Ecological genomics of Darwin's finches:

Connecting genotypes, phenotypes, and fitness to understand the process of speciation

Marc-Olivier Beausoleil

Faculty of Science Redpath Museum and Department of Biology McGill University Montréal, Québec, Canada

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"À mes parents, Lucie et Claude"

Pour l'insatiable curiosité et le profond émerveillement que vous m'avez transmis.



Map of the Galápagos Archipelago with the world as inset (Robinson's projection). The archipelago is located on the equator (dashed line), inside the red box about 1000 km East of the mainland Ecuador, South America. The sampling sites are shown in light grey on Santa Cruz island. Names in parentheses are older designations of the islands.

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"Wherever information reproduces, there is evolution"

Martin A. Nowak, 2006 Evolutionary Dynamics: Exploring the Equations of Life

Abstract

One of the fundamental goals of evolutionary biology is to understand what Darwin called the "mystery of mysteries": the emergence of biological diversity. At the core of the theory of ecological speciation is the process of divergent natural selection, which occurs when distinct heritable phenotypes are advantageous in different environments, while intermediate phenotypes are selected against.

Since Darwin, significant progress has been made in understanding the processes that can explain or prevent the formation of new species. However, many aspects of ecological speciation are cryptic. In particular, linking genotypes, phenotypes, and fitness of organisms, and uncovering how these connections can influence interactions between different species, has been a major challenge to understanding how natural populations evolve in response to environmental changes across time and space.

In my dissertation, I investigate how natural selection in different environments shapes, at the genomic and phenotypic level, a community of Darwin's finches, which are iconic for the study of ecological speciation and adaptive radiation. I use long-term genetic and phenotypic data from ground finches (*Geospiza* spp.) coexisting on Santa Cruz Island in the Galápagos as well as field observations.

Despite many years of study on the finches, little is known about individual space use and habitat preference. In my first chapter, I used radio telemetry data on five medium ground finches (*G. fortis*) to show that they prefer dry-forest habitat, as well as noting for the first time a communal roosting behaviour. This study shows that radio telemetry is a valuable method to understand the

movement ecology of these birds and the role of space use in an ecological speciation.

In my second chapter, I used 9 years of mark-recapture data from over 600 *G. fortis* to understand how disruptive selection changes based on climatic conditions. Although disruptive selection is present throughout the study, I discovered temporal variation in fitness as a function of beak size: disruptive selection was strongest in years preceded by a dry season with high precipitation. Therefore, the results establish a direct link between climatic factors and natural selection in Darwin's finches and demonstrate how temporal modulation of fitness functions can impact population differentiation.

Adaptive radiations can be visualized with a fitness landscape, a topographic-like graph with peaks and valleys that associates trait values with fitness. In my third chapter, I characterized the topology of the fitness and adaptive landscape (with mean trait and fitness) of a Darwin's finches community using apparent lifespan as a fitness proxy. Using a 17-year dataset, I identified five phenotypic modes (*G. fuliginosa*, *G. fortis* small and large, *G. magnirostris*, and *G. scandens*) close to the five peaks on the fitness landscape. In contrast, the adaptive landscape has four peaks, suggesting that some species experience relaxed selection and might fuse in the future.

In my last chapter, I sequenced the whole genomes of over 400 Darwin's finches to connect genotypes, phenotypes, and fitness, characterizing adaptive landscapes based on population allele frequencies. Using a genome-wide association study, I found that loci associated with beak morphology in different species of Darwin's finches are closer to adaptive peaks compared to loci not linked to beaks. These adaptive landscapes provide a framework that helps understand the loci under selection.

Overall, my work shows that connecting genotypes, phenotypes, and fitness helps to understand the mechanisms underlying adaptive radiation by uncovering how divergent natural selection drives genetic and phenotypic change, both within and between closely related and interacting species. Moreover, my work is a testimony to the enduring role that the adaptive landscape concept can play in explaining how organisms adapt to a changing world.

Résumé

L'un des objectifs fondamentaux de la biologie évolutive est de comprendre ce que Darwin appelait le « mystère des mystères » : l'émergence de la diversité biologique. Au cœur de la théorie de la spéciation écologique se trouve le processus de sélection naturelle divergente, qui se produit lorsque des phénotypes héréditaires distincts sont avantageux dans différents environnements, tandis que les phénotypes intermédiaires sont éliminés par la sélection naturelle.

Depuis Darwin, des progrès significatifs ont été réalisés au niveau de notre compréhension des processus pouvant favoriser ou empêcher la formation de nouvelles espèces. Cependant, de nombreux aspects de la spéciation écologique sont cryptiques. En particulier, établir un lien entre les génotypes, les phénotypes et la valeur adaptative (*fitness*) des organismes, et découvrir comment ces connexions peuvent influencer les interactions entre différentes espèces, a été un défi majeur pour comprendre comment les communautés naturelles réagissent aux changements environnementaux à travers le temps et l'espace.

Dans ma thèse, j'étudie comment la sélection naturelle dans différents environnements façonne, au niveau génomique et phénotypique, une communauté de pinsons de Darwin, qui sont emblématiques pour l'étude de la spéciation écologique et de la radiation adaptative. J'utilise des données génétiques et phénotypiques à long terme de pinsons Géospizes (*Geospiza* spp.) coexistant sur l'île de Santa Cruz aux Galápagos ainsi que des observations sur le terrain.

Malgré de nombreuses années d'études sur les pinsons, on sait peu de choses sur l'utilisation individuelle de l'espace et la préférence d'habitat de ces oiseaux. Dans mon premier chapitre, j'ai utilisé des données de radiotélémétrie sur cinq Géospizes à bec moyen (*G. fortis*) pour montrer

qu'ils préfèrent un habitat de forêt sèche, tout en notant pour la première fois un comportement de rassemblement à un dortoir communautaire. Cette étude montre que la radiotélémétrie est une méthode précieuse pour comprendre l'écologie du mouvement de ces oiseaux.

Dans mon deuxième chapitre, j'ai utilisé 9 ans de données de marquage-recapture de plus de 600 *G. fortis* pour comprendre comment la sélection disruptive change en fonction des conditions climatiques. Bien que la sélection disruptive soit présente tout au long de l'étude, j'ai découvert une variation temporelle dans la fonction de *fitness* : la sélection disruptive était plus forte, les années précédées d'une année avec une saison sèche comportant de fortes précipitations. Par conséquent, les résultats établissent un lien direct entre les facteurs climatiques et la sélection naturelle chez les pinsons de Darwin et démontrent comment la modulation temporelle des fonctions de *fitness* peut avoir un impact sur la différenciation des populations.

Les radiations adaptatives peuvent être visualisées avec un paysage de *fitness* phénotypique, un graphique de type topographique avec des montagnes et des vallées, qui associent les valeurs de trait au *fitness*. Dans mon troisième chapitre, j'ai caractérisé la topologie du paysage du *fitness* et adaptatif d'une communauté de pinsons de Darwin en utilisant la durée de vie apparente comme indicateur de valeur adaptative. À l'aide d'un ensemble de données de 17 ans, j'ai identifié que les cinq modes phénotypiques (*G. fuliginosa*, *G. fortis* petit et grand, *G. magnirostris* et *G. scandens*) étaient proches des cinq pics du paysage de *fitness*. En revanche, le paysage adaptatif, une version plus lissée du paysage de *fitness*, à quatre pics, suggère que certaines espèces subissent une pression de sélection moins importante et pourraient éventuellement fusionner.

Dans mon dernier chapitre, j'ai séquencé les génomes entiers deplus de 400 pinsons de Darwin pour connecter les génotypes et le *fitness*, caractérisant les paysages adaptatifs basés sur les fréquences alléliques populationnelles. À l'aide d'une étude d'association pangénomique, j'ai découvert que les locus associés avec des morphologies de becs dans différentes espèces de pinsons de Darwin sont placés à proximité de pics adaptatifs comparés aux locus qui ne sont pas liés à la morphologie des becs. Ces paysages adaptatifs fournissent un outil qui aide à comprendre les locus sélectionnés et à prédire comment les populations pourraient atteindre des pics adaptatifs. Dans l'ensemble, mon travail montre que la connexion des génotypes, des phénotypes et du *fitness* aide à comprendre les mécanismes sous-jacents à la radiation adaptative en découvrant comment la sélection naturelle divergente entraîne des changements génotypiques et phénotypiques, à la fois au sein et entre des espèces étroitement liées et en interaction. De plus, mon travail témoigne du rôle durable que le concept de paysage adaptatif peut jouer pour expliquer comment les organismes s'adaptent à un monde dynamique.

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Contributions to Original Knowledge

The chapters in this thesis bring original scholarship contributions for the partial fulfillment of the degree of Doctor of Philosophy.

Chapter 1 addresses the movement and space use of the medium ground finch (*Geospiza fortis*) in the arid coastal zone of Santa Cruz Island (Beausoleil et al. 2022). This is the first analysis using telemetry to explore the ecological and evolutionary importance of space use in Darwin's finches. Most notably, I quantified the area used by the finches and found the individual habitat preference based on plant communities, but also found an undescribed communal roosting behaviour. Finally, this study invites new research to be done using similar techniques or using novel technologies to facilitate data acquisition and get movement patterns at a broader spatial and temporal scale in order to answer unsolved ecological and evolutionary questions.

Chapter 2 aims to find the role of temporally varying disruptive natural selection in maintaining species divergence in a population of Darwin's finches (*Geospiza fortis*) which is composed of small and large beak morphotypes (Beausoleil et al. 2019b). To achieve this, I constructed yearly fitness functions associating individual beak size phenotypes with their survival to extract selection coefficients. As many studies look at natural selection in the wild, few look at how variable it can be. This study uncovers the role of varying disruptive selection in fostering or preventing species divergence. However, in order to know the agent of selection, measuring selection in relation to ecological variables is needed. For this, I explored the quantitative relationship between the strength of nonlinear selection and precipitation patterns. To my knowledge, this is the first study using the strength of disruptive selection with an ecological variable to find a putative selective

agent involved in species divergence.

Chapter 3 is focused on the characterization of fitness and adaptive landscapes in a community of ground-dwelling Darwin's finches (Beausoleil et al. 2023b). While fitness landscapes have been extensively studied, no study, however, has explored the fitness landscape, let alone the adaptive landscapes, of a natural community which covers almost the full spectrum of phenotypes between the species. Using wild individual birds from a long-term capture-mark-recapture study, I constructed a fitness landscape from beak morphologies and apparent survival, but also quantified an empirical adaptive landscape, a smoother version of the fitness landscape. I used the inferred adaptive peaks from the fitness landscape with population genetics to explore how potential evolutionary constraints might prevent populations from reaching their adaptive peaks. For this, I developed a metric called 'prospective selection' which estimates the amount of selection that would be required, given genetic covariances, to climb to a particular peak. Interest is rising for these kinds of analyses, but this is the first exploiting fitness and adaptive landscapes for a naturally occurring population.

