawal and Fishbein 2006) and/or nutritional properties of seeds, and these important areas require further study.

The results of the exclusion experiments showed that ground finches can have a strong effect on the composition of seed banks. Finch predation decreases seed density, alters the species composition and trait distribution of seeds within seedbanks, and shifts both the taxonomic and phylogeneic diversity of intact seeds. Importantly, the effect of finch predation on seed banks varies between study sites as does the composition of finch communities. This pattern is consistent with a link between the distribution of finch beak sizes within a community and finch seed selectivity – e.g. communities with more large beaked finches would be exposed to greater predation pressure on large seeds. The coupling of the ecological effect of seed availability on finch evolution and the ecological effect of finch predation on seed bank composition suggests that finches could alter their own evolutionary trajectories. However, I found that the effect of finch predation on seed banks was not consistently translated to equivalent shifts in the emergent above ground vegetation. I therefore suggested that other factors influencing seed survival and plant recruitment may cause a decoupling of eco-evolutionary interactions between finches and plants.

These findings constitute a significant contribution to our current understanding of the role of eco-evolutionary interactions in complex natural communities. Nonetheless, there are still key questions that remain outstanding, including: to what extent do evolutionary changes in finch beak morphology influence plant communities and the fitness of individual plant species? And what are the long-term effects of these eco-evolutionary interactions given the high background variability in the environment? The spatial setting of the archipelago provides an ideal opportunity to perform additional exclusion experiments that could help address these and similar questions. For example, it is well documented that there are differences in beak size distributions among focal species across the different islands, which is information that could be used to make predictions about seed preferences. In addition, to more fully understand the potential importance of seed predation on plant community structure more data is needed about the processes shaping seed germination and plant recruitment. For example, it would be valuable to experimentally test whether plant recruitment is limited by space and/or seed abundance (Muller-Landau et al. 2002), and whether there might be potential trade-offs between seed defense traits, germination success, and seedling survival (Crawley 2014).

## *Environmental context influencing reciprocal interactions*

In Chapter 4, I studied seed predation by ground finches on *Tribulus cistoides* and explored whether there is evidence to suggest reciprocal ecological and evolutionary dynamics between ground finches and the *T. cistoides* plants upon which they feed. I showed that finches can significantly decrease seed survival and impose selection on fruit defense traits. I also found some evidence suggesting a potential divergence in fruit morphology in relation to different selection pressures among islands. However, to quantify the potential strength of selection imposed by finches, it is necessary to establish the heritability of the seed traits that finches are selecting for—which could be explored using common garden experiments and molecular analyses. In addition, other ecological processes that might constrain evolutionary responses in fruit morphology to seed predation by finches could be further examined. For instance, it would be valuable to explore the strength of potentially opposing selection pressures on *T. csitoides* fruits during dispersal and germination.

A main conclusion from my work on the Galápagos finch-plant system is that ecological interactions and strength of selection vary over both space and time. It is likely that the different species compositions of finch communities across islands and yearly climatic fluctuations underlie much of this variation. Such variation emphasizes the importance of considering the geographic mosaic (Thompson 2005) in the study of eco-evolutionary dynamics, especially in natural systems within heterogenous landscapes (Brunner et al. 2019).

Collectively, my thesis deepens our current understanding of the interplay between ecological and evolutionary processes shaping communities of species. At larger scales, the role of these interactions has received more attention, and here I use an emblematic insular system to show how the incorporation of ecophylgenetic approaches can help us to disentangle the effects of the multiple factors driving species assembly. At a finer scale, I have shown how ecological and evolutionary dynamics can interact and feedback into one another, but I also suggest that such eco-evolutionary dynamics might not necessarily scale-up in natural systems against a background of high environmental variability.

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# APPENDIX

## Supplementary Information Chapter 2

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**Supplementary Information S1**| List of plant checklists, public databases, and literature sources

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**Source area analysis**

Previous studies have suggested a close relationship between the Galápagos flora and the flora of the northwestern regions of South America (Hooker 1847; Svenson 1946; Porter 1976, 1984). To establish the source pool of species from which the native Galápagos flora is derived, we examined 15 putative source regions within America, indexed as follows: 1= Argentina, 2 = Bolivia, 3 = Brazil, 4 = Chile, 5 = Colombia, 6 = Ecuador, 7 = Guyanas, 8 = Mesoamerica (Mexico plus Central America), 9 = North America, 10 = Paraguay, 11 = Perú, 12 = The Cocos Island, 13 = Uruguay, 14 = Venezuela, 15 = West Indies.

First, we calculated a similarity index (SI), as the proportion of the Galápagos non-endemics angiosperms present in each of the 15 potential source areas. Second we estimated the probability of each region being the source of origin of a Galápagos species chosen at random ($p_i$) following Papadopulus et al. (2011):

$$p_i = (1/N_s) \sum_{j=1}^{N_s} (O_{i,j} / \sum_{i=1}^{N_R} O_{i,j})$$

Where $N_s$ is the number of species included, $N_R$ is the number of source regions, and $O_{i,j}$ is the presence (1) or absence (0) of species $j$ in region $i$. A list of species included in the analysis (216 species) and their presence (1) or absence (0) on each region is presented below.

**Supplementary Information S2|** Species dispersal strategy information

Information on species dispersal strategies was compiled from the literature listed below and the following online databases: The LEDA Traitbase: A database of life-history traits of Northwest European flora <www.leda-traitbase.org> (Kleyer et al. 2008), Royal Botanic Gardens Kew Seed Information Database (SID) <http://data.kew.org/sid>, FRUBASE <http://ebd10.ebd.csic.es/mywork/frubase/> (Jordano 1995), and BROT: plant trait database for Mediterranean Basin species <www.uv.es/jgpausas/brot> (Paula et al. 2009; Paula and Pausas 2013). We considered evidence from direct observations or authors' inferences based on diaspore morphology.

Authors and database managers use multiple systems to classify dispersal methods, usually according to the information available on species biology and environmental context. For purposes here, we classify species in to two broad groups: those with and without long-distance dispersal strategies. Species reported as having zoochory (animal dispersal), anemochory (wind dispersal), or hydrochory (water dispersal) dispersal were considered as species with long-distance dispersal strategies, and species with unassisted dispersal as species without long-distance dispersal strategies (Willson 1993; Gómez and Espadaler 1998; Thomson et al. 2010). To maximize the number of species included in our data set, we defined these four categories as follows:

(1) Zoochory – animal dispersal, which included: diaspore ingested by animals intentionally or accidentally (when the evidence consists of direct observations), diaspore carried by animals intentionally (except insects) or accidentally (e.g. when the diaspore have an adhesive mechanism or when there was direct observational evidence).

(2) Anemochory – wind dispersal, which included diaspore blown by the wind, with the exception of tumbleweeds.

(3) Hydrochory – water dispersal, diaspore transported on the surface or submerged in water currents; dispersal triggered by raindrops was excluded.

(4) Unassisted dispersal – no reported dispersal vector, which included seeds that disperse solely by dropping to the ground near or beneath the parent plant, or are actively dispersed by the parent plant, such as explosive dehiscence.

These four categories of dispersal are considered non-exclusive because species can have several methods of dispersal, and different authors might use different criteria to assign a dispersal mechanism

Additionally, for species without recorded dispersal strategies, we used diaspore morphology descriptions from the literature to assign likely seed dispersal strategies (Pijl 1982; Willson et al. 1990; Hughes et al. 1994). We considered diaspores that have wings, plumes, or tufts of hairs structures as being wind-dispersed; diaspores that have fleshy structures, pulp or arils as being dispersed by animal ingestion; diaspores with hooks, awns, sticky hairs or other adherent structures as being dispersed on the fur and feathers of animals; corky diaspores with internal air chambers as being dispersed by water; and plants with explosive mechanisms for releasing diaspores, or with no obvious morphological structure that could be associated with the above dispersal vectors, as to being dispersed without assistance. (data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.43b1t).

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**Supplementary Information S3 |** Species distribution within the Galápagos archipelago.

Information of species distribution was obtained from Wiggins and Porter (1971) and Jaramillo Díaz et al. (2015). We present below the list of the 373 native Galápagos angiosperm species considered in this study to estimate island phylogenetic structure metrics for the 14 main islands. We indicate their endemic status and presence (1) or absence (0) on each island, indexed as follows: 1 = Darwin, 2 = Española, 3 = Fernandina, 4 = Floreana, 5 = Genovesa, 6 = Isabela, 7 = Marchena, 8 = Pinta, 9 = Pinzon, 10 = San Cristóbal, 11 = Santa Cruz, 12 = Santa Fé, 13 = Santiago, and 14 = Wolf. Species names were standardized according to The Plant List 1.1 <http://www.theplantlist.org/> and the Taxonomic Name Resolution Service <http://tnrs.iplantcollaborative.org> (Boyle et al. 2013). Unresolved and unmatched taxa names were excluded. Higher taxonomic membership_of each species was then standardized according to APG III (Angiosperm Phylogeny Group 2009).

| **Species** | **Status** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acacia insulae-iacobi* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Acacia macracantha* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Acacia rorudiana* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Acalypha abingdonii* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Acalypha flaccida* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Acalypha parvula* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Acalypha velutina* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Acalypha wigginsii* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Acmella darwinii* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Ageratum conyzoides* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Alternanthera echinocephala* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Alternanthera filifolia* | Endemic | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Alternanthera flavicoma* | Endemic | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Alternanthera galapagensis* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Alternanthera halimifolia* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Alternanthera helleri* | Endemic | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Alternanthera nesiotes* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Alternanthera* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *rugulosa* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Alternanthera snodgrassii* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Alternanthera subscaposa* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Alternanthera vestita* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Amaranthus anderssonii* | Endemic | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| *Amaranthus furcatus* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Amaranthus scleranthoides* | Endemic | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Amaranthus squamulatus* | Native | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| *Anredera ramosa* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Anthephora hermaphrodita* | Native | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Aristida divulsa* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Aristida repens* | Endemic | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Aristida subspicata* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Aristida villosa* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| *Atriplex peruviana* | Native | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| *Avicennia germinans* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Baccharis steetzii* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Bastardia viscosa* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Batis maritima* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Bidens riparia* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Blechum pyramidatum* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Blutaparon rigidum* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Boerhavia coccinea* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Boerhavia erecta* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Boerhavia tuberosa* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Borreria ericaefolia* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 |
| *Bowlesia palmata* | Native | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Brachiaria multiculma* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Brachycereus nesioticus* | Endemic | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Brickellia diffusa* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| *Bulbostylis juncoides* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Bursera graveolens* | Native | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Calandrinia galapagosa* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Calceolaria* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *dichotoma* | | | | | | | | | | | | | | | |
| *Capraria biflora* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Capraria peruviana* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Capsicum galapagoense* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cardiospermum corindum* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Castela galapageia* | Endemic | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Castilleja scorzonerifolia* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cenchrus platyacanthus* | Endemic | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Centella asiatica* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Chiococca alba* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Chrysanthellum pusillum* | Endemic | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Cissampelos glaberrima* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Cissampelos pareira* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Cissus verticillata* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Commelina diffusa* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Conocarpus erectus* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Corchorus orinocensis* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Cordia andersonii* | Endemic | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Cordia leucophlyctis* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Cordia lutea* | Native | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Cordia polycephala* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cordia revoluta* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Cordia scouleri* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Cranichis ciliata* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cranichis lichenophila* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cranichis werffii* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cressa truxillensis* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Crotalaria incana* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Crotalaria pumila* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Croton scouleri* | Endemic | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Cryptocarpus pyriformis* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Cuphea carthagenensis* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Cuscuta acuta* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Cuscuta gymnocarpa* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cyclopogon werffii* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cyclospermum laciniatum* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Cyperus anderssonii* | Endemic | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Cyperus confertus* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Cyperus distans* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cyperus drummondii* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Cyperus esculentus* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| *Cyperus grandifolius* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Cyperus laevigatus* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cyperus ligularis* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cyperus squarrosus* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Dalea tenuicaulis* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Darwiniothamnus lancifolius* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Darwiniothamnus tenuifolius* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Delilia inelegans* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Delilia repens* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Desmanthus virgatus* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Desmodium procumbens* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Dichondra microcalyx* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Dicliptera peruviana* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Distichlis spicata* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dodonaea viscosa* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Drymaria cordata* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Drymaria monticola* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Drymaria rotundifolia* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Duranta dombeyana* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Duranta erecta* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Duranta mutisii* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Eclipta prostrata* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Eleocharis acutangula* | Native | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Eleocharis atropurpurea* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Eleocharis maculosa* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Eleocharis montana* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Eleocharis mutata* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Eleocharis sellowiana* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Encelia hispida* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| *Enydra maritima* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Enydra sessilifolia* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |

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| *Epidendrum spicatum* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Eragrostis ciliaris* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Eragrostis mexicana* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Eragrostis pastoensis* | Native | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Erigeron alternifolius* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Eriochloa pacifica* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Erythrina velutina* | Native | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *Euphorbia abdita* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Euphorbia amplexicaulis* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Euphorbia equisetiformis* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Euphorbia galapageia* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Euphorbia nummularia* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Euphorbia punctulata* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Euphorbia recurva* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Euphorbia viminea* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Evolvulus convolvuloides* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Evolvulus simplex* | Native | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Exodeconus miersii* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Fimbristylis dichotoma* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Froelichia juncea* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Froelichia nudicaulis* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Fuertesimalva insularis* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Galactia striata* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Galium canescens* | Native | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Galium galapagoense* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Galvezia leucantha* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Gossypium darwinii* | Endemic | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Gossypium klotzschianum* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Govenia utriculata* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Grabowskia boerhaaviifolia* | Native | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Habenaria alata* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Habenaria distans* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Habenaria monorrhiza* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Heliotropium anderssonii* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |

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| *Heliotropium angiospermum* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Heliotropium curassavicum* | Native | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Heliotropium indicum* | Native | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Herissantia crispa* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Hibiscus diversifolius* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Hippomane mancinella* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Homolepis glutinosa* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Hydrocotyle galapagensis* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Hydrocotyle umbellata* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Hypericum thesiifolium* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Hypoxis decumbens* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Hyptis gymnocaulos* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hyptis spicigera* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Iochroma ellipticum* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Ionopsis utricularioides* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| *Ipomoea habeliana* | Endemic | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| *Ipomoea imperati* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ipomoea incarnata* | Native | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Ipomoea pes-caprae* | Native | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Ipomoea triloba* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Ipomoea tubiflora* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Jaegeria gracilis* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Jaltomata werffii* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Jasminocereus thouarsii* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Justicia galapagana* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Kallstroemia adscendens* | Endemic | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Klaprothia fasciculata* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Kyllinga brevifolia* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Kyllinga pumila* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Laguncularia racemosa* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Lantana peduncularis* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Laportea aestuans* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Lecocarpus lecocarpoides* | Endemic | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |

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| *Lecocarpus pinnatifidus* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lemna aequinoctialis* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Linum cratericola* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Linum harlingii* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Liparis nervosa* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Lippia rosmarinifolia* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Lippia salicifolia* | Endemic | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lobelia xalapensis* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Ludwigia erecta* | Native | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Ludwigia leptocarpa* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Ludwigia peploides* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Lycium minimum* | Endemic | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| *Macraea laricifolia* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Macroptilium atropurpureum* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Maytenus octogona* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Mecardonia procumbens* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Mentzelia aspera* | Native | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Merremia aegyptia* | Native | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Miconia robinsoniana* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Microchilus weberianus* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Mollugo cerviana* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Mollugo crockeri* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Mollugo flavescens* | Endemic | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Mollugo floriana* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| *Mollugo snodgrassii* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Muhlenbergia microsperma* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Najas guadalupensis* | Native | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Nama dichotoma* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Neptunia plena* | Native | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Nicotiana glutinosa* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Nolana galapagensis* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Ombrophytum subterraneum* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Opuntia echios* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Opuntia galapageia* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Opuntia helleri* | Endemic | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Opuntia insularis* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Opuntia megasperma* | Endemic | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Opuntia saxicola* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

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| *Oxalis dombeyi* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Oxalis megalorrhiza* | Native | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| *Panicum alatum* | Native | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Panicum arundinariae* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Panicum dichotomiflorum* | Native | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Panicum hirticaule* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Parietaria debilis* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Parkinsonia aculeata* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Paspalidium geminatum* | Native | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Paspalum distichum* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Paspalum galapageium* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Paspalum paniculatum* | Native | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Paspalum penicillatum* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Paspalum redundans* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Paspalum vaginatum* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Passiflora colinvauxii* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Passiflora foetida* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Passiflora suberosa* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Pectis subsquarrosa* | Endemic | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Pectis tenuifolia* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Pennisetum pauperum* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Peperomia galioides* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Peperomia inaequalifolia* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Peperomia petiolata* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Peperomia rotundata* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Pernettya howellii* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Persicaria acuminata* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Persicaria hydropiperoides* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Persicaria punctata* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Phaseolus mollis* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Phoradendron berteroanum* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Phyla strigulosa* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Phyllanthus caroliniensis* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Physalis angulata* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |

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| *Physalis galapagoensis* | Endemic | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Physalis pubescens* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| *Phytolacca octandra* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Pilea baurii* | Endemic | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Pilea peploides* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Piscidia carthagenensis* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Pisonia floribunda* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Plantago galapagensis* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Pleuropetalum darwinii* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Plumbago coerulea* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plumbago zeylanica* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Polygala anderssonii* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Polygala galapageia* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Polygala sancti-georgii* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Polygonum galapagense* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Ponthieva maculata* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Portulaca howellii* | Endemic | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Prescottia oligantha* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Prosopis juliflora* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Psidium galapagaeum* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Psychotria angustata* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Psychotria rufipes* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Pycreus bipartitus* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Pycreus polystachyos* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Ranunculus flagelliformis* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Rhizophora mangle* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Rhynchosia minima* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Rhynchospora contracta* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Rhynchospora corymbosa* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Rhynchospora nervosa* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Rhynchospora rariflora* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Rhynchospora rugosa* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Rhynchospora tenuis* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Rorippa nana* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Ruellia floribunda* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Ruppia maritima* | Native | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Rytidostylis carthagenensis* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Salvia insularum* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Salvia occidentalis* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Salvia prostratus* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Salvia pseudoserotina* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Sarcocornia fruticosa* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sarcostemma angustissimum* | Endemic | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Scaevola plumieri* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Scalesia affinis* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Scalesia aspera* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Scalesia atractyloides* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Scalesia baurii* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Scalesia helleri* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Scalesia incisa* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Scalesia microcephala* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Scalesia pedunculata* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Scalesia stewartii* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Scalesia villosa* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Scleria distans* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Scleria gaertneri* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Scoparia dulcis* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Scutia spicata* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Senna occidentalis* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Senna pistaciifolia* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Senna uniflora* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Sesuvium edmonstonei* | Native | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Sesuvium portulacastrum* | Native | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Setaria parviflora* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Setaria setosa* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Sicyocaulis pentagonus* | Endemic | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Sicyos villosus* | Endemic | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sida salviifolia* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Sida spinosa* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Sisyrinchium galapagense* | Endemic | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Solanum americanum* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Solanum cheesmaniae* | Endemic | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Solanum edmonstonei* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Solanum erianthum* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Soliva anthemifolia* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Spermacoce dispersa* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Spermacoce linearifolia* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Spermacoce perpusilla* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Spermacoce remota* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Spermacoce rotundifolia* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Spermacoce suberecta* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sporobolus indicus* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Sporobolus pyramidatus* | Native | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Sporobolus virginicus* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Stenotaphrum secundatum* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Stuckenia pectinata* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Stylosanthes sympodialis* | Native | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Tephrosia cinerea* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Tetramerium nervosum* | Native | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Teucrium vesicarium* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Tillandsia insularis* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Tiquilia darwinii* | Endemic | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Tiquilia fusca* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Tiquilia galapagoa* | Endemic | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Tiquilia nesiotica* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Tournefortia psilostachya* | Native | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Tournefortia pubescens* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Tournefortia rufo-sericea* | Endemic | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |
| *Trianthema portulacastrum* | Native | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Trichoneura lindleyana* | Endemic | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Trisetum howellii* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Tropidia polystachya* | Native | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Uniola pittieri* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Utricularia foliosa* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Vallesia glabra* | Native | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Verbena grisea* | Endemic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Verbena townsendii* | Endemic | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Vigna adenantha* | Native | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Vigna luteola* | Native | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Volkameria mollis* | Native | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *Waltheria ovata* | Native | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Zanthoxylum fagara* | Native | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 |

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**Supplementary Information S4 |** Phylogenetic structure of the Galápagos archipelago using the reduced phylogeny.

Phylogenetic structure of Galápagos flora was estimated using an alternative phylogeny that has a better tip resolution, but include a reduced set of data (34,304 species see details in Methods). Phylogenetic structure was estimated using three potential source pools (small, medium and large). The standard effect sizes of phylogenetic diversity (SES.PD) and mean pairwise distances (SES.MPD) calculated from 999 random draws from the phylogeny are presented below. Negative values indicate phylogenetic clustering. Significant patterns relative to the null model are marked with an asterisk (*).

| | Species pool | SES.PD | SES.MPD |
|---|---|---|---|
| **Small** | Native species | -6.21* | -9.76* |
| | Native species, non endemics | -4.25* | -3.91* |
| **Medium** | Native species | -5.50* | -9.94* |
| | Native species, non endemics | -3.43* | -4.15* |
| **Large** | Native species | -5.77* | -9.97* |
| | Native species, non endemics | -3.46* | -4.43* |

**Supplementary Information S5 |** Phylogenetic logistic regression evaluating the predictors of plant species colonization success of the Galápagos archipelago.

To examine the effects of dispersal strategy and the climatic suitability on the success of plant species colonizing the Galapagos archipelago, we fit phylogenetic logistic regression models with presence/absence of species in the archipelago (P/A, 0 = absence, 1 = present) as response variable. Here, we present the models fit for the complete set of data obtained for dispersal strategy (4339 species) and climatic suitability (11,934 species) independently. Species dispersal strategy was coded as a binary variable representing species' long-distance dispersal strategy (LDD, 0 = absence, 1 = present). The climatic suitability of the archipelago for each species was described using two variables (see methods): niche dissimilarity (ND, lower values indicate higher similarity) and niche overlap (NO, higher values indicate greater overlap). In addition, we present (marked with an a asterisk *) the models fit with an alternative re-categorization of dispersal strategy, considering the number of dispersal strategies that species have, in order to test if multiple long dispersal strategies could have favor colonization success (Vander Wall and Longland 2004; Vargas et al. 2015). For the latter, we classified dispersal strategy (DS) into four categories: DS = 1 (species with unassisted dispersal), DS = 2 (species with one long-distance dispersal strategy), DS = 3 (species with two long-distance dispersal strategies), and DS = 4 species with three long distance dispersal strategies. As in the main analysis, zoochory, hydrochory, and anemochory were considered long-distance dispersal strategies. In order to be able to compare these models, we fit them only using species that had data on both dispersal and climatic suitability (3,029 species).

| Parameter | Coefficient | z value | 95% CI | *P* values | AIC |
|---|---|---|---|---|---|
| Model: P/A ~ ND | | | | | 1446.2 |
| ND | -0.940 | -9.622 | (-1.293 – -0.663) | $p < 0.001$ | |
| Model: P/A ~ NO | | | | | 1569.1 |
| NO | 0.256 | 4.903 | (0.212 – 0.292) | $p < 0.001$ | |
| Model: P/A ~ LDD | | | | | 1503.6 |
| LDD | -0.684 | -3.329 | (-0.982 – -0.304) | $p = 0.001$ | |
| Model: P/A ~ ND* | | | | | 929.2 |
| ND | -3.508 | -13.247 | (-3.949 – -2.884) | $p < 0.001$ | |
| Model: P/A ~ ND + DS* | | | | | 951.7 |
| ND | -2.593 | -8.236 | (-2.954 – -2.289) | $p < 0.001$ | |
| DS | -0.266 | -2.018 | (-0.488 – 0.099) | $p < 0.044$ | |
| Model: P/A ~ DS* | | | | | 1151.5 |
| DS | -0.593 | -2.946 | (-0.980 – -0.090) | $p < 0.003$ | |

## References

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**Supplementary Information S6 |** Phylogenetic diversity of island assemblages (SES.PD).

Standardized effect sizes of phylogenetic diversity (SES.PD) were calculated for species assemblages on each of the 14 main islands, with and without including endemic species. We use the regional phylogeny reduced to species native to the archipelago (216 native non-endemic plus 156 endemic species) as the regional species pool. SES.PD has a greater sensitivity to terminal structure of the phylogenies, which makes it better suited for exploring assembly processes relevant at a small temporal and spatial scale (Mazel et al. 2015). SES.PD values for each island are listed below. Positive values correspond to over dispersed assemblages, whereas negative values correspond to clustered assemblages, significant values indicated by an asterisk.

| **Island** | **SES.PD** | **SES.PD non-endemics** |
|---|---|---|
| Darwin | -0.447 | -0.460 |
| Espanola | -2.764* | -2.538* |
| Fernandina | -0.064 | -0.123 |
| Floreana | -1.096 | 0.164 |
| Genovesa | -1.945* | -1.625* |
| Isabela | 1.328 | 0.066 |
| Marchena | -2.403* | -2.251* |
| Pinta | 1.084 | 0.456 |
| Pinzón | 0.108 | 0.061 |
| San Cristóbal | 1.292 | -0.550 |
| Santa Cruz | 1.728* | -0.140 |
| Santa Fé | -2.169* | -1.985* |
| Santiago | 0.411 | -0.042 |
| Wolf | -1.616 | -1.854* |

## References

Mazel, F., Davies, T.J., Gallien, L., Renaud, J., Groussin, M., Münkemüller, T., et al. (2015). Influence of tree shape and evolutionary time-scale on phylogenetic diversity metrics. *Ecography*.doi:1APA

**Supplementary Information S7 |** Multiple linear regression models of island phylogenetic structure (SES.MPD).

Standardized coefficient estimates and associated statistics for the top $AIC_C$ models ($\Delta AIC_C < 4$) of island phylogenetic structure (SES.MPD) regressed against various combinations of predictors. Predictor variables: area = A ($km^2$), endemism = E (proportion of endemic species on each island), island isolation (km) = I, annual precipitation (mm) = P, and annual mean temperature = T (°C). Predictor variables were log transformed and standardized to a mean of 0 and a standard deviation of 1.