The goal in chapter 4 is to explore the features of genetic adaptive landscapes in order to resolve the connections between genotypes, phenotypes and fitness. For this, I examined the genomic markers associated with beak length and found their associations with individual fitness. The construction of these genetic adaptive landscapes, using population allele frequencies, can then be used to compare how the loci associated with beak morphology are closer to their adaptive peaks compared to other genomic markers that are not associated with beak morphologies. This represents the first time a genetic adaptive landscape has been estimated for wild species and can help determine the genetic markers behind ecological speciations by finding if population allele frequencies are close to their adaptive peaks.

Thesis Format

I wrote a manuscript-based thesis style which contains a general introduction, followed by chapters representing each of the manuscripts I have prepared for publication, and finally a general discussion that summarizes the overall body of work. Short linking statements between each chapter help connect the ideas in the thesis. Three chapters, which are published in peer-reviewed journals, are reproduced here with permission from the original sources. I received permission from all coauthors to include the manuscripts in this thesis. Each published chapter was edited to standardize the thesis format, but the content has not changed. An ethical statement accompanies each chapter regarding the Animal Use Protocols and the Scientific investigation permits required to work with vertebrates and in the Galápagos National Park. Links to the code and data can be found in the 'Data and scripts' sections.

Chapter 1:

Beausoleil, Marc-Olivier, Carlos Camacho, Julio Rabadán-González, Kristen Lalla, Roxanne Richard, Paola L. Carrión, Andrew P. Hendry, and Rowan D. H. Barrett. 2022. Where did the finch go? Insights from radio telemetry of the medium ground finch (*Geospiza fortis*). *Ecology and Evolution*, *12*(4):e8768. (DOI: 10.1002/ece3.8768; Electronic supplementary material is available online on the Ecology and Evolution website).

Data and scripts:

Data and scripts are available on Dryad at 10.5061/dryad.qbzkh18kc and FigShare.

Ethical statement:

Field work was conducted under the University of Massachusetts Amherst Animal Use Protocols #2017-0005 and the Galápagos National Park (Permiso de investigación científica #PC-28-19).

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H. Koop, Jeffrey Podos, Diana M. T. Sharpe, Andrew P. Hendry, and Rowan D. H. Barrett. 2019.
Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*). *Proceedings of the Royal Society B: Biological Sciences*, 286(1916):20192290. (DOI: 10.1098/rspb.2019.2290; Electronic supplementary material is available online at 10.6084/m9.figshare.c.4738814).

Data and scripts:

The script used for analysis can be found on GitHub: beausoleilmo/temporal_fitness_landscape. Data available from the Dryad Digital Repository: 10.5061/dryad.zcrjdfn6q.

Ethical statement:

Fieldwork was conducted under the University of Massachusetts Amherst Animal Use Protocols for 2003, 2004, 2005, 2006: #23-10-09; 2007, 2008, 2009: #26-10-16; 2010, 2011: #2009-0063; and the University of Utah for 2008 and 2009 IACUC #07-08004. The Galápagos National Park

Service permit, Permiso de investigación científica, are as follows: 2003, 2004, 2005, 2006, 2007: #PC-009-98; 2008: #PC-01-08; 2009: #PC-21-07, Ext. 01-09; 2010 and 2011: #PC-58-10.

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Data and scripts:

The data and scripts are archived on Borealis dataverse at Beausoleil, M.-O., P. L. Carrión, J. Podos, C. Camacho, J. Rabadán-González, R. Richard, K. Lalla, J. A. M. Raeymaekers, S. A. Knutie, L. F. De León, J. A. Chaves, D. H. Clayton, J. A. H. Koop, D. M. T. Sharpe, K. M. Gotanda, S. K. Huber, R. D. H. Barrett, and A. P. Hendry. 2023. Data and code for "The fitness landscape of a community of Darwin's finches". Borealis dataverse, 10.5683/SP3/0YIWSE, and on GitHub at beausoleilmo/adaptive.landscapes.finches.

Ethical statement:

Field work was conducted under the University of Massachusetts Amherst Animal Use Protocols (2003-2006; #23-10-09, 2007-2009; #26-10-16, 2010-2011; #2009-0063, 2012-2013; #2009-0063, 2014-2016; #2013-0087, 2017-2020; #2017-0005) and University of Utah Protocols (2008-2010; #07-08004, 2010-2013; #10-07003) and the Galápagos National Park (Permiso de investigación científica, 2003-2007; #PC-009-98, 2008; #PC-01-08, 2009; #PC-21-07, 2010-2011; #PC-58-10, 2012; #PC-03-12, 2013; #PC-17-13, 2014; #PC-29-14, 2015; #PC-26-15, 2016; #PC-36-16, 2017; #PC-14-17, 2018; #PC-03-18, 2019-2020; #PC-28-19).

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A. H. Koop, Diana M. T. Sharpe, Sarah K. Huber, Kiyoko M. Gotanda, Andrew P. Hendry, Daniel Wegmann, and Rowan D. H. Barrett, In preparation.

Data and scripts:

The data (non-genomic) and scripts will be archived on Borealis dataverse, and on GitHub at barrettlabecoevogeno/ATLAS-Genomics-Finches. Genomic data will be available on NCBI.

Ethical statement:

Field work was conducted under the University of Massachusetts Amherst Animal Use Protocols (2010-2011; #2009-0063, 2017-2019; #2017-0005) and University of Utah Protocols (2010; #07-08004, 2010-2013; #10-07003) and the Galápagos National Park (Permiso de investigación científica, 2010; #PC-58-10, 2011; #PC-58-10, 2017; #PC-14-17, 2018; #PC-03-18, 2019; #PC-28-19). Genetic permit: MAE-DNB-CM-2018-0123-O and MAE-DNB-CM-2016-0041-M-0005. Canadian Food Inspection Agency permits: 2010, A-2010-05844-2; 2011, A-2011-06827-2; 2017, A-2017-01555-4; 2018-2019, A-2019-02563-4. Genomic data produced and analysed in this chapter were generated in collaboration with the McGill Genome Centre Montréal, and the Genetic Diversity Centre (GDC), ETH Zurich.

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Contribution of Authors

I (M.-O.B.) am the first author of all research found in this thesis. Conducting these studies required the collaborative effort of a large team of scientists. Below, I provide their initials with their contributions. You can find their complete names in the list of authors from the published manuscripts on page xvii and following.

Chapter 1: M.-O.B, C.C., J.R.G. conceptualized the study and performed (and programmed) the formal analysis. M.-O.B, C.C., R.R. administered the project, M.-O.B, C.C., A.P.H. acquired funding, M.-O.B, C.C., J.R.G., A.P.H., R.D.H.B. supervised the study. M.-O.B, C.C., J.R.G., K.L., R.R., P.C.A., A.P.H., R.D.H.B. wrote the paper and M.-O.B, C.C., J.R.G., R.R. prepared the visualization of the data. M.-O.B, C.C., J.R.G., K.L. developed the methodology and curated the data, and R.R., P.C.A. helped collect the data. M.-O.B, C.C., J.R.G., A.P.H. validated the analyses. M.-O.B, C.C., J.R.G., K.L., R.R., A.P.H. provided the resources (study material) needed to conduct the study.

Chapter 2: M.-O.B., A.P.H. and R.D.H.B. conceived the study and wrote the paper. M.-O.B., J.P., A.P.H. and R.D.H.B. designed the research. M.-O.B., A.P.H., J.A.M.R., L.F.D.L., D.H.C., J.P. and R.D.H.B. coordinated the study. M.-O.B., S.A.K., L.F.D.L., S.K.H., J.A.C., J.A.M.R., D.H.C., J.A.H.K., J.P. and A.P.H. collected the data. M.-O.B., L.K.M. and L.O.F. conducted statistical analyses. All authors contributed to revisions and gave final approval for publication.

Chapter 3: M.-O.B. and A.P.H. conceptualized the study, supervised (with R.D.H.B.), wrote the original draft and validated the study. M.-O.B. curated the data, developed the methodology and software for the formal analysis including visualization. M.-O.B., A.P.H., P.C.A., J.P., C.C., J.R.G., R.R., K.L., J.A.M.R., S.A.K., L.F.D.L., S.K.H., J.A.C., D.H.C., J.A.H.K., D.M.T.S., K.M.G., and R.D.H.B. reviewed and edited the manuscript. M.-O.B., P.C.A., J.P., C.C., J.R.G., R.R., K.L., J.A.M.R., S.A.K., L.F.D.L., S.K.H., J.A.C., D.H.C., J.A.H.K., D.M.T.S., K.M.G., and R.D.H.B. reviewed and edited the manuscript. M.-O.B., P.C.A., J.P., C.C., J.R.G., R.R., K.L., J.A.M.R., S.A.K., L.F.D.L., S.K.H., J.A.C., D.H.C., J.A.H.K., D.M.T.S., K.M.G., and A.P.H. collected the data. M.-O.B., J.P., J.A.M.R., D.H.C., L.F.D.L., J.A.C., D.M.T.S., K.M.G., R.D.H.B., and A.P.H acquired funding.

Chapter 4: M.-O.B. conceptualized the study, wrote the original draft, validated the study, and curated the data. M.-O.B., A.P.H, D.W., and R.D.H.B. supervised the project. M.-O.B., I.S., X.W., L.P.S., and D.W. developed the methodology and software for the formal analysis. M.-O.B., P.C.A., J.P., C.C., J.R.G., R.R., K.L., J.A.M.R., S.A.K., L.F.D.L., S.K.H., J.A.C., D.H.C., J.A.H.K., D.M.T.S., K.M.G., and A.P.H. collected the data. M.-O.B., I.S., X.W., and L.P.S. coordinated and executed the laboratory work including DNA extractions, quantification, library preparation, sequencing and processing the data. M.-O.B., I.S., X.W., L.P.S., P.C.A., J.P., C.C., J.R.G., R.R., K.L., J.A.C., D.H.C., J.A.H.K., D.M.T.S., K.M.G., D.W., S.K.H., J.A.C., D.H.C., J.A.H.K., D.M.T.S., K.M.G., D.W., R.D.H.B. and A.P.H. reviewed and edited the manuscript. M.-O.B., J.P., J.A.M.R., D.H.C., L.F.D.L., J.A.C., D.M.T.S., K.M.G., A.P.H, D.W., and R.D.H.B. acquired funding.

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General Introduction

Field of study and theoretical background

At the heart of evolutionary ecology is the goal of answering a perennial question in biology: what are the factors involved in the formation, persistence, or extinction of species (Darwin 1859; Coyne and Orr 2004; Nosil 2012; Hendry 2017)? The ecological theory of adaptive radiation aims to explain how and why species form and how populations diverge in their traits due to their environment. The theory suggests that adaptive radiation proceeds via three processes (Schluter 2000): 1. populations and species become phenotypically different because they exploit different environments, 2. resource competition drives phenotypic differentiation and 3. reproductive isolation arises from divergent natural selection of a genetically-based trait (ecological speciation; figure 2; Schluter 2001; Sobel et al. 2010; Nosil 2012). In other words, adaptive radiation can be summarized as the formation of new species that occurs through phenotypic divergence from ecological causes (figure 3). Therefore, the main mechanism explaining species formation is divergent natural selection in which a single population splits because at least two distinct trait means are favoured, meaning they have a high fitness, and intermediate phenotypes have a lower fitness. Although many studies have explored natural selection in the wild, few have attempted to study the link between genotypes, phenotypes and fitness, especially of intermediate phenotypes of an ongoing adaptive radiation in the wild. In this thesis, I focus on characterizing divergent natural selection in natural populations.