| **Model** | **A** | **E** | **I** | **P** | **T** | **adjR$^2$** | **logLik** | **AICc** | **Weight** |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.617 | | | | 0.536 | 0.451 | -18.829 | 50.102 | 0.268 |
| 2 | | | | 0.586 | | 0.289 | -21.251 | 50.901 | 0.180 |
| 3 | 0.510 | | | | | 0.198 | -22.092 | 52.584 | 0.078 |
| 4 | | | | 0.519 | 0.294 | 0.322 | -20.315 | 53.074 | 0.061 |
| 5 | | | -0.494 | | 0.485 | 0.302 | -20.509 | 53.463 | 0.050 |
| 6 | | -0.546 | | | 0.684 | 0.285 | -20.679 | 53.803 | 0.042 |
| 7 | 0.500 | -0.268 | | | 0.646 | 0.450 | -18.181 | 53.863 | 0.041 |
| 8 | | | -0.424 | | | 0.112 | -22.812 | 54.023 | 0.038 |

We also fit a model including the estimated minimum age (million years) of each island as a measure of island ontogeny. The standardized coefficients, estimated by averaging the parameters from the top $AIC_C$ models ($\Delta$ $AIC_C < 4$), are presented below. Confidence intervals are shown in parentheses (CI). In these analyses, isolation and endemism were not among the predictors of top $AIC_C$ averaged models, which we interpreted as a lack of support for both predictors. Results show that phylogenetic structure (SES.MPD) is associated with estimated minimum island age, such that older islands tend to show more overdispersed assemblages. This pattern suggests that in older islands, although there was more time available for speciation events, there was also more time for species colonization and extinction.

| **Predictor variable** | **Coefficient (z)** | **Adjusted Standard error** | **95% CI** | ***P* values** |
|---|---|---|---|---|
| Area | 0.710 | 0.201 | (0.269 – 1.152) | $p = 0.002$ |
| Age | 0.554 | 0.225 | (0.053 – 1.056) | $p = 0.030$ |
| Temperature | 0.787 | 0.279 | (0.192 – 1.382) | $p = 0.009$ |
| Precipitation | 0.586 | 0.234 | (0.077 – 1.096) | $p = 0.024$ |

Standardized coefficient estimates and associated statistics for the top $AIC_C$ models ($\Delta AIC_C < 4$) are presented below.

| **Model** | **A** | **Age** | **P** | **T** | **adjR$^2$** | **logLik** | **AICc** | **Weight** |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.753 | 0.554 | | 0.901 | 0.624 | -15.512 | 48.524 | 0.331 |
| 2 | 0.616 | | | 0.536 | 0.451 | -18.829 | 50.102 | 0.151 |
| 3 | | | 0.586 | | 0.344 | -21.251 | 52.901 | 0.101 |

# Supplementary Information Chapter 3

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**Supplementary Table 1 |** Correlation tests on finch-plant interaction strengths among years.

Using finch feeding observations, we tested the correlation of species interaction strengths among years (2003-2007), at the two study sites El Garrapatero (EG) and Academy Bay (AB) to examine how conserved are these interactions through time. In the table we provide Spearman's Rank correlation values (r) and significance values ($P$). Significant correlations at $P$ =< 0.05 are in gray shade.

**Study Site AB**

**Study Site EG**

| **Year** | **2003** | **2004** | **2005** | **2006** | **2007** |
|---|---|---|---|---|---|
| **2003** | | r = 0.620<br>$P < 0.001$ | r = 0.512<br>$P = 0.002$ | r = 0.403<br>$P = 0.022$ | r = 0.424<br>$P = 0.015$ |
| **2004** | r = 0.738<br>$P < 0.001$ | | r = 0.565<br>$P < 0.001$ | r = 0.547<br>$P = 0.001$ | r = 0.336<br>$P = 0.060$ |
| **2005** | r = 0.388<br>$P = 0.05$ | r = 0.611<br>$P < 0.001$ | | r = 0.464<br>$P = 0.007$ | r = 0.680<br>$P < 0.001$ |
| **2006** | r = 0.492<br>$P = 0.01$ | r = 0.623<br>$P < 0.001$ | r = 0.581<br>$P = 0.002$ | | r = 0.276<br>$P = 0.26$ |
| **2007** | r = 0.022<br>$P = 0.915$ | r = 0.125<br>$P = 0.543$ | r = -0.006<br>$P = 0.976$ | r = 0.020<br>$P = 0.923$ | |

**Supplementary Table 2 |** Information of DNA sequences used in phylogenetic analysis.

Accession numbers of sequences of two barcoding genes (*rbcL ~800pb* and *matK ~550pb)* used to estimate phylogenetic relationships of plants species present at the two study sites: El Garrapatero (EG) and Academy Bay (AB). For most of the species (58), tissue samples were collected in this study, and the sequencing performed in laboratories associated to Barcode of Life Database (BOLD). Sequences of species for which tissue samples were not available (22) were obtained from GenBank (indicated in Source). The sequences of congeneric relatives were used instead of seven species that lack sequence information (indicated in Note).

| **Species** | **Family** | **Accession number matK** | **Accession number rbcL** | **Source** | **Note** |
|---|---|---|---|---|---|
| *Abutilon depauperatum* | Malvaceae | VEGIS023-14\|SCE039\| | VEGIS023-14\|SCE039\| | This study (BOLD) | |
| *Acacia insulae-iacobi* | Fabaceae | VEGIS017-14\|SCE030\| | VEGIS017-14\|SCE030\| | This study (BOLD) | |
| *Acacia macracantha* | Fabaceae | VEGIS061-14\|SCE104\| | VEGIS061-14\|SCE104\| | This study (BOLD) | |
| *Acacia nilotica* | Fabaceae | JF270612.1 | JF265255.1 | GenBank | |
| *Acacia rorudiana* | Fabaceae | VEGIS052-14\|SCE031\| | VEGIS052-14\|SCE031\| | This study (BOLD) | |
| *Alternanthera echinocephala* | Amaranthaceae | VEGIS021-14\|SCE036\| | VEGIS021-14\|SCE036\| | This study (BOLD) | |
| *Alternanthera filifolia* | Amaranthaceae | VEGIS015-14\|SCE027\| | NA | This study (BOLD) | |
| *Amaranthus dubius* | Amaranthaceae | KX090202.1 | KX090210.1 | GenBank | |
| *Amaranthus sclerantoides* | Amaranthaceae | VEGIS071-14\|SCE135\| | VEGIS071-14\|SCE135\| | This study (BOLD) | |
| *Bastardia viscosa* | Malvaceae | NA | VEGIS080-14\|SCE159\| | This study (BOLD) | |
| *Bidens pilosa* | Asteraceae | VEGIS040-14\|SCE081\| | VEGIS040-14\|SCE081\| | This study (BOLD) | |
| *Blainvillea rhomboidea* | Asteraceae | AY297646.1 | VEGIS053-14\|SCE037\| | GenBank; This study (BOLD) | |
| *Boerhavia coccinea* | Nyctaginaceae | VEGIS025-14\|SCE046\| | VEGIS025-14\|SCE046\| | This study (BOLD) | |
| *Boerhavia erecta* | Nyctaginaceae | VEGIS057-14\|SCE091\| | VEGIS057-14\|SCE091\| | This study (BOLD) | |
| *Boerhavia tuberosa* | Nyctaginaceae | VEGIS036-14\|SCE075\| | VEGIS036-14\|SCE075\| | This study (BOLD) | |
| *Bursera* | Burseraceae | VEGIS062- | VEGIS062- | This study | |

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|---|---|---|---|---|---|
| *graveolens* | | 14\|SCE105\| | 14\|SCE105\| | (BOLD) | |
| *Cardiospermum corindum* | Sapindaceae | JN191108.1 | JN191144.1 | GenBank | |
| *Castela erecta* | Simaroubaceae | EU042853.1 | EU042991.1 | GenBank | Congeneric relative of *Castela galapageia* |
| *Castela galapageia* | Simaroubaceae | NA | VEGIS063-14\|SCE106\| | This study (BOLD) | |
| *Chrysanthellum pusillum* | Asteraceae | VEGIS070-14\|SCE133\| | VEGIS070-14\|SCE133\| | This study (BOLD) | |
| *Chloris virgata* | Poaceae | KP056921.1 | KP056831.1 | GenBank | |
| *Cordia dentata* | Boraginaceae | JQ587086.1 | JQ590888.1 | GenBank | Congeneric relative of *Cordia leucophlyctis* |
| *Cordia lutea* | Boraginaceae | NA | VEGIS035-14\|SCE074\| | This study (BOLD) | |
| *Cryptocarpus pyriformis* | Nyctaginaceae | VEGIS012-14\|SCE022\| | VEGIS012-14\|SCE022\| | This study (BOLD) | |
| *Croton scouleri* | Euphorbiaceae | VEGIS065-14\|SCE111\| | VEGIS065-14\|SCE111\| | This study (BOLD) | |
| *Desmodium procumbens* | Fabaceae | 0 | VEGIS004-14\|SCE007\| | This study (BOLD) | |
| *Desmodium distortum* | Fabaceae | JQ587588.1 | NA | GenBank | Congeneric relative of *Desmodium procumbens* |
| *Euphorbia ophthalmica* | Euphorbiaceae | VEGIS045-14\|SCE087\| | VEGIS045-14\|SCE087\| | This study (BOLD) | |
| *Evolvulus convolvuloides* | Convolvulaceae | VEGIS001-14\|SCE003\| | VEGIS001-14\|SCE003\| | This study (BOLD) | |
| *Evolvulus simplex* | Convolvulaceae | VEGIS032-14\|SCE063\| | VEGIS032-14\|SCE063\| | This study (BOLD) | |
| *Galactia striata* | Fabaceae | VEGIS060-14\|SCE102\| | VEGIS060-14\|SCE102\| | This study (BOLD) | |
| *Gossypium darwinii* | Malvaceae | JN201381.1 | JN243176.1 | GenBank | |
| *Heliotropium angiospermum* | Boraginaceae | VEGIS074-14\|SCE147\| | VEGIS074-14\|SCE147\| | This study (BOLD) | |
| *Hibiscus tiliaceus* | Malvaceae | JX517796.1 | JX572676.1 | GenBank | |
| *Ipomoea nil* | Convolvulaceae | VEGIS077-14\|SCE153\| | VEGIS077-14\|SCE153\| | This study (BOLD) | |
| *Ipomoea triloba* | Convolvulaceae | VEGIS038-14\|SCE079\| | VEGIS038-14\|SCE079\| | This study (BOLD) | |
| *Jasminocereus thouarsii* | Cactaceae | VEGIS027-14\|SCE050\| | VEGIS027-14\|SCE050\| | This study (BOLD) | |
| *Laportea aestuans* | Urticaceae | NA | VEGIS033-14\|SCE068\| | This study (BOLD) | |
| *Laportea* | Urticaceae | KF138015.1 | NA | GenBank | Congeneric |