Adaptive radiation

Adaptive radiation¹ is thought to be one of the main mechanisms generating biodiversity (Simpson 1953; Schluter 2000; Losos 2010; Soulebeau et al. 2015) due to the colonization of new environments (Landis et al. 2018), the evolution of key innovations (Rabosky 2017), or an environmental change such as the appearance of new resources or the removal of a group of competitors (Simpson 1953; Losos 2010). Many examples of adaptive radiation have been documented across the tree of life including plants (Columbines; Hodges and Arnold 1995), lizards (*Anolis* lizards; Williams 1983; Stroud et al. 2023), invertebrates (*Heliconius* butterflies; Arias et al. 2016, 2017; Supple et al. 2014), birds (Hawaiian honeycreepers; Amadon 1950, Darwin's finches; Grant 1999), and others (reviewed in Hernández-Hernández 2019; Gillespie et al. 2020).

One of the most spectacular examples of adaptive radiation is the African cichlid fishes. From a common ancestor, more than 1,700 species emerged (Kocher 2004; Seehausen 2006; Wagner et al. 2013; McGee et al. 2020; Abate and Noakes 2021; Santos et al. 2023). As a comparison, in Canada, there are about 1,200 species of fish including marine species (Coad et al. 1995). From a common ancestor, the African cichlid fishes rapidly diversified in feeding apparatus such as oral and pharyngeal jaw morphologies depending on their diet. Some jaw morphologies are adapted for scraping algae, crushing mollusks, eating leaves, insects, or other fish which allows the exploitation of varied resources. Together, these examples of adaptive radiation show how ecological causes can fuel the emergence of biological diversity.

Fitness landscapes

To illustrate the divergence of populations, a metaphor was developed to show the association of individual phenotypes to fitness called the fitness landscape (Wright 1932; Svensson and Calsbeek 2012; Dietrich and Skipper Jr 2012). Similar to topographic maps, fitness landscapes are shaped by mountains of high fitness and valleys of low fitness for a combination of phenotypes from

¹The term 'adaptive radiation' was coined by Osborn (1902).

individuals (figure 4). The contour lines of equal fitness are called isodapt². Ultimately, because evolution operates at the level of populations, the individual-phenotypic based fitness landscapes developed by Simpson (1944; 1953; Arnold et al. 2001; Svensson and Calsbeek 2012) can be extended into an adaptive landscape using the mean phenotype of a population and its mean fitness (Lande and Arnold 1983; Lande 1976, 1979; Schluter and Nychka 1994; Schluter 2000; Arnold et al. 2001; Arnold 2023). In this case the slope (linear; β) and curvature (quadratic; γ) at the trait mean (\bar{z}) on an adaptive landscape refers to the selection gradients. The original version of adaptive landscapes used gene combinations networks (Wright 1932), but genetic adaptive landscapes can also be constructed from mean allele frequencies for a given population and the fitness of each genotype (Lewontin and White 1960; Lewontin 2000).

In the literature, the concepts of fitness and adaptive landscapes fueled many ideas that researchers are still exploring today. Many synonyms have emerged to describe the 'landscapes' metaphor. In addition to fitness and adaptive landscapes, these include the 'individual selection surface' (Arnold 2023), 'selection surface' (Arnold 2023; Dietrich and Skipper Jr 2012), 'selection landscapes' (Simpson 1953), 'fitness surface', 'fitness function' or 'surface of selective value' (Schluter and Nychka 1994; Gavrilets 2004), 'performance surface', 'performance landscapes' (Arnold 2003; Holzman et al. 2022), 'adaptive topography' (Colgan and Cheney 1980; Gavrilets 2004; Lande 1976, 1979), 'fitness seascapes' (Mustonen and Lässig 2009), 'adaptive seascapes' (Merrell 1994), 'rugged landscape' (Kauffman and Levin 1987), 'evolutionary landscape' (Cambray and Mazel 2008), 'combinatorial maps' or 'combinatory landscapes' (Fontana et al. 1993), 'genotypic fitness landscapes' or 'genotypic fitness networks' (Patton et al. 2022), 'field of gene combinations' (Wright 1932), 'value landscape' (Eigen et al. 1989), and by extension 'genotype-fitness map' (de Visser and Krug 2014), 'genotype-to-fitness map', 'genotype-phenotype-fitness map', or 'phenotype-fitness landscape' (Hamel et al. 2020), 'phenotype-fitness map' (Bull et al. 2011; Venkataram et al. 2016; Kinsler et al. 2020), 'molecular' or 'mutational landscape' (Gillespie 1984, 1987, 1994; Rokyta et al. 2005), 'genotypic landscapes' (Blanquart et al. 2014), 'protein space'

²Coined by Lewontin and White (1960) which are similar to isoclines or isolines on a topographic map.

(Maynard Smith 1970, 1962; Perelson and Macken 1995; Firnberg et al. 2014), 'protein fitness landscape' (Meini et al. 2015), 'RNA landscapes' (Fontana and Schuster 1987; Fontana et al. 1993), 'holey landscapes' (Gavrilets 1997, 2004), 'functional landscapes' (Amor 2023; Skwara et al. 2023), and probably others (Stadler 2002, 1995). The concept has also inspired other fields of research such as engineering and computer science (Fodor et al. 2012; Richter and Engelbrecht 2014; Gendreau and Potvin 2019). Note that the term 'genomic landscape' is often used to describe the distribution of genomic features on a chromosome such as divergence between species and is not connected to the fitness or adaptive landscape concept (Ellegren et al. 2012; Ellegren 2013, 2014; Lawson and Petren 2017).

In the early development of the fitness landscape metaphor, it was recognized that they are not static representations of selection over time. Rather than being rigid as a rocky mountainous landscape and relatively invariant in time, they are dynamic entities (Simpson 1953)³ and are shaped by the life-history of the organism in the population and eco-evolutionary dynamics (Merrell 1994; Schluter 2000; Hendry 2017; McPeek 2017b,a; Arnold 2023). Recent publications are tackling this very subject and show that selection is indeed variable through time (Siepielski et al. 2009, 2011; Kingsolver and Diamond 2011; Morrissey and Hadfield 2012) and space (Siepielski et al. 2013), which shapes the fitness and adaptive landscapes (Bell 2010; Calsbeek and Cox 2012; Mira et al. 2015; Martin 2016; Houle et al. 2020; Martin and Gould 2020; Gillespie et al. 2020; Patton et al. 2022; Stroud et al. 2023). Therefore, a dynamic adaptive landscape would indicate a changing selection regime, which could in turn be related to environmental variables (figure 5).

In adaptive radiation, fitness landscapes are carved by natural selection in relation to the environmental features which associate fitness with ecological traits (Nosil 2012). Thus, we expect to find a rugged fitness landscape as in figure 4 (panel C and D) composed of peaks of high fitness and intermediate phenotypes of low fitness. Characterizing such rugged fitness landscapes has been elusive as trait and fitness data need to be quantified from individuals. Even more challenging is

³ To complete the representation of nature, all these elements must be pictured as in almost constant motion—rising, falling, merging, separating, and moving laterally, at times more like a choppy sea than like a static landscape—but the motion is slow and might, after all, be compared with a landscape that is being eroded, rejuvenated, and so forth, rather than with a fluid surface." (Simpson 1953 p. 159)

uncovering the 'genetic adaptive landscape', which requires individual genomic information from a population and quantifies the fitness of genotypes in relation to allele frequencies (Lewontin and White 1960). The topology of genetic adaptive landscapes could be characterized to find if genetic markers related to an ecological trait are closer to an adaptive peak or if they are found on an unstable adaptive landscape. Therefore, the characterization of fitness and adaptive landscapes that incorporate information about the connections between genotypes, phenotypes and fitness is missing from our current understanding of wild populations in adaptive radiations. Darwin's finches provide an exemplary system for addressing this challenge.

Study system

On the Galápagos Archipelago—situated in the Pacific Ocean, 1000 kilometers to the West of Ecuador—is home to 18 endemic species of the monophyletic Darwin's finches (also known as Galápagos finches, which in fact, are in the tanager family Thraupidae). These passerine birds are part of an adaptive radiation that started around 1.5 million years ago from a common ancestor thought to originate Central or South America (Lack 1947; Sato et al. 2001; Petren et al. 2005; Lamichhaney et al. 2016, 2015). However, more recently, a group of species collectively referred to as the ground finch (*Geospiza*, Gould) emerged about 100,000 to 400,000 years ago (Lamichhaney et al. 2015). On Santa Cruz Island, the second largest island in the Galápagos Archipelago, four of these ground finches can be found: the blunt beaked small, medium and large ground finches (*Geospiza fuliginosa, Geospiza fortis*, and *Geospiza magnirostris*) that crack small to large seeds of a diversity of plant species (Smith et al. 1978; De León et al. 2014; Carvajal-Endara et al. 2020) and the pointy beaked cactus finch (*Geospiza scandens*) which consumes nectar, pollen, and seeds of the *Opuntia* cactus (Grant 1999). Variation in the climate, which changes the availability of food types (seeds, flowers, pollen, nectar, caterpillars, etc.) was shown to be the ecological driver of natural selection and explain the diversity of beaks (Lack 1947; Smith et al. 1978; Grant and Grant 1993).

Studying adaptive radiation and speciation using Darwin's ground finches, an often cited textbook example of evolution by natural selection (Futuyma and Kirkpatrick 2017; Emlen and

Zimmer 2020; Arnold 2023), is of considerable interest to tackle ecological and evolutionary questions regarding the emergence of species (Ranganath 2018). Previous studies on these birds found that the major ecological traits behind the emergence of the new species are beak size and shape, but also body size including the muscles that allow beak articulation (Lack 1947; Bowman 1961; Grant 1999; Genbrugge et al. 2011). When resources are scarce due to extreme climatic events, the different species of Darwin's finches tend to increase specialisation on particular food types (Smith et al. 1978; Grant and Grant 1993, 2014; Grant 1999; Grant and Grant 2002; De León et al. 2014). Further, beak traits are highly heritable (Boag 1983), with a genetic basis that includes some large effect genes (e.g., HMGA2 and DLK1; Chaves et al. 2016; Lamichhaney et al. 2016; Rubin et al. 2022; Enbody et al. 2023). Beaks have also been studied for their developmental pathways (Abzhanov et al. 2004, 2006; Campas et al. 2010; Mallarino et al. 2011; Masly and Azom 2022) and mechanics (Herrel et al. 2005a,b, 2009; Soons et al. 2010). Moreover, they are used by the species to mate assortatively (Ratcliffe and Grant 1983; Huber et al. 2007; Podos 2010; Grant and Grant 2018) and show variation linked with individual fitness (Grant and Grant 1995, 2014; Hendry et al. 2009; Beausoleil et al. 2019, 2023). However, it should be noted that hybridization, although rare, probably due to assortative mating (Podos 2010), is possible between species and may produce viable offspring (Grant and Grant 1998, 2016, 2019, 2020). Introgression, the movement of alleles from one population to another, was demonstrated in the striking hybridization of a G. magnirostris (male large ground finch) and a G. fuliginosa (female small ground finch) on Daphne Major, which produced four fledglings (Grant 1999). Evidence of this process has also been detected via the genetic remnants of an extinct population of unusually large G. magnirostris in an extant population of G. fortis (Grant and Grant 2021). With this background of knowledge, ground dwelling Darwin's finches provide an excellent opportunity to study the process of adaptive radiation and the emergence of novel biodiversity.