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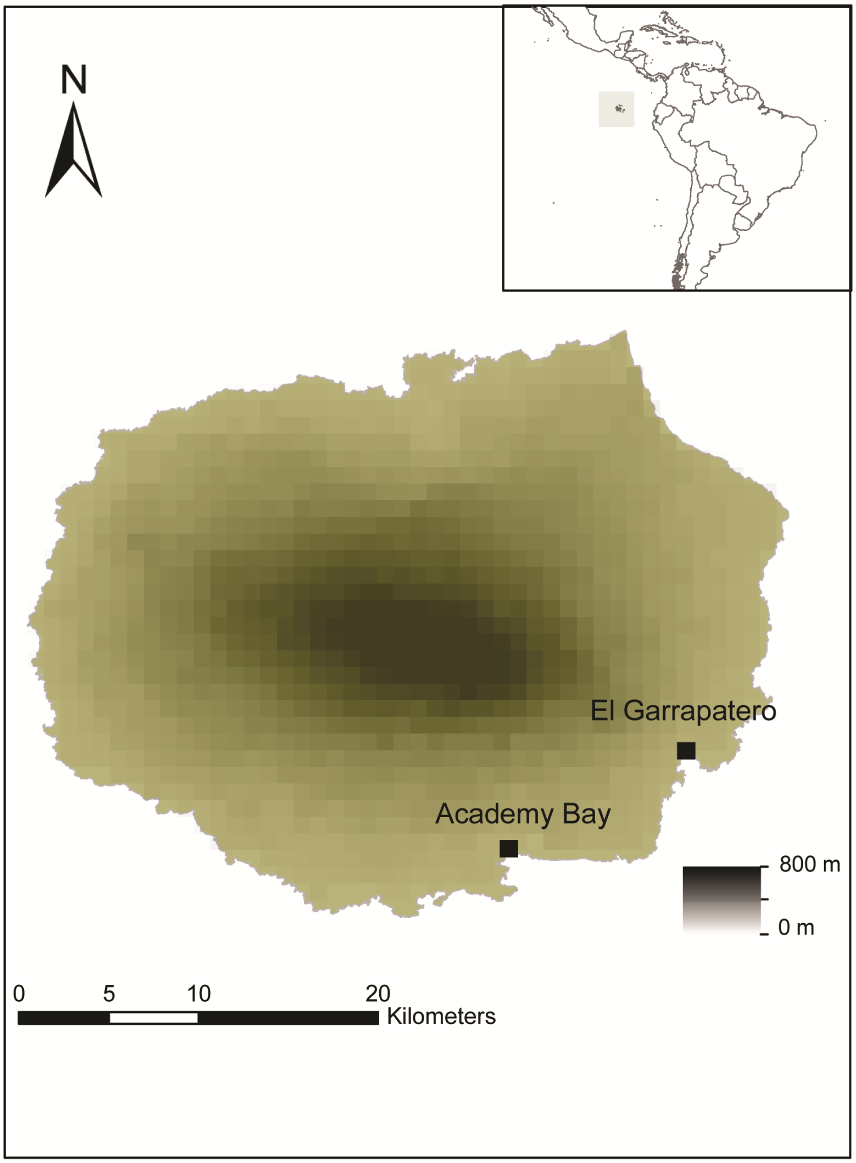
|---|---|---|---|---|---|
| *bulbifera* | | | | | relative of *Laportea aestuans* |
| *Lantana camara* | Verbenaceae | GU134977.1 | GU135140.1 | GenBank | |
| *Lantana peduncularis* | Verbenaceae | VEGIS037-14\|SCE077\| | VEGIS037-14\|SCE077\| | This study (BOLD) | |
| *Lycium minimum* | Solanaceae | VEGIS016-14\|SCE029\| | VEGIS016-14\|SCE029\| | This study (BOLD) | |
| *Maytenus octogona* | Celastraceae | VEGIS042-14\|SCE083\| | VEGIS042-14\|SCE083\| | This study (BOLD) | |
| *Mentzelia aspera* | Loasaceae | VEGIS022-14\|SCE038\| | VEGIS022-14\|SCE038\| | This study (BOLD) | |
| *Merremia aegyptia* | Convolvulaceae | VEGIS079-14\|SCE158\| | VEGIS079-14\|SCE158\| | This study (BOLD) | |
| *Momordica charantia* | Cucurbitaceae | VEGIS068-14\|SCE127\| | VEGIS068-14\|SCE127\| | This study (BOLD) | |
| *Mollugo flavescens* | Molluginaceae | VEGIS069-14\|SCE130\| | VEGIS069-14\|SCE130\| | This study (BOLD) | |
| *Opuntia echios* | Cactaceae | VEGIS056-14\|SCE049\| | VEGIS056-14\|SCE049\| | This study (BOLD) | |
| *Oxalis dombeyi* | Oxalidaceae | VEGIS054-14\|SCE044\| | VEGIS054-14\|SCE044\| | This study (BOLD) | |
| *Parkinsonia aculeata* | Fabaceae | JX495738.1 | JX571869.1 | GenBank | |
| *Passiflora foetida* | Passifloraceae | VEGIS066-14\|SCE121\| | VEGIS066-14\|SCE121\| | This study (BOLD) | |
| *Pectis tenuifolia* | Asteraceae | KJ525291.1 | VEGIS005-14\|SCE009\| | GenBank | |
| *Physalis pubescens* | Solanaceae | EF438943.1 | KJ773744.1 | GenBank | |
| *Piscidia carthagenensis* | Fabaceae | KU176188.1 | KM219829.1 | GenBank | |
| *Plantago major* | Plantaginaceae | KJ593055.1 | KJ593615.1 | GenBank | |
| *Portulaca oleracea* | Portulacaceae | VEGIS043-14\|SCE084\| | VEGIS043-14\|SCE084\| | This study (BOLD) | |
| *Porophyllum ruderale* | Asteraceae | KJ525334.1 | VEGIS029-14\|SCE055\| | GenBank; This study (BOLD) | |
| *Prosopis juliflora* | Fabaceae | VEGIS039-14\|SCE080\| | VEGIS039-14\|SCE080\| | This study (BOLD) | |
| *Rhynchosia minima* | Fabaceae | VEGIS002-14\|SCE005\| | VEGIS002-14\|SCE005\| | This study (BOLD) | |
| *Sarcostemma viminale* | Apocynaceae | JQ024993.1 | JQ025085.1 | GenBank | Congeneric relative of *Sarcostemma angustissimum* |
| *Scalesia affinis* | Asteraceae | NA | VEGIS055-14\|SCE048\| | This study (BOLD) | |
| *Scalesia aspera* | Asteraceae | EU118426.1 | NA | GenBank | Congeneric relative of |

| | | | | | |
|---|---|---|---|---|---|
| | | | | | *Scalesia affinis* |
| *Scutia spicata* | Rhamnaceae | VEGIS014-14\|SCE025\| | VEGIS014-14\|SCE025\| | This study (BOLD) | |
| *Senna obtusifolia* | Fabaceae | VEGIS075-14\|SCE150\| | VEGIS075-14\|SCE150\| | This study (BOLD) | |
| *Senna occidentalis* | Fabaceae | KJ638445.1 | KJ773879.1 | GenBank | |
| *Sida ciliaris* | Malvaceae | VEGIS044-14\|SCE085\| | VEGIS044-14\|SCE085\| | This study (BOLD) | |
| *Sida salvifolia* | Malvaceae | VEGIS078-14\|SCE154\| | VEGIS078-14\|SCE154\| | This study (BOLD) | |
| *Sida sp* | Malvaceae | VEGIS046-14\|SCE088\| | VEGIS046-14\|SCE088\| | This study (BOLD) | |
| *Sida spinosa* | Malvaceae | KJ663783.1 | DQ006105.1 | GenBank | |
| *Stylosanthes sympodialis* | Fabaceae | VEGIS073-14\|SCE146\| | VEGIS073-14\|SCE146\| | This study (BOLD) | |
| *Tephrosia decumbens* | Fabaceae | 0 | VEGIS031-14\|SCE061\| | This study (BOLD) | |
| *Tiquilia sp* | Boraginaceae | VEGIS072-14\|SCE144\| | VEGIS072-14\|SCE144\| | This study (BOLD) | |
| *Tournefortia psilostachya* | Boraginaceae | VEGIS034-14\|SCE072\| | VEGIS034-14\|SCE072\| | This study (BOLD) | |
| *Tournefortia pubescens* | Boraginaceae | VEGIS047-14\|SCE092\| | VEGIS047-14\|SCE092\| | This study (BOLD) | |
| *Tribulus cistoides* | Zygophyllaceae | VEGIS009-14\|SCE018\| | VEGIS009-14\|SCE018\| | This study (BOLD) | |
| *Trianthema portulacastrum* | Aizoaceae | VEGIS041-14\|SCE082\| | VEGIS041-14\|SCE082\| | This study (BOLD) | |
| *Vallesia glabra* | Apocynaceae | VEGIS064-14\|SCE107\| | VEGIS064-14\|SCE107\| | This study (BOLD) | |
| *Volkameria aculeatum* | Lamiaceae | KJ012820.1 | EF125096.1 | GenBank | Congeneric relative of *Volkameria molle* |
| *Waltheria ovata* | Malvaceae | VEGIS028-14\|SCE054\| | VEGIS028-14\|SCE054\| | This study (BOLD) | |
| *Zanthoxylum fagara* | Rutaceae | VEGIS076-14\|SCE152\| | VEGIS076-14\|SCE152\| | This study (BOLD) | |

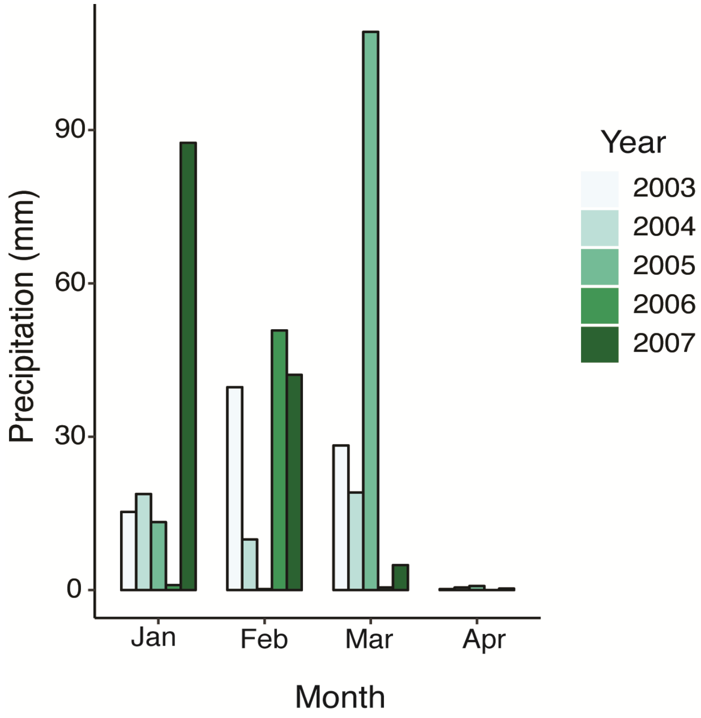
**Supplementary Figure 1** | Map showing study sites on Santa Cruz Island.

Our study was performed on Santa Cruz Island, one of the main islands of the Galápagos archipelago, located ~1000km west from Ecuador in South America. Feeding observations, vegetation surveys, and finch exclusion experiments were performed at two sites located in dry lowland forest. Academy Bay (AB; 0° 44' 21.3" S, 90° 18 '06.3" W) and El Garrapatero (EG; 0° 41' 15.7" S, 90° 13' 18.3" W).



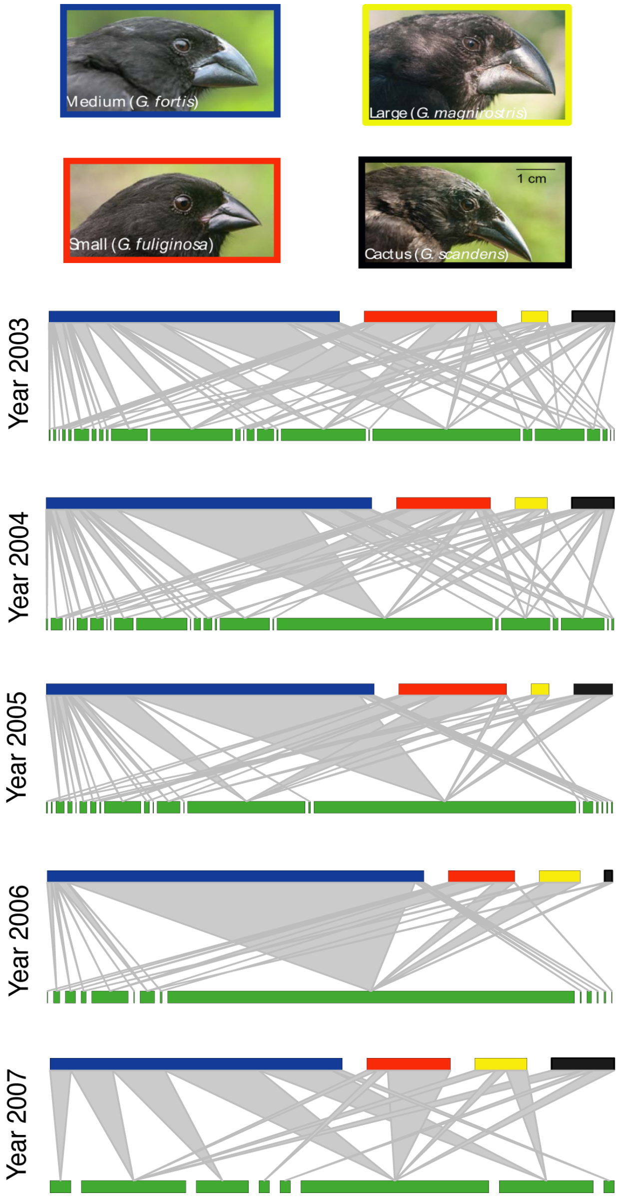
**Supplementary Figure 2** | Variation in precipitation from 2003 to 2007 in Santa Cruz Island.

Feeding observations and plant surveys were performed form during the wet season (January -March) from 2003 to 2007. Bars represent the cumulative precipitation (mm) per month from January to April. Santa Cruz experienced significantly higher precipitation at the beginning of the wet season in 2007 and towards the end of the wet season in 2006. Data provided by the Charles Darwin Research Station.



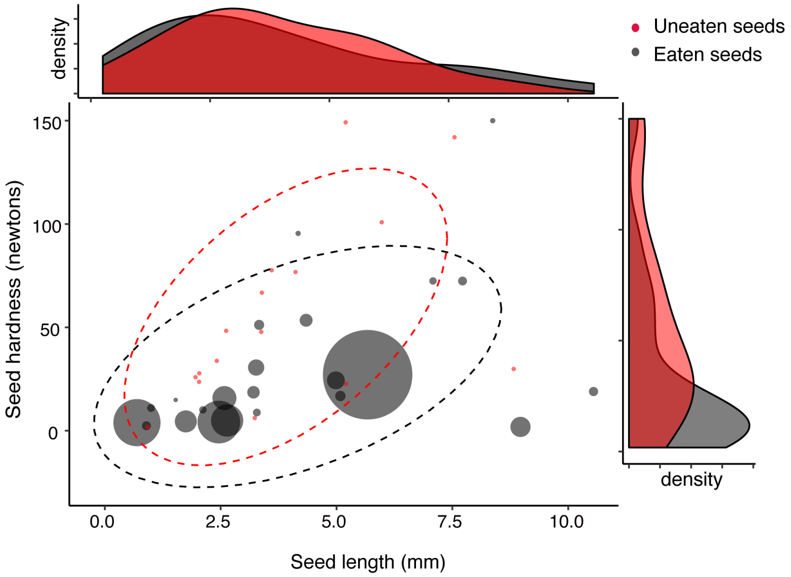
**Supplementary Figure 3** | Finch-plant interactions represented as bipartite networks for each year from 2003 to 2007 at Academy Bay (AB).

Finch-plant interactions at AB represented as bipartite networks for each year (2003-2007). Upper level boxes represent finch species *G. fortis* (blue), *G. fuliginosa* (red), *G. magnirostris* (yellow), and *G. scandens* (black). Lower level boxes represent plant species. Grey lines indicate the frequency of interactions. Photos provided by Luis F. De León.



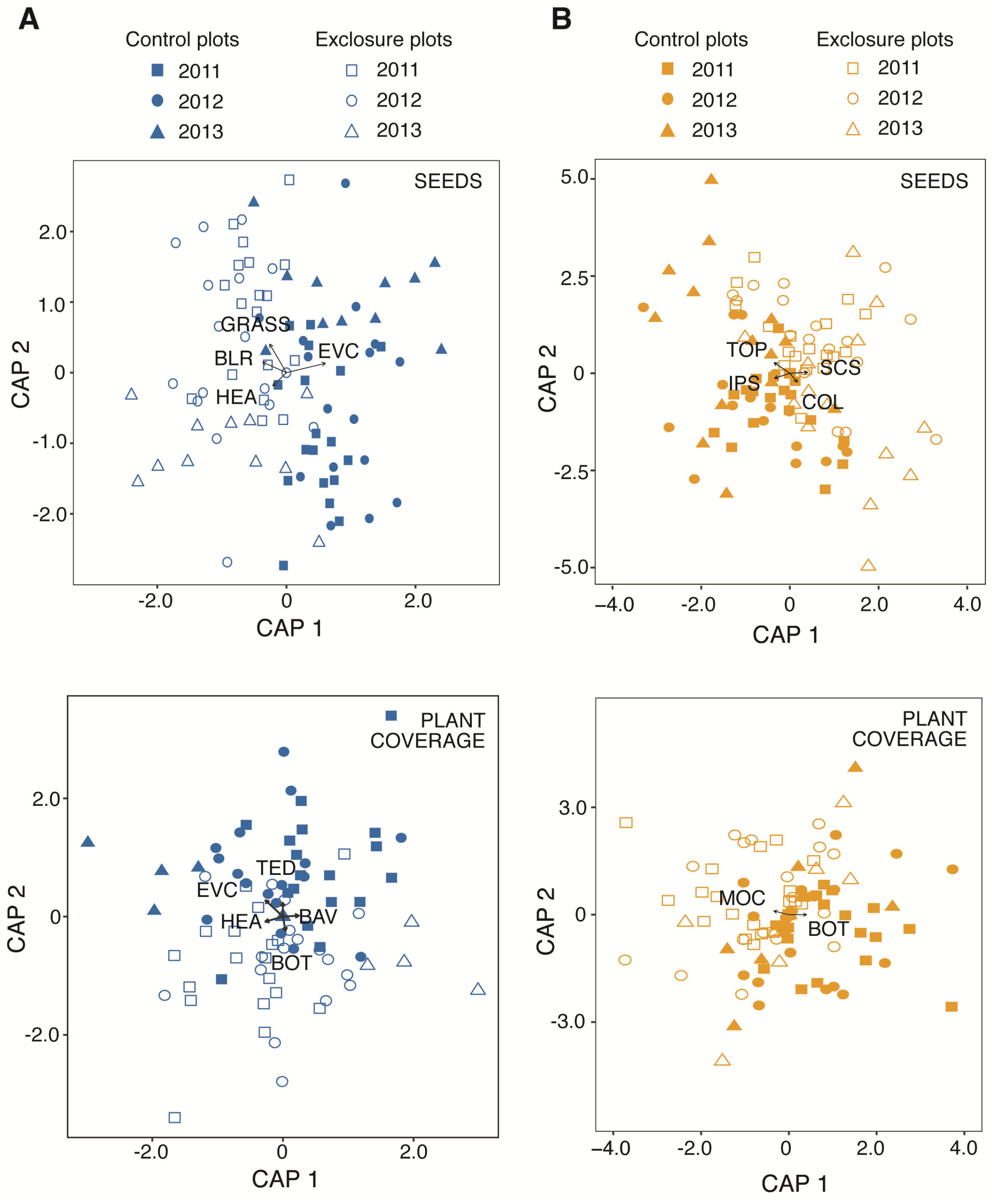
**Supplementary Figure 4 |** Length and hardness distribution of eaten and uneaten seeds by finches at Academy Bay (AB).

Distribution of length and hardness of eaten (in gray) and uneaten (in red) seeds at AB. The size of the gray circles (eaten seeds) represents the number of feeding observations. Finches tend to eat softer seeds (t = -2.12, *P* = 0.041), but there was no difference in seed size (t = 0.016, *P* = 0.987).



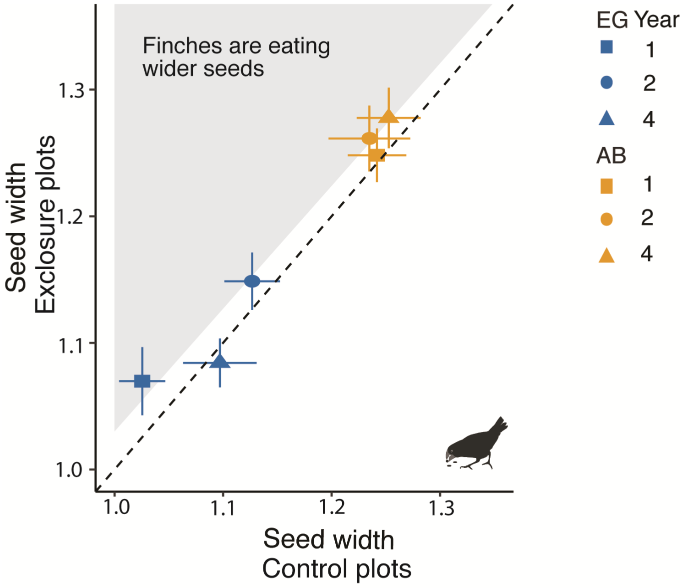
**Supplementary Figure 5 |** Partial constrained analysis of coordinates testing species composition differences between exclosure and control plots.

To test the effect of finches on species composition we performed partial constrained analysis of principal coordinates (partial CAP; see methods). Plots show variation on species composition between control and exclosure plots, in seeds (upper plots) and above ground plant coverage (lower plots), at El Garrapatero (A) and Academy Bay (B). Increased relative abundance of species associated to large difference in species composition (CAP 1 and CAP 2) are show with black arrows. Species names represented by abbreviations as follow. EVC (*Evolvulus convolvuloides*); BLR (*Blainvillea rhomboidea*); HEA (*Heliotropium angiospermum*); TED (*Tephrosia decumbens*); BAV (*Bastardia viscosa*); BOT (*Boerhavia tuberosa*); TOP (*Tournefortia psilostachya*); IPS (*Ipomoea* sp.); COL (*Cordia leucophlyctis*); SCS (*Scutia spicata*); MOC (*Momordica charantia*). A significant effect of finches was observed on seeds at EG (F = 1.635, $P$ = 0.001) and on plants at AB (F = 1.919, $P$ = 0.048), but not on seeds at AB (F = 1.00, $P$ = 0.073) or plants at EG (F = 1.377, $P$ = 0.117).


A
Control plots
2011
2012
2013
Exclosure plots
2011
2012
2013
SEEDS
GRASS
BLR
EVC
HEA
CAP 2
CAP 1
2.0
1.0
0
-1.0
-2.0
-2.0
0
2.0
PLANT COVERAGE
TED
EVC
HEA
BAV
BOT
B
Control plots
2011
2012
2013
Exclosure plots
2011
2012
2013
SEEDS
TOP
SCS
IPS
COL
5.0
2.5
-2.5
-5.0
–4.0
–2.0
4.0
PLANT COVERAGE
MOC
BOT
3.0
-3.0

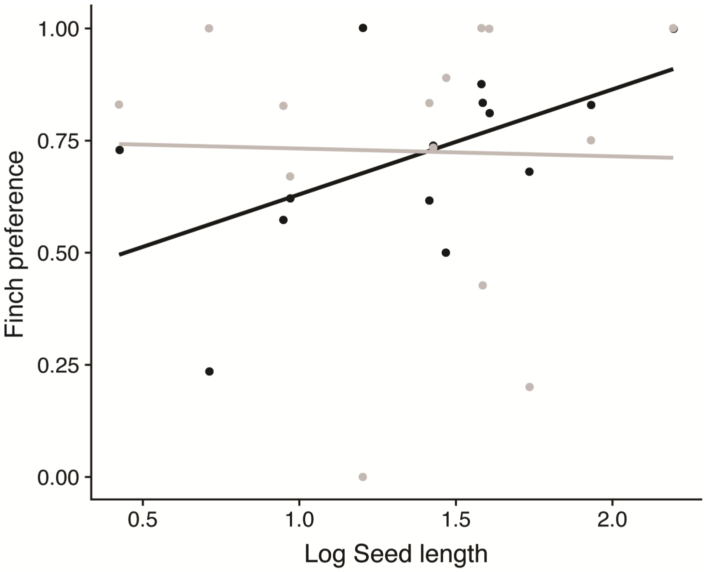
**Supplementary Figure 6** | Distribution of seed width in exclosure and control plots.

Distribution of mean weighted seed width (log) and in exclosure and control plots at the two study sites El Garrapatero (EG) and Academy Bay (AB). Finches tended to eat wider seeds, but the effect was not significant (t = -0.673, *P* = 0.502).



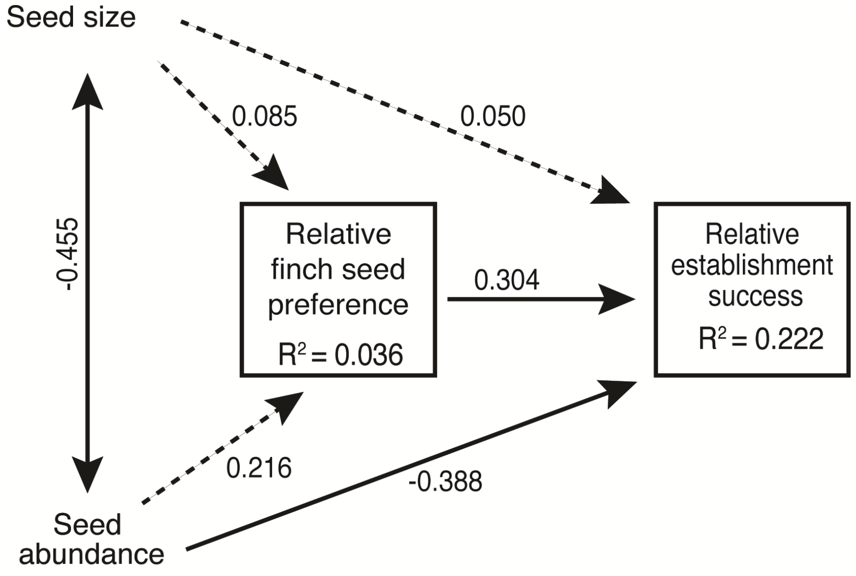
**Supplementary Figure 7** | Relationship between relative finch preference and seed length.

We compared the relationship of relative finch preference observed in the exclosure experiment and seed length at the two study sites. For this we used a subset of 14 species that were present at the two sites. We found the relationship is strong at Academy Bay, black line, ($\beta = 0.234 \pm 0.103$, $t = 2.273$, $P = 0.0422$, Adjusted $R^2 = 0.243$, $N=12$), than at El Garrapatero, gray line, ($\beta = -0.017 \pm 0.187$, $t = 2.273$, $P = -0.092$, Adjusted $R^2 = 0.08$, $N=12$).



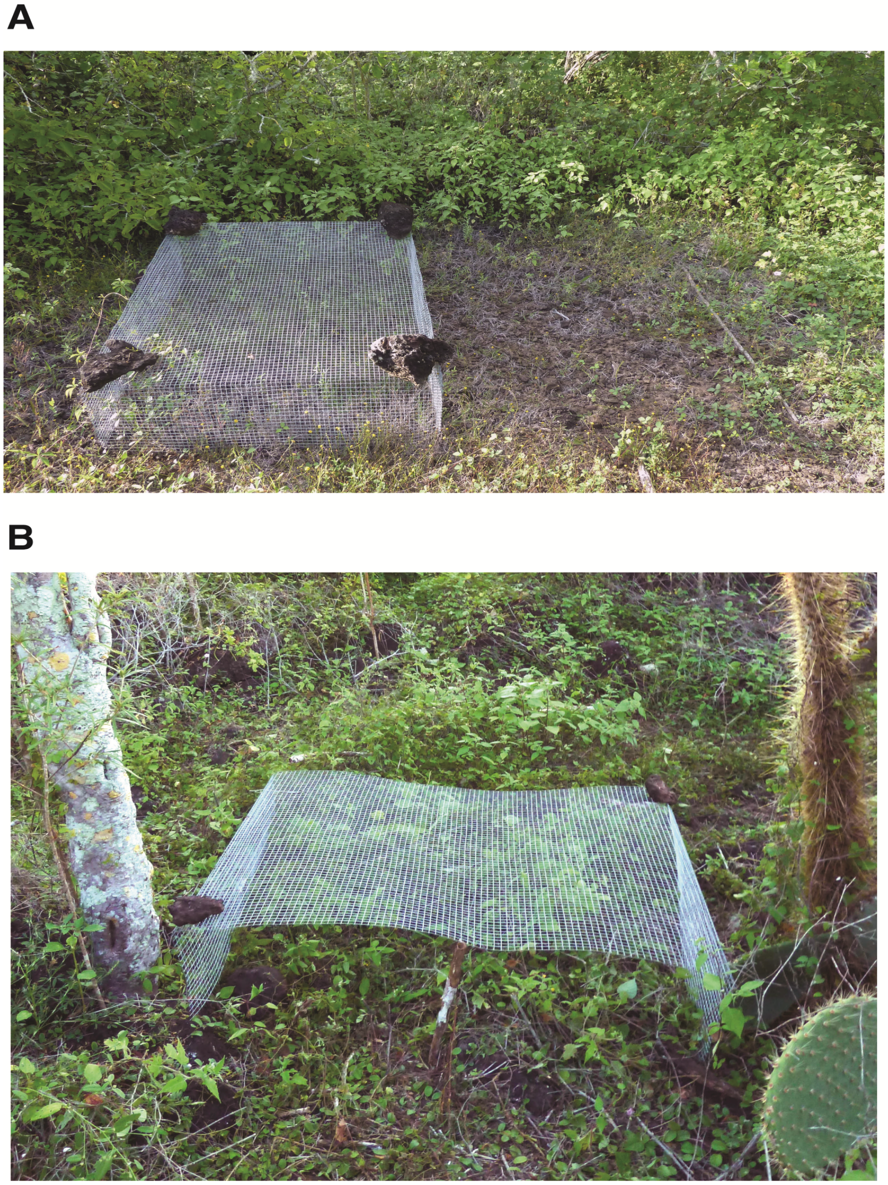
**Supplementary Figure 8** | Path diagram showing structural equation models estimates of direct and indirect factors influencing establishment success.