To investigate the process of adaptive radiation in Darwin's finches, I contributed to and used the capture-mark-recapture data collected on ground finches over a 17-year period at El Garrapatero (Santa Cruz island, Galápagos, Ecuador; (0°41′22.9″ S, 90°13′19.7″ W). At this location, the four

sympatric ground finches species have five phenotypic modes (Lack 1947; Ford et al. 1973; Herder et al. 2006; Foster et al. 2008; Beausoleil et al. 2019). More specifically, there are two distinct beak size populations of medium ground finch (*G. fortis*, small and large 'morphs') which are connected with intermediate beak phenotypes (and a diet associated with intermediate seed size and hardness). These two *G. fortis* beak morphs lie between the smaller (*G. fuliginosa*) and larger ground finches (*G. magnirostris*) (Hendry et al. 2006; Foster et al. 2008; De León 2010; De León et al. 2011, 2014; Beausoleil et al. 2019).

Summary of thesis content

I here study Darwin's finches to explore the theory of ecological adaptive radiations, focussing on divergent natural selection in wild populations. The thesis has four chapters: 1. Where did the finch go? Insights from radio telemetry of the medium ground finch (*Geospiza fortis*), 2. Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*), 3. The fitness landscape of a community of Darwin's finches, and 4. Exploring genetic adaptive landscapes in Darwin's finches. I used the long-term capture-mark-recapture survey on populations of ground finches (*G. fuliginosa*, *G. fortis* small and large, *G. magnirostris*, and *G. scandens*) inhabiting Santa Cruz Island to study the ecological speciation of these birds.

Although Darwin's finches have sparked research interest in evolutionary biology for many decades (Darwin 1839; Snodgrass 1902; Lack 1947; Grant and Grant 2002; Enbody et al. 2023), the movement ecology of Darwin's finches and quantifying its importance in evolution is lacking. In the first chapter, I asked: What is the home range and habitat use of the *G. fortis*? Five medium ground finch (*G. fortis*) equipped with radio-telemetry devices provided evidence for a preference in the dry-forest habitat as well as the first documentation of communal roosting behaviour (Beausoleil et al. 2022). This study highlights that spatial ecology of Darwin's finches is a valuable avenue of research to better understand the ecological factors involved in the evolutionary dynamics of populations regarding foraging activities and roosting behaviour.

In the second chapter, my main questions were: Is there a significant association between
beak size and fitness for *G. fortis* and are selection coefficients correlated with precipitation patterns? In addition, what is the relationship between the strength of selection and environmental variation (Beausoleil et al. 2019)? Specifically, I studied how disruptive selection changes based on climatic conditions using more than 600 *G. fortis* from a 9-year capture-mark-recapture survey. The results indicate that disruptive selection between the small and large beak morphotypes is significant in certain years. I further showed that the strength of selection increases with the amount of precipitation in the dry season of the preceding year. This relationship between selection gradients and an environmental variable shows how precipitation is involved as a selective agent, likely due to its impact on seed availability. More importantly, this chapter demonstrates how a temporally changing fitness function can play a role in population divergence.

For the third chapter, the overarching question was: What is the shape and features of a fitness landscape in a community of Darwin's finches? I estimated fitness and adaptive landscapes to show mountains of high fitness and valleys of low fitness for different phenotypes, with the aim of characterizing an adaptive radiation of Darwin's ground finches (Beausoleil et al. 2023). Using apparent lifespan as a measure of fitness, I leveraged 17 years of capture-mark-recapture data to uncover the topology of the fitness and adaptive landscapes. The results showed that the five beak size modes composed of *G. fuliginosa*, *G. fortis* small and large, *G. magnirostris*, and *G. scandens* are near five distinct fitness peaks. However, the adaptive landscape only had four peaks. I further introduce a metric, called 'prospective selection' to determine the amount of selection that would be required for each species or morph to reach their nearest adaptive peaks. In summary, this chapter elevates the adaptive landscape as a quantitative tool to characterize adaptive radiations and provides a framework to study the constrained evolutionary path that leads to adaptive peaks.

In the last chapter, I tackled the question: What is the architecture of a genetic adaptive landscape in Darwin's finches? I characterized genetic adaptive landscapes from population allele frequencies using more than 400 whole genomes of individual Darwin's finches (*G. fuliginosa*, *G. fortis* small and large morphs, and *G. magnirostris*). I identified loci putatively associated with beak length using a genome-wide association study, and found that they are located closer to regions of

the genome that have been targets of natural selection ('adaptive peaks') compared to loci without association with beak morphology. It shows how genetic adaptive landscapes can be used in order to find adaptive loci that are linked with a trait targeted by selection. More research needs to focus on making connections between phenotypic adaptive landscapes and genetic adaptive landscapes, especially regarding how gene interactions can shape the genetic adaptive landscape. Finally, I argue that the genetic adaptive landscape could help answer questions about the genetic basis of adaptation.

Together, my chapters shed light on the mechanisms involved in adaptive radiation that can either foster or impede the formation of novel species. The work in this thesis shows how linking genotypes, phenotypes, and fitness, and understanding how these connections vary across time and space, can sharpen our understanding of the process of adaptive radiation. More specifically, I demonstrated how the adaptive landscape concept is useful for describing the process of evolution in wild populations. Finally, this work reinforces the value of contributing to and maintaining long-term projects. The databases they provide help answer important questions about the spatio-temporal dynamics that are at the heart of evolutionary ecology.



Figure 2: Graphical representation of ecological speciation as described by the theory of adaptive radiation. The speciation continuum is shown as a gradient shaded line (top) from initiation of speciation to completion. Panel A refers to divergent natural selection and shows a reduction in fitness (red dashed line as a fitness function) of intermediate phenotype (black line as the phenotypic distribution) through time $(t_1, ..., t_n)$ and the separation of population means (from μ_0 to μ_1 and μ_2). Panel B is a representation of the emergence of reproductive isolation where an original population interbreeds freely (lines connecting the large dots show the ability to interbreed), but through time stops exchanging genes. Panel C shows that there is a genetic link between divergent natural selection and reproductive isolation with different colours associated with different genotypes.



Figure 3: Adaptive radiation showing that from an ancestral species (panel A) there is the emergence of species (as shown by the hypothetical phylogenetic tree) with phenotypic and ecological diversity (panel B) due to ecological causes (panel C-D) here shown in a hypothetical example with different bird species equipped with diverse beak morphologies adapted at exploiting different resources. Note that panel D is a two-dimensional representation of the fitness landscapes shown in panel C.



Figure 4: Hypothetical fitness landscapes showing a flat surface (panel A in 3 dimensions, B in 2 dimensions) with phenotypes having the same fitness and mountains with peaks of high fitness and valleys of low fitness (panel C in 3 dimensions, D in 2 dimensions) for each phenotypic combination on the plane. The black contour lines are the 'isodapt' and the colour shading from blue (low) to red (high) show the different fitness values for specific combination of trait 1 and trait 2 values.



Figure 5: Hypothetical relationship between the strength of selection as a function of an environmental variable from the same population through time or in different populations from different environments. This type of relationship can be used to find if an environmental variable is an agent of selection in a population. In this case, each large grey point in the graph represents a selection coefficient or gradient (here curvature as γ) which was extracted from the slope of a fitness function relating individual phenotypes and fitness in a particular environment shown as the inset for which selection gradients are represented as large red points (see Conner and Hartl 2004 for an equivalent graph for linear gradients, β).

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"I have long felt that biology ought to seem as exciting as a mystery story, for a mystery story is exactly what biology is."

> Richard Dawkins, 1976 The Selfish Gene

Chapter 1

Where did the finch go? Insights from radio telemetry of the medium ground finch (*Geospiza fortis*)

This chapter is republished from an Open Access article: Beausoleil, M.-O.¹, C. Camacho^{2, 3}, J Rabadán-González⁴, K. Lalla⁵, R. Richard¹, P. L. Carrión¹, A. P. Hendry¹ and R. D. H. Barrett¹. 2022. Where did the finch go? Insights from radio telemetry of the medium ground finch (*Geospiza fortis*). *Ecology and Evolution 12*(4):e8768, licensed under Attribution 4.0 International (CC BY 4.0)

Author affiliations:

¹ Redpath Museum and Department of Biology, McGill University. Montréal, QC. Canada

² Department of Biological Conservation and Ecosystem Restoration, Instituto Pirenaico de Ecología—CSIC, Jaca, Spain

³ Department of Biology, Centre for Animal Movement Research (CAnMove), Lund University, Lund, Sweden

⁴ Observation.org Spain, Seville, Spain

⁵ Department of Natural Resource Sciences, McGill University, Sainte-Anne-de-Bellevue, QC. Canada

1.1 Abstract

Movement patterns and habitat selection of animals have important implications for ecology and evolution. Darwin's finches are a classic model system for ecological and evolutionary studies, yet their spatial ecology remains poorly studied. We tagged and radio-tracked five (three females, two males) medium ground finches (*Geospiza fortis*) to examine the feasibility of telemetry for understanding their movement and habitat use. Based on 143 locations collected during a 3-week period, we analyzed for the first time home range size and habitat selection patterns of finches at El Garrapatero, an arid coastal ecosystem on Santa Cruz Island (Galápagos). The average 95% home range and 50% core area for *G. fortis* in the breeding season was 20.54 ha \pm 4.04 ha *SE* and 4.03 ha \pm 1.11 ha *SE*, respectively. For most of the finches, their home range covered a diverse set of habitats. Three finches positively selected the dry-forest habitat, while the other habitats seemed to be either negatively selected or simply neglected by the finches. In addition, we noted a communal roosting behavior in an area close to the ocean, where the vegetation is greener and denser than the more inland dry-forest vegetation. We show that telemetry on Darwin's finches provides valuable data to understand the movement ecology of the species. Based on our results, we propose a series of questions about the ecology and evolution of Darwin's finches that can be addressed using telemetry.

1.2 Introduction

The way in which animals move across the landscape has important implications for ecology and evolution: migration influences nutrient transfers, dispersal influences speciation, habitat choice influences natural selection, and home ranges influence competition (Nathan 2008; Holyoak et al. 2008; Jeltsch et al. 2013). Hence, our knowledge of any model system in ecology and evolution benefits critically from an understanding of how an organism moves across its landscape. Darwin's finches on the Galápagos Islands are a classic system in evolutionary ecology (Grant and Grant 2014; Grant 1999), with a long history of research on morphological variation (Grant 1999; Lack 1947), growth and development (Grant 1981), diet (De León et al. 2014), mate choice and species recognition (Grant and Grant 1997; Podos 2001), genomics (Chaves et al. 2016; Enbody et al. 2021; Lamichhaney et al. 2016, 2018, 2015), and habitat use (Grant and Grant 2014; Grant 1999). However, their movement ecology is poorly understood. At a small scale, direct observations and capture-recapture studies have shed some light on their natal and breeding dispersal (Grant 1999), and breeding territory size (Boag and Grant 1984; Grant and Grant 1989; Price 1984). At a larger scale, genetic studies have revealed that migratory movement is limited, but not absent, between islands but high within islands (De León et al. 2010; Lamichhaney et al. 2018; Lawson et al. 2019; Petren et al. 2005). Yet there is a knowledge gap between the small and large scale movement studies, especially for finches' daily movement routines, home range (Burt 1943), and core area size (loosely defined as a smaller portion of the home range). For example, our knowledge of the movement of finches across the landscape, including permanent (dispersal) and intermittent (normal activities of food gathering, mating, and caring for young) displacements, is limited. Furthermore, although some information is available on breeding territory size (Boag and Grant 1984) and flocking behaviour of non-breeding ground finches during the dry season (Schluter 1982; Swash and Still 2005) and on dispersal of captive-reared mangrove finches (*Camarhynchus heliobates*; Cunninghame et al. 2017), almost no information exists on habitat use or patterns of commuting behaviour in Darwin's finches. Therefore, scientists and conservation biologists lack basic information about the habitat selection patterns of the finches, their daily movement routines across the landscape, and the intrinsic and extrinsic factors influencing such movements.

The Island of Santa Cruz encompasses diverse habitats that provide numerous opportunities for finches to select particular environments (Grant 1999; Reeder and Riechert 1975). But, determining the movement of birds on a large territory comes with a logistical challenge: the difficulty of tracking individual finches. Darwin's finches can be challenging to recapture/resight since they can move long distances and aggregate in wandering flocks after the breeding season or when dry conditions preclude breeding (Schluter 1982; Swash and Still 2005). In addition, the large population sizes occupying a broad territory compared to the limited number of banding sites, and the fact that some individuals with larger beaks are able to remove their bands, makes it a challenge to track individuals

by standard mark-recapture methods. Further, GPS tags are generally still too heavy for finches due to their small body size (body mass $22 \text{ g} \pm 6 \text{ g}$ [average $\pm 2x SD$]). Telemetry methods (e.g., radio-tracking) might provide direct information on the movement and behaviour of individual finches and radio tags are small enough to be deployed on finches, yet they have not been extensively used in the Galápagos (exceptions include Cunninghame et al. 2017; Fessl et al. 2010). Concerns about the use of telemetry generally stem from the perception that data collection will be challenging due to features of the landscape (e.g., dense vegetation, inaccessible areas due to the volcanic structure of the landscape).

Despite these concerns, telemetry in general, and Very-High Frequency (VHF) radiotelemetry in particular, has been used to investigate movement patterns in small birds (Kenward 2001; White and Garrott 1990), thus informing habitat selection (Camacho et al. 2014), foraging range and roosting (Ginter and Desmond 2005), post-fledging dispersal (Fisher and Davis 2011), and migration (Bégin-Marchand et al. 2021). This approach has also been used on rare occasions in Darwin's finches in the Galápagos, primarily for conservation purposes. Miniature radio-transmitters have been previously deployed on the woodpecker finch (*Camarhynchus pallidus*; Cunninghame et al. 2017; Fessl et al. 2010), and also on the critically endangered mangrove finch (*C. heliobates*) to track the movement of captive-reared juveniles (Cunninghame et al. 2013, 2015, 2017). However, the utility of these methods for eco-evolutionary studies of Darwin's finches captured and released in the wild is unknown. Thus, we here explore the extent to which radio-transmitter tagging methods are effective in this context.

Our aims are threefold: (a) Explore Darwin's finch movement and space use associated with different behaviours (e.g., diurnal activity, nesting, and roosting); (b) Ascertain data quantity and quality to determine what kind of insights can be gained in a three-week data collection period (the duration of battery life of the miniature radio-transmitters); and (c) Identify the limitations of using radio-telemetry methods given the topography of the volcanic terrain. To fulfil these aims, we deployed VHF radio-telemetry tags on a focal sample of five medium ground finches (*Geospiza fortis*) on Santa Cruz in the Galápagos, Ecuador. We then estimated the home range and core

area of these birds in the arid coastal zone and characterized their habitat selection patterns and movement behaviour. Finally, we discuss the potential utility of these methods for addressing three key unresolved questions, which we believe would advance our understanding about the behaviour, ecology, evolution, and conservation of Darwin's finches: (a) What ecological factors influence finch's home range size and location?; (b) How does finch movement impact their ecological interactions with other taxa?; and (c) What factors influence roosting behaviour in finches?

1.3 Materials and Methods

1.3.1 Capture and trasnmitter deployment

Our study took place at El Garrapatero, Santa Cruz Island, Galápagos, Ecuador ($0^{\circ}41'22.9''$ S, $90^{\circ}13'19.7''$ W) from 22 February to 13 March 2019 (20 days), during the breeding season of Darwin's finches. This population has been studied since 2003, with systematic data on behaviour, feeding ecology, and morphology collected on an annual basis (Beausoleil et al. 2019; De León et al. 2011; Hendry et al. 2009; Knutie et al. 2019; Podos 2007). Our test sample consisted of five medium ground finches (*Geospiza fortis*)—three females and two males (table 1.1)—captured at the same dry-forest sites we use during our long-term systematic mist netting operations at El Garrapatero (Beausoleil et al. 2019; De León et al. 2014; Hendry et al. 2009). Only actively breeding individuals (i.e., adult females showing either an active or regressing brood patch, and adult males showing a cloacal protuberance (Pyle et al. 1997)) were tagged to reduce the variability in home range differences (Pagen et al. 2000; Streby et al. 2011). We determined sex based on plumage colouration (Grant 1999; Price 1984).

Each individual was fitted with a 0.56 g PicoPip Ag376 VHF radio transmitter (pulse length: 30 ms, pulse rate: 60 ppm, for about three-week battery life; Biotrack Ltd. UK). To attach the radio transmitter, we used a custom-made leg-loop harness made of a thin elastic band glued (cyanoacrylate) to the transmitter with a biodegradable paper in between to allow the harness to detach itself after two to three months (Naef-Daenzer 2007). We fitted the harness around the bird's legs and placed the transmitters on the bird's back (synsacrum) as described in Rappole and Tipton

(1991) (figure A.1) and cut the antenna to a final length of 11 cm to allow birds to move freely and avoid risks of entanglement (Dougill et al. 2000). The radio transmitter and harness represented <3% of the body mass of each individual (Murray and Fuller 2000). For each bird, we measured tarsus length to the nearest 0.01 mm as an index of structural size (Senar and Pascual 1997) and body mass to the nearest 0.1 g using a digital balance to adjust the size of the harness on which the VHF is attached. Individuals were banded with numbered Monel metal bands and a unique combination of plastic colour bands for ease of identification in the field. Birds were released immediately after being measured and equipped with transmitters. The time from capture and tagging to release did not exceed 15 min.

1.3.2 Bird tracking

Tracking sessions began 24 h after tagging to facilitate resumption of normal behaviour and activity, as confirmed by relocation and direct observation of tagged birds. Two observers simultaneously tracked radio-tagged individuals for three- to five-hour sessions, usually in the morning between 0600 h and 1100 h, when birds are most active. They were also tracked opportunistically earlier (between 0500 h and 0600 h, before detecting any visual (e.g., flying silhouettes against the sky) or acoustic (e.g., dawn chorus) sign of bird activity) and later in the day (1700 h and 1800 h, after bird activity ceased in the evening; figure A.2) in order to locate the roosting sites. Each observer used a 3-element antenna connected either to an ICOM IC-R20 (Icom Inc., JP) or a SIKA (Biotrack Ltd., UK) portable receiver to record signal strength and direction. Sometimes the birds could be located and directly observed by tracking the VHF signal to its source (the nest or its immediate surroundings), and so their precise location was recorded using a Samsung A3 and J7 Pro phones with a Memento Database program (MementoDB Inc., mementodatabase.com) and ObsMapp, observation.org/apps/obsmapp). Most often, to estimate their position we used bitriangulation of fixes based on an azimuthal telemetry model within the R-package razimuth (50,000 iterations with 5,000 burn-in; 600 prior due to detection range of antenna in the field; version 0.1.0; Gerber et al. 2018; R Core Team 2021; R version 4.0.3). Directional bearings were estimated from

accessible sites along the main road and the path to the beach. Bearings at angles around 90° to each other were generally preferred to obtain accurate estimates (mean of biangulation points = $79.7^{\circ} \pm 3.1^{\circ} SE$, n = 90). Bearings that resulted in clearly erroneous estimates (e.g., those over the sea) were also removed from the data set prior to analyses. Unusable locations represented 23% of the initial data set (n = 286 fixes), and so the final sample size included 219 fixes acquired with telemetry (table 1.2). We recorded additional fixes only after >20 min to minimize sample clustering. The birds were relocated sequentially at regular intervals to minimize bias in relocation effort. The average time between consecutive relocations on the same day was 2.31 h (range 1.67-2.78 h, SE =0.19 h, n = 5). Observers also recorded the location of bird nests (when possible) and the tagged birds' activity, either diurnal activity or roosting. Observers either triangulated nests (n = 1 bird) or found them (n = 3 birds) by estimating the approximate location of tagged birds and then moving closer using the signal strength until the nest was found and the identity of the bird was confirmed through their colour band combinations. For one bird, the nest could not be located directly due to its limited accessibility (but see figure A.9). The location of roosts was estimated for all birds by biangulation during the night (figure A.2).

Direct observation of the behaviour of the tagged individuals within the first 2-3 days after tagging enabled us to confirm their nesting status. The duration and periodicity of behavioural observations differed among individuals depending on the time needed to confirm their nesting status. Males collecting material to build their nests left the nest and returned back at short (1-5 min) regular intervals. Females incubating eggs or brooding chicks tended to remain in the nest for periods of at least 45 min (see Austin et al. 2019 for comparisons with other birds). Thus, the total time of observation per bird was \leq 30 min in males (one single session) and 90-180 min in females (60 min sessions on 2-3 consecutive days). This information also enabled us to link movement patterns, as determined from the radio-tracking data, to the breeding stage of each bird and, therefore, to infer changes in the bird's breeding status throughout the study period. For instance, females that remained stationary (i.e., no apparent change in the signal strength or direction regardless of the tracking position) for 45 min or longer were assumed to continue incubation or nursing tasks. By

contrast, rapid periodic changes in the strength of the signal from the location of the nest was taken as an indication of continued building activity in males or offspring provisioning in females (Orr 1945; Price et al. 1983).