We performed test for direct and indirect effect of seed size, seed abundance, and relative finch preference on the relative establishment success of annual plant species within exclosure plots using structural equation models (see methods). The path diagram show the regression estimates between factors. The arrows show the direction of the effect. Significant regression estimates at *P* =< 0.05 are in show by solid arrows. $R^2$ of the two factors used as response variables are also shown. Seed size and Seed abundance were included as covariates indicated by the double arrow. Plans species that show lower establishment success have seeds that are less eaten by finches and tend to be more abundant. Suggesting a tradeoff between seed predation and establishment success.



**Supplementary Figure 9** | Exclosure and sham-control plots.

Pictures of a exclosure plot (A) and a sham-control plot (B) used in the finch exclusion experiment. 20 paired experimental plots (exclosure and control) were established in 2010 at El Garrapatero and Academy Bay. Five sham-control, also paired plots, which are opened at both sides to allow finches to enter, were established at each site on 2011 to test the cage effect. Photos provided by Luis F. De León.



# Supplementary Information Chapter 4

## List of contents

**Supplementary Information S1** | Information about populations sampled

**Supplementary Information S1: Table S1.** Geographic information on *Tribulus cistoides* populations sampled in this study. The columns provide information on the island, population ID, latitude, longitude, and the years when sampling was performed for each collection site. Populations marked with (*) were sampled to perform the analysis of mericarp hardness in 2017.

| **Island** | **Population ID** | **Latitude (°S)** | **Longitude (°W)** | **2015** | **2016** | **2017** |
|---|---|---|---|---|---|---|
| Baltra | AP2 | -0.444 | -90.273 | no | yes | no |
| Baltra | CH | -0.483 | -90.277 | no | yes | no |
| Española | BG | -1.354 | -89.660 | no | yes | no |
| Española | PS | -1.371 | -89.745 | no | yes | no |
| Floreana | CC | -1.277 | -90.481 | no | yes | no |
| Floreana | CD | -1.279 | -90.473 | yes | yes | yes |
| Floreana | CM | -1.281 | -90.469 | yes | yes | yes |
| Floreana | LB | -1.287 | -90.490 | yes | no | no |
| Floreana | PN | -1.277 | -90.488 | no | yes | yes |
| Floreana | POB | -1.237 | -90.449 | no | no | yes |
| Floreana | WC | -1.282 | -90.480 | yes | no | yes |
| Isabela | AP | -0.945 | -90.955 | yes | yes | yes |
| Isabela | ECR* | -0.937 | -90.978 | yes | yes | yes |
| Isabela | RSA* | -0.941 | -90.967 | yes | yes | yes |
| Isabela | RTP* | -0.952 | -90.973 | yes | no | yes |
| Isabela | RVS* | -0.930 | -90.985 | yes | no | yes |
| Isabela | TP* | -0.948 | -90.974 | yes | yes | yes |
| San Cristóbal | LB2 | -0.922 | -89.615 | yes | yes | yes |
| San Cristóbal | RLB | -0.915 | -89.615 | yes | no | no |
| San Cristóbal | USFQ | -0.896 | -89.609 | yes | yes | yes |
| Seymour Norte | TT | -0.401 | -90.291 | no | yes | no |
| Santa Cruz | AB* | -0.738 | -90.302 | yes | yes | yes |
| Santa Cruz | DP | -0.585 | -90.354 | yes | yes | yes |
| Santa Cruz | EG* | -0.686 | -90.223 | yes | yes | yes |
| Santa Cruz | EG2 | -0.677 | -90.227 | yes | yes | yes |
| Santa Cruz | ITC | -0.488 | -90.280 | yes | yes | no |
| Santa Cruz | ITC2* | -0.542 | -90.319 | yes | yes | yes |
| Santa Cruz | MGN* | -0.574 | -90.333 | yes | yes | yes |
| Santa Cruz | TB* | -0.746 | -90.319 | yes | yes | yes |
| Santa Cruz | EG3* | -0.689 | -90.221 | no | no | yes |

## **Supplementary Information S2 |** Relationship between *Tribulus cistoides* fruit morphology and hardness

To evaluate the relationship between mericarp morphology and mericarp hardness, we first tested for variation in hardness of the mericarp surface. Hardness was measured at six locations of each mericarp (upper spine, ventral surface, left side of ventral surface, right side of ventral surface, dorsal surface, and distal end; Supplementary Information S2: Fig. S1a) using a Shore D scale (0-100 value) with a handheld durometer (Asker, Super Ex, Type D, Kyoto, Japan). These locations are likely to be the most directly involved in protecting seeds because finches usually hold the mericarps between their beaks transversally, pressing down on the ventral and dorsal surface of the mericarps, or laterally, pressing down on the left and right side, before cracking the ventral wall to obtain the seeds. Mericarps are held along the middle of the mericarp, between the upper and lower spines (when present), however sometimes during the manipulation of the mericarp the upper spines are intentionally broken off.

We evaluated how mericarp hardness varied across the mericarp surface, and if hardness varied among islands, populations or individual mericarps, using linear mixed effects models. We fit the following model using the *lmer* function in the lme4 v. 1.1-14 package (Bates et al. 2015) of R: Hardness measure = mericarp location + island + population(island) + mericarp(population(island)) + error; mericarp, island and population were included as random effects (parentheses indicate hierarchically nested factors), and mericarp location was treated as a fixed effect. The statistical significance of random effects were evaluated using likelihood-ratio tests with the *rand* function in R, while the *P*-value of the fixed factor was obtained using the *anova* function in the lmerTest v. 2.0-36 package (Kuznetsova et al. 2017) with the denominator degrees-of-freedom determined according to the Satterthwaite correction. Post-hoc Tukey-Kramer tests were performed using the *glht* function in the package multcomp v. 1.4-8 (Hothom et al 2013) to identify specific differences in hardness among locations on the mericarp. All data were standardized (mean = zero and standard deviation = one) across islands and populations prior to analysis.

We found that mericarp hardness varied substantially among locations on the surface of mericarps ($F_{5,\ 235} = 15.301$, $P < 0.001$). The hardest mericarp locations were the left side of ventral surface (mean hardness on a Shore D scale ± SD: 56.365 ± 1.679), right side of the ventral surface (53.542 ± 1.679), and along the dorsal surface (52.615 ± 1.679); no significant post hoc differences were detected among these locations (Supplementary Information S2: Fig. S1b). Mericarp distal end (46.094 ± 1.670), upper spine (47.198 ± 1.679), and ventral surface (49.948 ± 1.679) were relatively softer locations (Supplementary Information S2: Fig. S1b). The hierarchical analysis of variation did not detect significant variation among islands ($P = 1$ obtained using *ranova* function); after removing Island from models, mericarp explained more than twice the amount of variation than population (variance 27.63 and 12.18, respectively).

We tested for relationships between mericarp hardness and morphological traits by performing three independent principal component analyses on measurements of hardness and morphology. First, a principal component analysis of mericarp hardness measured from the six locations on the mericarp surface (Supplementary Information S2: Table S1), and the first principal component was used in subsequent analyses representing mericarp global hardness ($PC1_{\text{Global hardness}}$), because all traits positively load on this axis, explaining 55% of the total variation (Supplementary Information S2: Table S1). Second, a principal component analysis of mericarp hardness measured from the three hardest locations on the mericarp surface, which were expected to be most directly involved in protecting seeds from finch predation (Supplementary Information S2: Table S2). Again the first component was used in subsequent analyses representing mericarp local hardness ($PC1_{\text{Local hardness}}$). Third, we performed a principal component analysis of mericarp morphology using the six morphological measurements of mericarps (Supplementary Information S2: Fig. S3a; Table S3). The first principal component was used to represent mericarp size ($PC1_{\text{size}}$) because all traits positively loaded on this axis, explaining 44% of the total variation (Supplementary Information S2: Table S3).

Finally, we confirmed the relationships between morphology and the hardness measurements collected using the durometer using a portable materials testing system (FLS-1 Tester, Lucas Scientific; Supplementary Information S2: Fig. S2a) to provide a separate, independent measure of mericarp hardness. We estimated the loading and fracture characteristics in the middle position of the ventral surface of 34 mericarps. Displacement-controlled compression tests were applied to the mericarp (11.2 ± 1.2 SD mm/min loading rate, 500N load cell) until mericarp fracture (i.e. ventral surface breaking/cracking) using a wedge-shaped indentor that simulated beak-seed contact. Load-displacement curves were acquired (sample rate=50 samples/sec) and used to estimate maximum load (N) applied to a mericarp just prior to fracture (Supplementary Information S2: Fig. S2b). Then, we conducted a mixed model regression between the first principal component of the six durometer measurements ($PC1_{Hardness}$) and the single measurement collected from the portable materials testing system. The regression was performed using the function *lmer* with population included as a random factor. Island was not included in the model because all mericarps used in this analysis were from Santa Cruz island. A log-likelihood-ratio test was used to evaluate the significance of the random effect of population. The dependent variable, maximum load (as measured from the portable materials testing system), was log-transformed to meet the assumptions of ANOVA and standardized (mean = 0, standard deviation = 1) to facilitate the interpretation of results and contrasts. This analysis revealed a marginally statistically significant positive relationship between the two hardness measures ($\beta = 0.18 \pm 0.009$, $\chi^2 = 3.645$, $P = 0.056$, $R^2_{marginal} = 0.104$, n = 34; Fig. S2 below) and a non-significant population component of variation was explained by differences among population ($\chi^2 = 0$, $P = 1$, n = 6). This analysis showed the relationships between mericarp morphology and mericarp hardness were repeatable across different methods for measuring mericarp hardness

**Supplementary Information S2: Table S1.** Summary of principal component analysis of mericarp hardness measured from six locations on the mericarp surface (see Supplementary Information S2 Fig. S1).

| Mericarp location | Principal Component<br>1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Ventral surface | -0.44 | 0.14 | -0.17 | 0.74 | -0.32 | 0.33 |
| Left side of ventral surface | -0.44 | 0.18 | -0.24 | 0.14 | 0.73 | -0.39 |
| Right side of ventral surface | -0.42 | 0.20 | -0.50 | -0.52 | -0.48 | -0.18 |
| Upper spine | -0.44 | 0.15 | 0.36 | -0.39 | 0.24 | 0.66 |
| Distal end | -0.42 | -0.12 | 0.69 | 0.05 | -0.27 | -0.50 |
| Dorsal surface | -0.23 | -0.93 | -0.21 | -0.05 | 0.07 | 0.10 |
| **Summary** | | | | | | |
| Standard deviation | 1.81 | 0.93 | 0.78 | 0.68 | 0.63 | 0.61 |
| Proportion of variance | 0.55 | 0.14 | 0.10 | 0.08 | 0.07 | 0.06 |
| Cumulative proportion of variance | 0.55 | 0.70 | 0.79 | 0.87 | 0.94 | 1.00 |

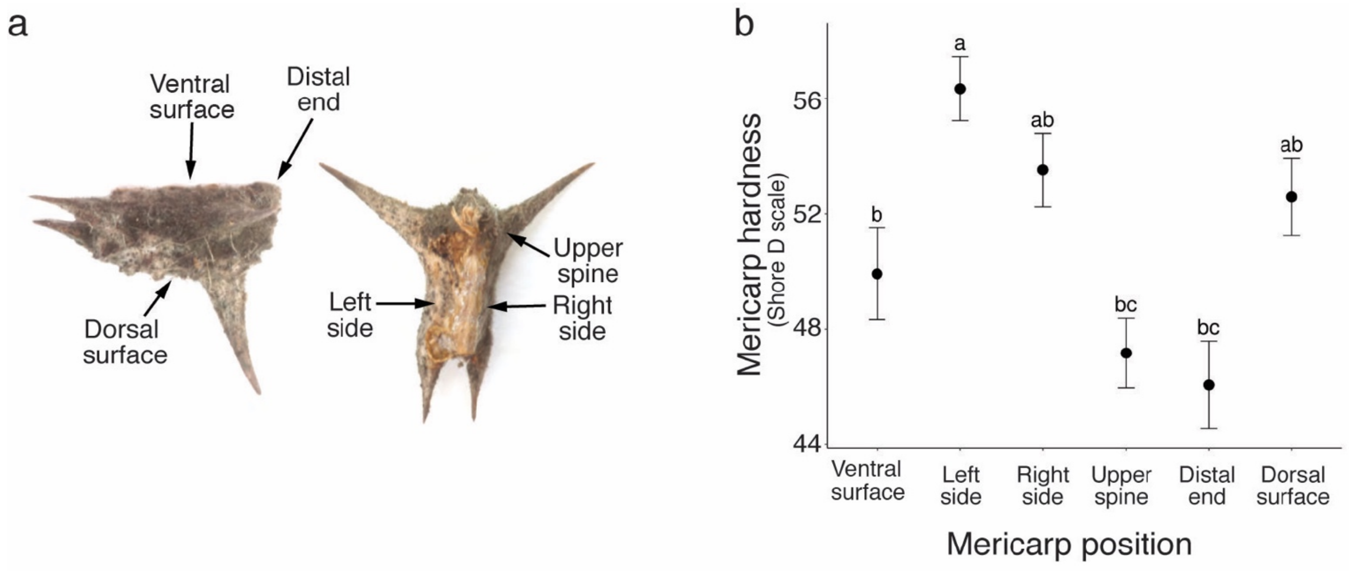
**Supplementary Information S2: Table S2.** Summary of principal components analysis of mericarp hardness measured from the three hardest locations on the mericarp surface that we expect to be most directly involved in protecting seeds from finch predation (left side of ventral surface, right side of the ventral surface, and ventral surface; see above).