Prior to radio-transmitter attachment on the birds, we estimated relocation error under field conditions by placing the VHFs in random locations around the capture site and letting 'blinded' observers find their position by taking bearing measurements. Then, as a measure of the error, we calculated the mean Euclidean distance between the estimated locations (using the razimuth package, see above) and the actual (georeferenced) location of the VHFs (figure A.7).

1.3.3 Roost count

The tagged finches used a communal roosting area located outside the nesting area (except incubating females; see '1.4 Results' on page 39). We detected the communal roosting area by locating the birds 1 h before dawn (0500 h - 0600 h). During this time, we considered a bird roosting if there was no apparent change in its signal strength or direction regardless of the tracking position. Given that one of our goals was to determine space use by the finches, we gathered data on the number of other (non-tagged) finches using the communal roosting area. Once the location of roosting sites had been identified, two observers conducted a direct count of birds entering the roost during the evening (table A.1; Video A1 linked here and still image of video 1.3). The site of the main roost was adjacent to the ocean, so the observers stood back-to-back perpendicularly to the shoreline to monitor all potential entrances (observer location 0°41'36.56" S, 90°13'18.16" W). These counts began near sunset (1800 h), before any bird was seen around the roosting area. The observers counted any finch or group of finches entering the roost and subtracted the (small) number of finches exiting the roost area (see table A.1). To avoid double-counting, every observer informed their partner about birds passing from one visual range to another and flying out of the roost. Medium ground finches are the most abundant species in the study area (Beausoleil et al. 2019). However, during the census, we counted all finch species together, because it is difficult to distinguish between Darwin's finch species from a distance due to similar plumage and size, especially under poor

lighting conditions. The count lasted approximately one hour, until finches stopped entering the roost.

1.3.4 Home range, core area and habitat selection analyses

For home range and habitat selection analyses, we combined the data from different sources (i.e., VHF-inferred fixes, direct observation, and location of capture), after transformation to UTM coordinates. The azimuthal telemetry model (ATM) traceplot was visually inspected to ensure proper mixing of the Markov chain Monte Carlo (MCMC) chain for the concentration parameter κ (which controls the uncertainty in the ATM; see Gerber et al. 2018; figure A.3 and figure A.4). The minimum number of points needed for accurate home range estimation was determined for each bird from the plateau of the rarefaction curve of minimum convex polygons (MCP 100%). To estimate home range size and core area, we used a bivariate normal kernel function using 'kernelUD' (Utilization distribution) at 95% and 50%, respectively, from the adehabitatHR package (version 0.4.19; Calenge 2006). For the smoothing parameter (h) for kernel estimation, we used the reference bandwidth (href) and constrained the area to be terrestrial (i.e., excluding the ocean). We used the sf library (version 0.9.8; Pebesma 2018) to intersect the home ranges with the habitat types—as detailed below—and calculated the proportion of bird locations within habitat types and range overlap of habitat types for each finch. We mapped our results using ggplot (version 3.3.3; Wickham 2016) and used satellite images and field observations for validation (figure A.5) to make our own habitat type polygons in QGIS (QGIS Development Team 2021, version 3.16; Google Earth Pro 7.3.3.7786 2021). We categorized habitat types used by the finches as 'beach', 'inland water' (a pond that can temporarily dry out), 'Manzanillo forest' (coastal zone dominated by the tree *Hippomane* mancinella (poison apple) and other trees), 'dry-forest' dominated by Opuntia echios (prickly pear cactus) and Bursera graveolens (incense tree), and 'paved road' encompassing a parking lot and road.

For the habitat selection analysis, we calculated the proportion of each habitat type within each home range (i.e., availability) and tested whether birds spent more or less time (the number of relocations) in each habitat than would be expected from its availability. Specifically, for each finch we compared the expected number of relocations in a habitat to the number of observed locations within that habitat with a chi-square test. We calculated the Bonferroni corrected 95% confidence interval (from the proportion of observed locations of the bird in certain habitats to the total number of observations for that bird) as in Neu et al. (1974) and the direction of habitat selection (negative, neutral or positive) as in Sierro et al. (2001). Specifically, if the observed area calculated as a proportion of a given habitat type in the home range was smaller than the lower bound of the Bonferroni confidence limit based on the proportion of bird locations in a particular habitat type, the bird was assumed to positively select the habitat. In the case where the proportion was greater than the upper confidence limit, it was considered to negatively select that habitat. In the case where the value lies inside the confidence interval, the bird was 'neutral' with respect to that habitat. As a quantitative preference value for habitat selection, we also calculated the Jacobs' index, in which a value of zero indicates a random utilisation of the habitats whereas a positive or negative value indicates a positive or negative selection of a habitat type, respectively (Jacobs 1974; Lechowicz 1982). Jacobs' index has been used in other habitat selection studies (Revilla et al. 2000) and, contrary to the selection ratio, it is independent of the relative abundance of each habitat available to the birds (Jacobs 1974). To determine diurnal and nocturnal differences in commuting behaviour, we calculated the average distance (mean of all distances of the located finch to their nest) that the finches travelled from their nest during the day or at night.

1.4 Results

Our sample of medium ground finches included three females at different stages of the breeding cycle and two nest-building males (table 1.1). The two males continued building nests throughout most of the tracking period, and one female (JP4645, table A.2) completed its clutch and then initiated incubation. The other females were already incubating (LF1234) or feeding offspring (KGSK2033) at the time of tagging. The resignted birds (all but LF1234) showed no sign of negative impact of the radiotags on their diurnal behaviours. The tags remained in their original position

until the end of the study in all but one bird: male LF0126 removed its tag after two weeks. The tag antenna was found bent, which may indicate that the bird was able to remove it with the beak once inside the nest.

We collected a total of 143 locations with a mean number of 28.6 locations per bird (range: 23-31; figure 1.1, table 1.2). Of these locations, 81.1% (116 points) were estimated with the azimuthal telemetry model, 15.4% (22 points) through direct observation, and 3.5% (5 points) from mist-netting (capture locations). The minimum number of fixes required for accurate home range estimation ranged from 17 to 28 locations depending on the bird (figure A.6). The mean relocation error was 30.11 m ±8.98 m *SE* (range 13.13-70.93 m, n = 6). The total number of finches observed entering the communal roosting area in one evening was 669 finches (table A.1).

The mean home range size (kernel 95%) was 20.54 ha ±4.04 ha *SE* (range 7.58-29.09 ha, n = 5, table 1.2) and the mean core area (kernel 50%) was 4.03 ha ±1.11 ha *SE* (range 1.17-6.60 ha, n = 5). The tagged finches overlapped in their core areas, from 61% (76% for home range) from LF1233 on JP4645 and 43% (77% for home range) from LF1233 on LF0216 to <30% overlap in the other core areas (figure 1.1, table A.3). The finches moved a greater distance (3.7 times more) on average from their nests to the roosting area (247 m ±25 m *SE*, n = 4) compared to the distance they travelled during their daily activity (67 m ±22 m *SE*, n = 4; figure A.8). The average daily commute distance (regardless if it is during day or night) was 102 m ±21 m *SE*. Female JP4645 travelled to the communal roosting area at night during the egg-laying stage, but remained on the nesting territory during the incubation stage (figure A.9). The incubating female LF1234 also remained on the putative nesting territory during the night (figure A.9), suggesting that the use of the communal roost is contingent upon the nesting status.

Overall, the highest proportions of habitat types observed in the finches' home ranges were arid zone dry-forest (55.20%) and coastal zone 'Manzanillo forest' (35.54%) (table A.4). Three finches (JP4645, LF0216, and LF1233) showed a positive selection for the dry-forest whereas one finch (KGSK2033) used this habitat less than expected by chance (figure 1.2, table 1.3 and table A.4). The rest of the habitat types were either negatively selected or not selected (figure 1.2,

table 1.3). However, for only one male (LF0216), the use of a particular habitat (dry-forest) deviated significantly from random expectation in a positive direction ($\chi^2 = 16.21$, p-value = 0.001, df = 3; figure 1.2, table 1.3 and table A.4).

1.5 Discussion

1.5.1 Exploring Darwin's finch movement and space use

We have shown that radio tags can be used to track the movements of individual medium ground finches for at least a three-week period and, therefore, determine their habitat selection patterns. Other, mostly arboreal, finches such as the woodpecker finch and the mangrove finch, have been tracked in previous studies (Cunninghame et al. 2013, 2015, 2017; Fessl et al. 2010), yet our study is the first to use VHF tracking for any ground finch species. The resulting fine-scale temporal and spatial data on activity patterns revealed aspects of finch biology that are invaluable for understanding the ecology and evolution of these birds. For example, we identified nesting places, foraging areas, and roosting sites that together delimit the home range of these ground finches. All the nests were located on cacti, which are found in abundance in the dry-forest (Grant 1999). Further, daily movement patterns of the finches from the arid habitat to the coastal habitat illustrate the importance of movement and multiple habitat use during the breeding season.

No estimates of the home range size of breeding *Geospiza fortis* are available in the literature for comparison, since previous studies focused on nesting territory (i.e., the confined area around the nest), estimated from observations of males' territorial behaviour (Boag and Grant 1984). Using VHF tracking, we were able to follow the finches not only over their nesting territory, but also over the entire area in which they live and move (i.e., the full home range for the given period of time). The smallest home range we estimated using the minimum convex polygon method was 33.700 m² (3.37 ha, figure 1.1a, table 1.2), and the largest range was 172.500 m² (17.25 ha, figure 1.1b, table 1.2) with an average of 101.600 m² (10.16 ha ±2.25 ha SE, n = 5). The only previous estimates of nesting territory size for *G. fortis*, calculated as minimum convex polygons, are respectively 0.2% (203.6 m²) and 0.5% (477.8 m²) of the estimated home range size in this study (Boag and Grant 1984), indicating that relatively large areas are required to meet the spatial needs of breeding finches.

Home range size and habitat selection patterns often vary during the annual cycle (Rühmann et al. 2019; Stanley et al. 2021; Wiktander et al. 2001). We found that the smallest (7.58 ha) and the largest (29.09 ha) home range size corresponded to an egg-laying bird (JP4645; table 1.1 and table 1.2) and a chick-rearing bird (KGSK2033), which is consistent with general expectations for birds (e.g., Kolts and McRae 2017; Zurell et al. 2018). However, we also found marked differences between both nest-building males (LF0216 and LF1233 with home ranges of 14.86 ha and 24.71 ha, respectively). With a small sample of 5 individuals that differed in sex and breeding stage, we are limited in the strength of inference that can be made about how these factors impact range sizes.