| **Mericarp location** | **Principal Component** | | |
|---|---|---|---|
| | **1** | **2** | **3** |
| Ventral surface | -0.58 | 0.63 | -0.52 |
| Left side of ventral surface | -0.59 | 0.12 | 0.80 |
| Right side of ventral surface | -0.57 | -0.76 | -0.30 |
| **Summary** | | | |
| Standard deviation | 1.46 | 0.68 | 0.63 |
| Proportion of variance | 0.71 | 0.15 | 0.13 |
| Cumulative proportion of variance | 0.71 | 0.87 | 1.00 |

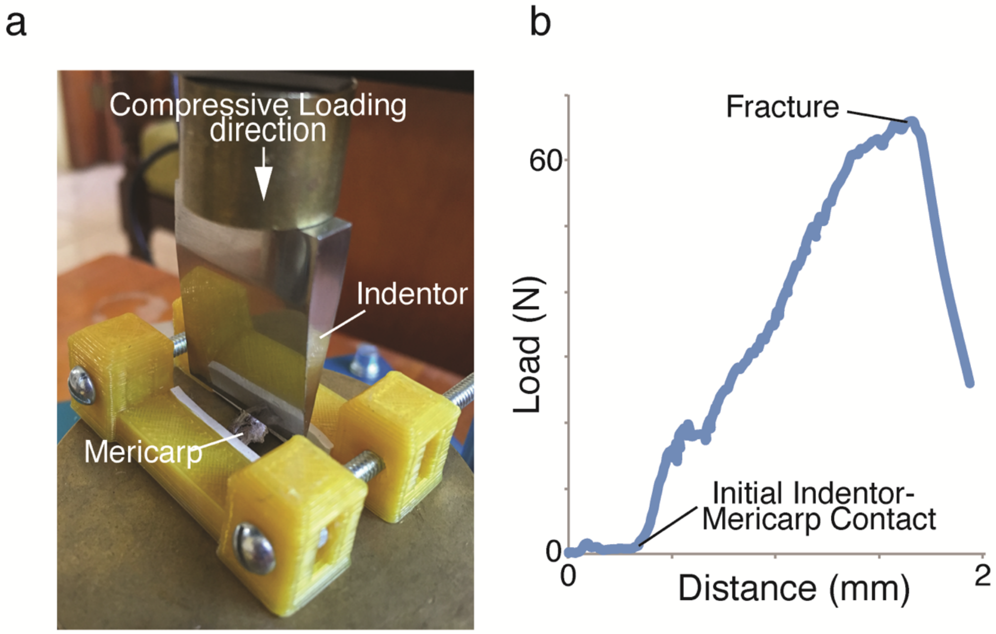
**Supplementary Information S2: Table S3.** Principal component analysis of mericarp morphology, using the six morphological measurements illustrated in Supplementary Information S2: Fig. S3b.

| **Mericarp** | **Principal Component** | | | | | |
|---|---|---|---|---|---|---|
| **location** | **1** | **2** | **3** | **4** | **5** | **6** |
| Length | 0.47 | 0.00 | -0.19 | -0.76 | -0.35 | 0.16 |
| Width | 0.28 | -0.64 | -0.15 | 0.44 | -0.54 | -0.05 |
| Depth | 0.45 | -0.45 | -0.09 | -0.04 | 0.76 | 0.05 |
| Upper spine size | 0.52 | 0.35 | 0.19 | 0.13 | -0.02 | -0.75 |
| Longest spine length | 0.47 | 0.37 | 0.30 | 0.37 | -0.04 | 0.64 |
| Spine position | 0.07 | 0.35 | -0.89 | 0.25 | 0.07 | 0.03 |
| **Summary** | | | | | | |
| Standard deviation | 1.63 | 1.18 | 0.98 | 0.76 | 0.53 | 0.36 |
| Proportion of variance | 0.44 | 0.23 | 0.16 | 0.10 | 0.05 | 0.02 |
| Cumulative proportion | 0.44 | 0.67 | 0.84 | 0.93 | 0.98 | 1.00 |

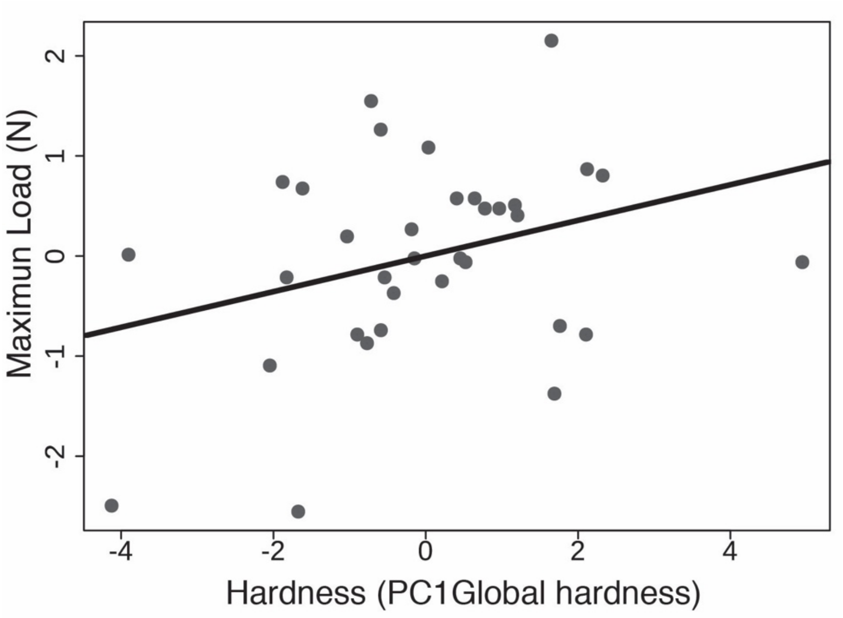
**Supplementary Information S2: Figure S1.** (a) Hardness was measured using a durometer at six different locations on the surface of mericarps as shown. (b) Post hoc Tukey test: different letters indicate statistically significant differences ($P < 0.05$) between groups.



**Supplementary Information S2: Figure S2.** (a) Photograph of the portable materials testing system used to verify the measures of mericarp hardness collected with the handheld durometer, including the wedge-shaped indentor that simulated beak-mericarp contact. (b) A representative load-displacement curve (N), with the maximum value followed by rapid decline indicating mericarp fracture.



**Supplementary Information S2: Figure S3.** Relationship between the maximum load (N) measured with the portable materials testing device and the first principal component ($PC1_{Global\ hardness}$) summarizing mericarp hardness measured at six locations with a durometer (see Supplementary Information S2: Fig. S1a). Units were standardized to a mean of zero and standard deviation of one prior to analysis.



## References:

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**:1–48.

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Kuznetsova A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: Tests in linear mixed effects models. *Journal of Statistical Software* **82**:1–26.

**Supplementary Information S3**. Fruit trait variation among individual plants

To examine variation in fruit morphological traits (i.e., width, length, upper spines size, mass, presence of lower spines) among individual plants, we performed hierarchical analysis of variance using the following model: Trait = population + plant(population) + schizocarp(plant(population)) + error, using the *lmer* function in lme4 v. 1.1-14 package (Bates et al. 2015). The three variance components (population, plant, schizocarp) were treated as nested random effects, with nesting indicated by parentheses, such that schizocarp was nested within plants, and plants were nested within populations. We estimated the percentage of variation associated with each factor and tested statistical significance with a likelihood-ratio tests using the function *rand* in lmerTest package v. 2.0-36 (Kuznetsova et al. 2017), with the option reml=TRUE. *P*-values for random effects were divided by 2 reflecting that these were 1-tailed tests (Littell et al. 1996). No data transformation was used for mericarp width, length and upper spines size. In the case of mericarp mass, we used a square-root transformation of the data before fitting the model to improve the normality of residuals. For the binary trait presence/absence of lower spines, we fit a logistic mixed-effects model using the *glmer* function in the lme4 package, and the significance of each component of variation was tested using likelihood-ratio tests with the *anova* function. In addition, using a similar model design, we tested the variance of each trait among schizocarps and plants within each population separately.

The morphology of *T. cistoides* mericarps varied considerably among schizocarps, plants, and populations (Supplementary Information 3: Table S1). All traits varied among plants except mericarp width. For mericarp length and upper spine size, the total variation explained by the effect of plant (21.82% and 5.86%, respectively) was higher than the variance attributed to the effects of either schizocarp (8.20% and 0%) or population (0% and 5.37%). For mericarp width and mass, the total variation explained by population (14.56% and 12.97%, respectively) was greater than the variation attributed to schizocarp (5.37% and 10.71%) or plant (1.88% and 5.63%). The presence of lower spines varied among schizocarps and plants, but not between the two populations. When we analyzed each population separately, we obtained similar results

(Supplementary Information 3: Table S2). Thus, in all examined traits we found a predominant variation among individual plants or populations.

**Supplementary Information S3: Table S1.** Variation of *T. cistoides* mericarp morphology among fruits (schizocarps), plants, and populations. Traits were obtained from 533 intact mericarps collected from two populations (EG and AB; 15 plants per population) in Santa Cruz island. For each mericarp trait, we fitted a linear mixed-effects model to estimate the percentage of variation of each component. Mean, ± standard deviation (SD), and range are shown for each trait, except for lower spines (†), for which we indicate the proportion of mericarps with presence of lower spines.

| **Source of variation** | **Width (mm)** | **Length (mm)** | **Upper spines size (mm)** | **Mass (g)** | **Lower spines present/absent** |
|---|---|---|---|---|---|
| Schizocarp | 5.37%* | 8.20%** | 0.00% | 10.71%*** | NA** |
| Plant | 1.88% | 21.82%*** | 5.86%*** | 5.63%* | NA*** |
| Population | 14.56%*** | 0.00% | 5.37%* | 12.97%*** | NA |
| **Mean ± SD (range)** | 2.76 ± 0.66<br>(0.52 - 4.69) | 6.50 ± 1.31<br>(3.29 - 10.65) | 9.97 ± 3.18<br>(1.51 - 16.38) | 0.05 ± 0.03<br>(0.002 - 0.184) | 0.83† |

*Note: P*-values were estimated using a likelihood-ratio test with one degree-of-freedom. Significant components of variation are marked with asterisks: (*) at $P < 0.05$, (**) at $P < 0.01$, and (***) at $P < 0.001$. In the case of the binary trait presence/absence of lower spines, we fitted a logistic regression mixed-effects model, and we only indicate the significance of each source of variation.

**Supplementary Information S3: Table S2.** Variation in *T. cistoides* mericarp morphology among schizocarps and plants within two populations. Traits were obtained from 533 intact mericarps collected from complete fruits of 15 plants from two *T. cistoides* populations (EG and AB) on Santa Cruz island. For each mericarp trait, we fit a linear mixed-effects model to estimate the percentage of variation expected by each component. In the case of the binary categorical (presence/absence) for lower spines, we fit a logistic mixed-effects model, and we indicate the significance of each source of variation.

| **Source of variation** | **Width (mm)** | **Length (mm)** | **Upper spines (mm)** | **Mass (g)** | **Lower spines (present/absent)** |
|---|---|---|---|---|---|
| **EG** | | | | | |
| Schizocarp | 1.47% | 7.39%* | 0.00% | 6.53% | NA* |
| Plant | 2.2% | 34.45%*** | 5.56%* | 10.29%** | NA*** |
| **AB** | | | | | |
| Schizocarp | 8.73%* | 9.27%* | 0.00% | 19.40%*** | NA* |
| Plant | 3.15% | 4.65% | 7.03%* | 1.76% | NA*** |

*Note:* Significant components of variation are marked with asterisks: (*) at $P < 0.05$, (**) at $P < 0.01$, and (***) at $P < 0.001$.

**References:**

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**:1–48.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS system for mixed models*. SAS Institute, Cary, North Carolina, USA.

Kuznetsova A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: Tests in linear mixed effects models. *Journal of Statistical Software* **82**:1–26.