Our data also revealed the existence of roosting activity in the Manzanillo forest and mangroves close to the sea (ranging from 0 m to 800 m). Darwin's finches typically aggregate during the non-breeding season to form large foraging flocks during the day (Schluter 1984). Our observations indicate that they may display gregarious behaviour also during the breeding season (except during incubation), even if roosting together at night requires birds to travel much longer distances than diurnal activities. This observation challenges the assumption that Darwin's finches roost in or close to their nests (e.g. <300 m; Boag and Grant 1984) and suggests that communal roosting may be advantageous to finches in general and non-incubating individuals in particular, although the exact benefits of roosts (e.g., reduced predation risk, foraging efficiency, or thermoregulation costs (Beauchamp 1999; Eiserer 1984; Lack 1968; Tebbich et al. 2010; Ward and Zahavi 1973)) remain to be explored.

1.5.2 Data quantity and quality ascertainment

Rarefaction curves of the minimum convex polygon reached a plateau at approximately 30 location points, indicating that moderate tracking effort is required to accurately calculate the home range size of a finch during the breeding season (figure A.6). This minimum number of fixes is similar to that reported for other breeding birds (Bechtoldt and Stouffer 2005; Camacho

et al. 2014), although more locations would probably be required for home range size estimation outside the breeding season due to flocking, post-fledging dispersal, or seasonal movements (Gula and Theuerkauf 2013). Our data also suggest that radio-tracking methods may be useful to collect enough data points even in the largely inaccessible landscape (i.e., dense vegetation, volcanic substrate) of the Galápagos (e.g., to infer the nest location based on diurnal activity locations; figure A.9). Most importantly, our data proved useful for shedding new light on key aspects of the natural history of Darwin's finches, such as their breeding behaviour, nest location, commuting behaviour, and habitat selection and use.

1.5.3 Identifying limitations of radio-tracking in finches

It is important to note that this is a pilot study aimed at providing preliminary data to test the utility of radio-tracking for improving understanding of movement ecology in Darwin's finches. Constraints on the duration of the tracking period due to the short (~ 3 weeks) battery life of miniature radio-transmitters restricted the volume of data that could be collected. This is a common limitation in telemetry studies of small, fast-moving birds, although its impact on home ranges and habitat selection estimates appears to be small compared to larger animals (Mitchell et al. 2019). In addition, we identified some challenges and limitations on telemetry specific to our study system. First, complex topography and dense vegetation in parts of the arid coastal zone represent a difficult environment to track finches. For example, we were unable to find the nest of the individual LF1234 (but see figure A.9). This limitation could be overcome using drones equipped with an antenna to track finches and with an onboard camera to film the location of the nest (Desrochers et al. 2018). A second limitation was the labour-intensive task of tracking finches with portable antennas in variable, but generally harsh, climatic conditions. A potential solution could be the implementation of automated radio tracking, consisting of a system of antennas distributed across the landscape, thus scanning a broader area with less effort (e.g., Cellular Tracking Technologies (CTT), Bridge et al. 2011; Motus, Taylor et al. 2017); or with an open source telemetry system (Gottwald et al. 2019). Such a network of antennas scattered in the landscape would be particularly useful for determining
the movement patterns of non-breeding finches flocking and moving long distances. Third, we observed tag removal by one individual (LF0126), which has also been identified as a limitation in other telemetry studies (Rechetelo et al. 2016). Of course, our tagging approach was temporary, with tag retention only required for long enough to complete the study (in our case three weeks). Finally, as is usually the case in radio-tracking studies, bearing error increased with distance of detection (between the observer and the radio transmitter), as well as with reduced orthogonality of bearings (Fuller et al. 2005). Here again, using drones could provide a solution by enabling access to terrain that is difficult for humans to traverse, thereby allowing shorter distance of detection and fully orthogonal bearings. From our experience, a drone used for mapping purposes in another study on the Galápagos islands seemed to be ignored by the finches (personal observations).

To summarize, although there are some constraints on the use of telemetry with Galápagos finches, we believe that all are surmountable and should not prevent researchers from studying the movement ecology of the finches at the individual level. We highly encourage the pursuit of this study and, for that reason, below we outline three long-standing questions about space use in finches that could be addressed using telemetry data.

1.5.4 Unanswered questions

What ecological factors influence finch's home range size and location?

Many factors can influence the space use of birds, such as food availability, habitat composition and configuration, population density, predator-prey interactions, human disturbance, topography, nesting site availability, climatic conditions, sex, age, social status, and flocking (Rolando 2002). In finches, territory size can change due to interrelated processes, such as fluctuations in rainfall (Grant 1999; Smith et al. 1978), food availability (Schluter 1984), and population densities (Boag and Grant 1984), although the effect of the spatial scale of environmental variation and movement remains to be examined. Obtaining accurate territory size (and home range) estimates at multiple spatial scales (e.g., from core to edge) should enable researchers to better understand the scalespecific mechanisms that shape territorial behaviour in these birds. On the other hand, post-fledging movements could be tracked to better understand the dispersal ecology of Darwin's finches (Gabela 2007). Using radio-transmitters for tracking non-breeding adults could also help determine how much flocking increases the chances of locating new food patches and when defending a patch of resources becomes more costly than searching for new patches (De León et al. 2014; Schluter 1984). Further, the Galápagos landscape is changing due to urbanization and agricultural intensification. Human-induced changes in the availability of resources might change the abundance and movement patterns of finches in certain environments, e.g., due to the introduction of fruits in agricultural areas (Swarth 1934), although tracking studies are needed to assess the true impact of these changes.

How does finch movement impact their ecological interactions with other taxa?

Movement is a key component shaping ecological interactions and coexistence of species (Jeltsch et al. 2013). For example, the cactus finch (*G. scandens*) is dominant over the medium ground finch (*G. fortis*; Boag and Grant 1984). Therefore, it is possible that, under certain social and ecological contexts (e.g., shortage of nest sites (Orr 1945) or nest-building material in humanaltered areas), some finches compete for breeding territories or adjust their social behaviour and/or home range size and location to local conditions, such as food availability, population density, and predation risk (Grant 1999; Kleindorfer et al. 2009). Home range size and overlap between species could be studied in relation to diet overlap to better understand the interspecific or intraspecific (with respect to the different beak morphotypes in *G. fortis*; Beausoleil et al. 2019) determination of their space use (Boag and Grant 1984).

Movement patterns in Darwin's finches can also be the basis of plant-animal interactions, for instance when granivorous finches disperse the seeds of the plants they use to build their nests (Camacho et al. 2018). Another application of telemetry on the finches could be to better understand the movement of finches in relation to the colonization and distribution of plants in the landscape, therefore shedding light on non-random seed dispersal by birds. Conservation biologists could benefit from this information as movement patterns of the finches could determine the spread of invasive plants (Buddenhagen and Jewell 2006; Camacho et al. 2018; Soria 2006).

Darwin's finches are becoming exposed to avian pathogens from other organisms such as

domestic chickens (*Gallus gallus*; Parker 2018; Wikelski et al. 2004). Tracking the movement of the potential hosts within islands can bring information on potential proximity of birds that are infected by introduced pathogens and further our understanding on the spread of diseases (Food and Agriculture Organization of the United Nations 2007). Therefore, studies gathering movement ecology information on finches could yield information about transmission of emergent imported diseases on the Galápagos affecting avian biodiversity.

What factors influence roosting behaviour in finches?

It has been noted that dense patches of *Opuntia* cacti in Daphne Major's crater were used as night roosts even for male finches holding territories (Boag and Grant 1984). However, our understanding of the roosting behaviour of Darwin's finches is limited and not much is known about the intrinsic and extrinsic factors driving variation in social behaviours. Communal roosting is relatively common in flocking birds (Beauchamp 1999; Eiserer 1984), and our observations suggest this behaviour is present in ground finches. Nevertheless, the extent to which roosting behaviour changes depending on the season (dry and wet) and life stage (breeding vs. non-breeding) remains unclear.

Further, a series of questions emerges from our observations. For example, does the type of roosting sites used differ in comparison to diurnal home ranges (Jirinec et al. 2016)? What are the fitness consequences of selecting a specific roosting location or habitat (for example, in relation to predation risk; Eiserer 1984)? Are there physiological and energetic advantages of selecting communal vs. solitary roosting sites? Do roosting sites in urban areas compared to natural environments differ in their characteristics? Is the communal roosting behaviour practiced only in coastal areas? How important is predation risk as a driving force for the evolution of roosting behaviour in insular ecosystems compared to continental ones (Eiserer 1984; Lack 1968)? Are roosting sites only used by *G. fortis* or shared with other species of finches? Is there a sex bias in roosting location?

The finches we tagged were roosting in the coastal zone of the island, which has a denser vegetation cover than the nesting sites. This could have implications regarding thermoregulation

costs and predation rates. Depending on within or between species interactions (e.g., dominance or the use of aggressive behaviour), there could be competition for higher quality positions within the roosting site, with outcomes determined by factors such as social structure (Mezquida et al. 2005; Smith et al. 2008).

To conclude, our study opens up new avenues of research to better understand the roosting behaviour and the movement ecology of Darwin's finches within islands. These can help understand the evolutionary dynamics of populations and complement our understanding of the ecology of the finches. The presence of urban and agricultural areas also provides a fertile ground to deepen our understanding of the effect of human activity on birds' behaviour.

1.6 Figures



Figure 1.1: Maps of home ranges for radio-tagged medium ground finches (a-e) at El Garrapatero on Santa Cruz Island, Galápagos. Each point represents the location of a finch



Figure 1.2: Jacobs' index showing direction of selection for each habitat type for each finch. The grey shading is only for distinguishing the habitat types.