**Supplementary Information S4** | Variation in seed predation

**Supplementary Information 4: Table S1.** Logistic mixed-effects models testing how seed predation per population varies among islands, years, and with finch community composition. Data from all islands are included. Finch community composition was considered as a fixed binary factor, with 0 indicating the absence (only *Geospiza fortis* present) and 1 indicating the presence of large-beaked finch species (i.e *G. magnirostris* and *G. conirostris*). (a) The model included finch community composition, year, and the interaction between both factors as fixed effects; (b) A separate model was fit for the year 2016, when the three additional islands were sampled (Baltra, Española, and Seymour Norte).

**a**

| | | $\chi^2$ | **P** |
|---|---|---|---|
| *Fixed effects* | Finch community | 1.54 | 0.214 |
| | Year | 213.12 | **< 0.001** |
| | Finch community x Year | 43.70 | **< 0.001** |
| *Random effect* | Island | 118.88 | **< 0.001** |

**b**

| | | **Estimate (Std. Error)** | ***Z*** | $\chi^2$ | **P** |
|---|---|---|---|---|---|
| **Year 2016** | | | | | |
| *Fixed effect* | Finch community | 0.86 (0.30) | 2.90 | | **< 0.004** |
| *Random effect* | Island | | | 39.12 | **< 0.001** |

*Note:* $\chi^2$ and *P*-values were estimated using Type II Wald tests. The effect of island was included as a random effect, and its $\chi^2$ and *P*-values were estimated using a likelihood-ratio test with one degree-of-freedom. Effects significant at $P < 0.05$ are shown in bold.

**Supplementary Information 4: Table S2**. Logistic mixed-effects models testing how the proportion of seeds depredated per mericarp varies among populations, islands, and finch community composition. 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. (a) Model including finch community composition, year, and the interaction between both factors as fixed effects. (b) Separate models were fit for each year.

**a**

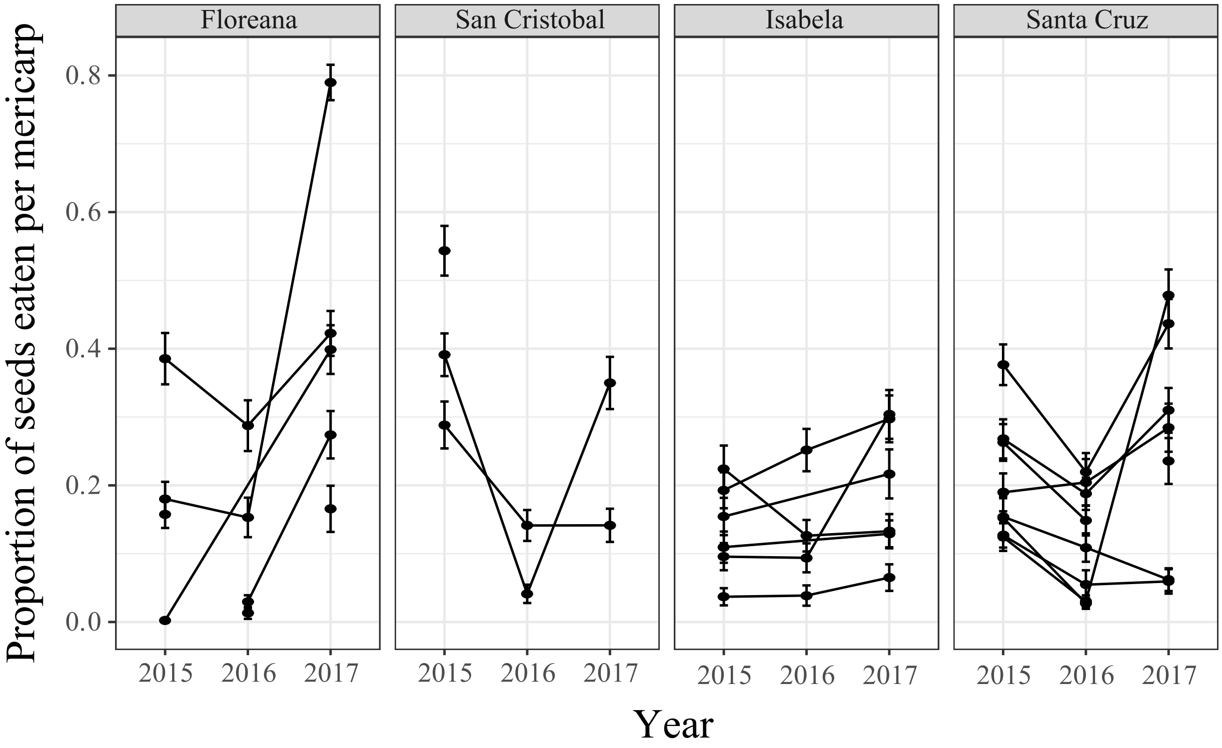
| | | $\chi^2$ | **P** |
|---|---|---|---|
| *Fixed effects* | Finch community | 7.14 | **0.008** |
| | Year | 158.60 | **< 0.001** |
| | Finch community x Year | 12.98 | **0.002** |
| *Random effects* | Population | 99.21 | **< 0.001** |
| | Island | 0.00 | 0.500 |

**b**

| | | **Coefficient (Std. Error)** | ***Z*** | $\chi^2$ | **P** |
|---|---|---|---|---|---|
| **Year 2015** | | | | | |
| *Fixed effect* | Finch community | -0.86 (0.35) | -2.45 | | **0.014** |
| *Random effects* | Population | | | 75.08 | **< 0.001** |
| | Island | | | 0.00 | 0.498 |
| **Year 2016** | | | | | |
| *Fixed effect* | Finch community | 0.10 (0.43) | 0.24 | | 0.809 |
| *Random effects* | Population | | | 24.26 | **< 0.001** |
| | Island | | | 0.00 | 0.500 |
| **Year 2017** | | | | | |
| *Fixed effect* | Finch community | -0.93 (0.45) | -2.07 | | **0.038** |
| *Random effects* | Population | | | 205.33 | **< 0.001** |
| | Island | | | 0.00 | 0.500 |

*Note:* $\chi^2$ and *P*-values of fixed factors were estimated using type II Wald tests and of random effects were estimated using likelihood-ratio test with one degree-of-freedom. Effects significant at $P < 0.05$ are shown in bold.

**Supplementary Information 4: Figure S1**. Variation in the proportion of seeds eaten per mericarp among populations, islands, years, and finch community composition.



**Supplementary Information S5** | Selection on *T. cistoides* fruit traits

**Supplementary Information 5: Table S1.** Logistic mixed-effects models testing for selection on mericarp traits imposed by finch seed predation**.** Standardized coefficients and standard errors (SE) averaged across the best-fitting models selected based on AIC values (Δ AIC < 2). The response variable is a binary variable in which 0 corresponds to mericarps with one or more seeds removed by finches, and 1 to intact 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.

| **Fixed effects** | **Standardized coefficient** | **SE** | ***P*** |
|---|---|---|---|
| Finch community | 1.93 | 0.48 | **0.003** |
| Year 2016 | 2.68 | 0.29 | **< 0.001** |
| Year 2017 | 0.66 | 0.27 | **0.016** |
| $PC1_{(Size)}$ | -0.28 | 0.10 | **0.008** |
| Upper spine size | 0.38 | 0.13 | **0.004** |
| Lower spines | 1.12 | 0.31 | **< 0.001** |
| Finch community x $PC1_{(Size)}$ | -0.01 | 0.04 | 0.892 |
| Finch community x Upper spine size | -0.25 | 0.09 | **0.007** |
| Finch community x Lower spines | -0.79 | 0.32 | **0.013** |
| Finch community x Year 2016 | -2.02 | 0.31 | **< 0.001** |
| Finch community x Year 2017 | -1.18 | 0.27 | **< 0.001** |
| Year 2016 x $PC1_{(Size)}$ | 0.14 | 0.14 | 0.297 |
| Year 2017 x $PC1_{(Size)}$ | 0.11 | 0.12 | 0.354 |
| Year 2016 x Upper spine size | 0.36 | 0.13 | **0.007** |
| Year 2017 x Upper spine size | 0.06 | 0.12 | 0.614 |
| Year 2016 x Lower spines | -0.67 | 0.22 | **0.002** |
| Year 2017 x Lower spines | -0.21 | 0.20 | 0.298 |

*Note:* Effects significant at $P < 0.05$ are shown in bold.

**Supplementary Information 5: Table S2**. Logistic mixed-effects models testing selection on mericarp traits imposed by finches**.** The response variable is the proportion of seeds that survived predation per mericarp. 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.

| | | $\chi^2$ | ***P*** |
|---|---|---|---|
| *Fixed effects* | Finch community | 7.03 | **0.008** |
| | Year | 158.99 | **< 0.001** |
| | $PC1_{(Size)}$ | 4.30 | **0.038** |
| | Upper spines size | 68.85 | **< 0.001** |
| | Lower spines | 23.11 | **< 0.001** |
| | Finch community x Upper spine size | 21.98 | **< 0.001** |
| | Finch community x Lower Spine | 23.70 | **< 0.001** |
| | Finch community x Year | 39.66 | **< 0.001** |
| | Year x $PC1_{(Size)}$ | 0.95 | 0.623 |
| | Year x Upper spine size | 1.80 | 0.406 |
| | Year x Lower spines | 0.95 | 0.623 |
| *Random effect* | Island | 0 | 0.500 |
| | Population | 76.85 | **< 0.001** |
| | Island x $PC1_{(Size)}$ | 0.00 | 0.500 |
| | Island x Upper spine size | 0.00 | 0.500 |
| | Island x Lower spines | 0.00 | 0.500 |

*Note:* Significance of fixed effects was estimated from the best-fitting model (selected based on AIC values), using Type II Wald tests and the significance of random effects was estimated using likelihood-ratio tests with one degree-of-freedom. Effects significant at $P < 0.05$ are shown in bold.

**Supplementary Information S6** | Effect of finch community composition on fruit morphology

**Supplementary Information 6: Table S1.** Morphological variation of *T. cistoides* mericarps associated with variation among populations, islands, years, and in relation to finch community composition. Finch community composition was considered as a categorical binary factor for each response variable, 0 indicating the absence (only *Geospiza fortis* present) and 1 the presence of large-beaked finch species (i.e. *G. magnirostris* and *G. conirostris*). (a) Linear mixed-effects models included finch community composition, year, and the interaction between these factors as fixed effects. In the case of the presence/absence of lower spines, we fit a logistic mixed-effects model. (b) Separate models were fit for each year; †denotes a separate analysis excluding data from islands sampled only in 2016. $\chi^2$ and *P* values were estimated using Type II Wald tests. Population and island were included as random effects, and the $\chi^2$ and *P*-values for these effects were estimated using a likelihood-ratio test with one degree-of-freedom. Effects significant at $P < 0.05$ are shown in bold.

**a**

| | **Effect** | **Width (mm)** | | **Length (mm)** | | **Upper spine size (mm)** | | **Lower spines (presence/absence)** | |
|---|---|---|---|---|---|---|---|---|---|
| | | $\chi^2$ | **P** | $\chi^2$ | **P** | $\chi^2$ | **P** | $\chi^2$ | **P** |
| | Finch community | 0.10 | 0.75 | 0.24 | 0.62 | 0.00 | 0.44 | 17.98 | **< 0.01** |
| | Year | 108.03 | **< 0.01** | 117.34 | **< 0.01** | 13.32 | **< 0.01** | 50.92 | **< 0.01** |
| | Finch community x Year | 16.56 | **< 0.01** | 41.60 | **0.03** | 53.90 | **< 0.01** | 47.03 | **< 0.01** |
| | Island | 0.00 | 0.50 | 11.90 | **<0.01** | 5.08 | **0.02** | < 0.01 | 0.49 |
| | Population | 588.00 | **< 0.01** | 553.5 | **< 0.01** | 589.60 | **< 0.01** | 1083.70 | **< 0.01** |
| **b** | | | | | | | | | |
| **2015** | Finch community | 2.02 | 0.15 | 0.29 | 0.59 | 0.31 | 0.57 | 2.79 | 0.09 |
| | Island | < 0.01 | 0.50 | 14.1 | **< 0.01** | 3.19 | 0.07 | 0.32 | 0.43 |
| | Population | 221.00 | **< 0.01** | 368.0 | **< 0.01** | 389.48 | **< 0.01** | 352.96 | **< 0.01** |
| **2016†** | Finch community | 0.86 | 0.36 | 0.71 | 0.40 | 0.12 | 0.72 | 26.99 | **< 0.01** |
| | Island | < 0.01 | 0.50 | 9.46 | **< 0.01** | 6.78 | **< 0.01** | 1.52 | 0.22 |
| | Population | 193.00 | **< 0.01** | 174.21 | **< 0.01** | 160.25 | **< 0.01** | 132.13 | **< 0.01** |
| **2016** | Finch community | 0.71 | 0.40 | 0.08 | 0.77 | 0.58 | 0.45 | 1.75 | 0.19 |
| | Island | 0.00 | 0.50 | 11.50 | **< 0.01** | 10.10 | **< 0.01** | 6.70 | **< 0.01** |
| | Population | 252.00 | **< 0.01** | 220.90 | **< 0.01** | 210.90 | **< 0.01** | 417.59 | **< 0.01** |
| **2017** | Finch community | 0.014 | 0.90 | 0.15 | 0.90 | 0.02 | 0.89 | 11.13 | **< 0.01** |
| | Island | 0.00 | 0.50 | 8.57 | **< 0.01** | 9.50 | **< 0.01** | < 0.01 | 0.50 |
| | Population | 235.00 | **< 0.01** | 340.09 | **< 0.01** | 214.90 | **< 0.01** | 728.21 | **< 0.01** |