Figure 1.3: Finches coming back to their roosting side 9 March 2019. The images were taken at about 18h10 near El Garrapatero's beach $(0^{\circ}41'38.54'' \text{ S}, 90^{\circ}13'16.53'' \text{ W})$. The video quality doesn't allow a proper finch count, but at least 50 finches were observed in about 5 min. (See https://ebird.org/hotspot/L3064040; Lalla 2019)

1.7 **Tables**

Date [†]	Band	Frequency (MHz)	Sex [¶]	Breeding stage	Tarsus (mm)	Mass (g)	Wing chord (mm)
2019-02-26	JP4645 [‡]	294	f	Laying eggs	21.92	21.6	69
2019-02-26	KGSK2033 [§]	191	f	Feeding young	20.71	19.7	68
2019-02-21	LF0216	154	m	Building nest	22.02	19.7	70
2019-02-26	LF1233	059	m	Building nest	22.31	26.1	79
2019-02-26	LF1234	206	f	Incubating	21.20	23.1	68

Table 1.1: Banding data for each Geospiza fortis captured

[†] Date when the finch was banded and/or a radio transmitter was deployed

[‡] Recaptured bird, first banded in 2013

[§] Recaptured bird, first banded in 2016

¶ m: male, f: female

Band	# days tracking	Duration of tracking period (days) [†]	# fixes [‡]	# of points [§]	Home range size 95% (ha)	Core area size 50% (ha)	MCP 100% (ha)	href smooth. ^{††}
JP4645	10	13	37	30	7.58	1.17	3.37	46.27
KGSK2033	10	15	41	23	29.09	6.37	17.25	76.54
LF0216	9	14	39	31	14.86	1.90	8.83	55.16
LF1233	7	8	48	29	24.71	4.13	9.50	67.41
LF1234	8	12	54	30	26.47	6.60	11.84	64.57
		Total	210	142	20.54	4.03	10.16	
		Total	219	143	$\pm 4.04^{\P}$	$\pm 1.11^{\P}$	\pm 2.25 ¶	

Table 1.2: Tracking parameters with home range and core area size estimates

[†] Number of days between the first and last tracking session (tracking span)

[‡] Number or bearings taken to bi-triangulate the position of the finches

[§] Including direct observations, 2019 capture location, and the location estimated from the fixes

¶ Mean \pm standard error (SE)

[#] Minimum convex polygon (MCP) estimation of the home range ^{††} Reference bandwidth smoothing (*href smooth.*), method of estimation of the smoothing parameter

Band	Habitat type	Proportion of habitat	Relocation number in	Expected number of	$oldsymbol{\chi}^2$	d	Proportion of observed locations	95% CI	Direction of selection	Jacobs' index
		in HR	habitat	relocations						
	Beach	0.032	1	0.96	0.001		0.033	0-0.118	Neutral	0.02
	Inland water	0.025	0	0.76	0.759		0.000	0-0	Negative	-
TDACAE	Manzanillo forest	0.158	1	4.75	2.957	0.072	0.033	0-0.118	Negative	-0.69
JF4040	Dry-forest	0.700	28	21.00	2.333		0.933	0.816-1.051	Positive	0.71
	Road paved	0.084	0	2.53	2.532		0.000	0-0	Negative	-1
	Total	1	30	30	8.58				I	
	Beach	0.124	5	2.86	1.596		0.217	0-0.439	Neutral	0.32
	Inland water	0.006	0	0.14	0.141	0.052	0.000	0-0	Negative	
	Manzanillo forest	0.430	15	9.90	2.631		0.652	0.396-0.908	Neutral	0.43
NG5N2033	Dry-forest	0.420	3	9.67	4.599		0.130	0-0.311	Negative	-0.66
	Road paved	0.019	0	0.43	0.431		0.000	0-0	Negative	-
	Total	1	23	23	9.40					
	Inland water	0.018	0	0.57	0.566		0.000	0-0	Negative	-1
	Manzanillo forest	0.428	4	13.28	6.483	0000	0.129	0-0.279	Negative	-0.67
LF0216	Dry-forest	0.511	27	15.85	7.850	100.0	0.871	0.721-1.021	Positive	0.73
	Road paved	0.042	0	1.31	1.309		0.000	0-0	Negative	-1.00
	Total	1	31	31	16.21					
	Beach	0.026	0	0.74	0.743		0.000	0-0	Negative	-1
	Inland water	0.020	0	0.58	0.582		0.000	0-0	Negative	-1
I E1733	Manzanillo forest	0.327	5	9.48	2.120	0.152	0.172	0-0.353	Neutral	-0.40
CC71 J71	Dry-forest	0.600	24	17.41	2.493		0.828	0.647 - 1.008	Positive	0.52
	Road paved	0.027	0	0.78	0.779		0.000	0-0	Negative	-1
	Total	1	29	29	6.72					
	Manzanillo forest	0.197	5	5.90	0.137		0.167	0.004-0.33	Neutral	0
I E1334	Dry-forest	0.781	23	23.42	0.008	0.255	0.767	0.582-0.952	Neutral	-0.04
+C71 J/1	Road paved	0.023	2	0.68	2.589		0.067	0-0.176	Neutral	0.51
	Total	1	30	30	2.73					

Table 1.3: Habitat selection analysis parameters

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Linking Statement 1

How animals move and interact with their environment has implications that generate ecoevolutionary dynamics. Chapter 1 contributed natural history information about the movement and space use of Darwin's finches. In particular, I showed how certain behaviors such as diurnal activities, nesting, and roosting change patterns of space use by exploiting different environments composed of diverse plant communities. Further, I discuss how telemetry can be used to answer questions about the behavior, ecology, evolution, and conservation of Darwin's finches. Extensions of this study could test if a fitness trade-off exists that would lead to character displacement of habitat preference (i.e., selection against habitat switching) or if there exists information-processing costs regarding search and efficiency of processing resources which would influence preference for a certain habitat. As shown in this study, space is an important factor involved in the ecology and evolution of Darwin's finches. However, this study does not bring a temporal perspective on the ecological and evolutionary factors involved in the speciation of Darwin's finches.

In the next chapter, I address questions regarding the temporal variation in disruptive selection of intermediate phenotypes in a population of Darwin's finches. In the theory of adaptive radiation, the formation of species is due to divergent natural selection, which is indistinguishable from disruptive selection when populations are speciating. However, for both, there will be a reduction of fitness of intermediate phenotypes in a population. I used a 9-year capture-mark-recapture dataset on a wild bimodal population of small and large morphs of medium ground finches (*G. fortis*) to determine how disruptive selection varies through time, but also to explore the associations between selection in different pairs of years and precipitation patterns at the study site.

"The whole landscape is a complex of the three elements [centripetal, centrifugal and linear selection], none in entirely pure form. To complete the representation of nature, all these elements must be pictured as in almost constant motion-rising, falling, merging, separating, and moving laterally, at times more like a choppy sea than like a static landscape—but the motion is slow and might, after all, be compared with a landscape that is being eroded, rejuvenated, and so forth, rather than with a fluid surface."

> George Gaylord Simpson, 1944 Tempo and mode in evolution.

Chapter 2

Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*)

This chapter is reproduced with permission from: M.-O. Beausoleil¹, L. O. Frishkoff², L. K. M'Gonigle³, J. A. M. Raeymaekers⁴, S. A. Knutie⁵, L. F. De León^{6,7}, S. K. Huber⁸, J. A. Chaves^{9,10}, D. H. Clayton¹¹, J. A. H. Koop¹², J. Podos¹³, D. M. T. Sharpe⁶, A. P. Hendry¹ and R. D. H. Barrett¹. 2019. Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*). *Proceedings of the Royal Society B: Biological Sciences* 286(1916):20192290.

Author affiliations:

- ¹ Redpath Museum and Department of Biology, McGill University. Montréal, QC. Canada
- ² Department of Biology, University of Texas at Arlington, Arlington, TX, USA
- ³ Department of Biological Sciences, Simon Fraser University, Burnaby BC V5A 1S6, Canada
- ⁴ Faculty of Biosciences and Aquaculture, Nord University, Bodø, Norway
- ⁵ Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA
- ⁶ Department of Biology, University of Massachusetts Boston, Boston, MA, USA
- ⁷ Centro de Biodiversidad y Descubrimiento de Drogas, Instituto de Investigaciones Científicas y Servicios de Alta Tecnología, Panamá, República de Panamá
- ⁸ Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA, USA

⁹ Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito, Quito, Pichincha, Ecuador

¹⁰ Galápagos Science Center, Puerto Baquerizo Moreno, Galápagos, Ecuador

¹¹ School of Biological Sciences, University of Utah, 257 South 1400 East, Salt Lake City, 84112 UT, USA

¹² Department of Biological Sciences, Northern Illinois University, 1425 W. Lincoln Hwy., DeKalb,
 IL 60115, USA

¹³ Department of Biology, University of Massachusetts, 221 Morrill Science Center, Amherst, MA, USA

2.1 Abstract

Disruptive natural selection within populations exploiting different resources is considered to be a major driver of adaptive radiation and the production of biodiversity. Fitness functions, which describe the relationships between trait variation and fitness, can help to illuminate how this disruptive selection leads to population differentiation. However, a single fitness function represents only a particular selection regime over a single specified time period (often a single season or a year), and therefore might not capture longer-term dynamics. Here, we build a series of annual fitness functions that quantify the relationships between phenotype and apparent survival. These functions are based on a 9-year mark-recapture dataset of over 600 medium ground finches (Geospiza fortis) within a population bimodal for beak size. We then relate changes in the shape of these functions to climate variables. We find that disruptive selection between small and large beak morphotypes, as reported previously for 2 years, is present throughout the study period, but that the intensity of this selection varies in association with the harshness of environment. In particular, we find that disruptive selection was strongest when precipitation was high during the dry season of the previous year. Our results shed light on climatic factors associated with disruptive selection in Darwin's finches, and highlight the role of temporally varying fitness functions in modulating the extent of population differentiation.

2.2 Introduction

Adaptive radiation can be envisioned as occurring on phenotypic fitness functions or surfaces that have multiple high-fitness peaks separated by low-fitness valleys (Simpson 1944; Arnold et al. 2001). While there are numerous studies of natural populations that infer such peaks and valleys (Schluter 2000), few consider the effects of temporal variation (Calsbeek et al. 2012). In birds, for example, the classic representations of fitness functions for Darwin's finches (Schluter and Grant 1984), African seed crackers (Smith 1993) and crossbills (Benkman 2003) do not provide estimates of disruptive selection across multiple years. Yet, temporal variation in fitness functions is very likely, which could facilitate or impede the process of adaptive radiation (Gosden and Svensson 2008). For instance, the presence of two discrete fitness peaks in one year might favour divergence; whereas a subsequent disappearance of those peaks might reverse any incipient divergence (Seehausen et al. 2008). Temporal variation in fitness functions might be common given that (i) estimates of directional selection can vary widely through time (Siepielski et al. 2017), (ii) many populations show substantial phenotypic changes on short time scales (Hendry et al. 2008) and (iii) several studies have documented speciation reversals, where formerly diverging species merge together again following environmental change (Seehausen et al. 2008; Kearns et al. 2018). However, direct assessments of temporal variation in fitness functions are generally lacking (Calsbeek et al. 2012).

Temporal variation in fitness functions could be driven by many factors including intrinsic dynamics, such as density or frequency dependence (Svensson and Sinervo 2000), or extrinsic factors, such as biotic or abiotic environmental change (Calsbeek et al. 2012). Hinting at the importance of one particular factor, Siepielski et al. (2017) found in a meta-analysis that 20–40% of temporal variation in directional selection could be explained by variation in precipitation. One context where variation in precipitation is expected to be particularly important is in neotropical environments with wet and dry seasons. These ecosystems can be subject to substantial interannual variation, most dramatically due to El Niño and La Niña events (Palmer and Pyle 1966). In such environments, many plants grow and reproduce predominantly during wet seasons; and so limited

rainfall within those seasons—as well as severe dry seasons—can lead to extended droughts that limit primary productivity and cause high mortality for primary consumers (Grant et al. 2000).

Two alternative predictions can be advanced for how the variation in precipitation could influence selection between alternative fitness peaks. On the one hand, harsh conditions strengthen selection against maladapted individuals; hence increasing the strength of disruptive selection between alternative peaks. This prediction infers that niche differentiation between competing species should be greater when resources are more limited (Grant et al. 1976; Smith et al. 1978). On the other hand, harsh conditions could increase competition among common phenotypes; hence lowering the heights of the fitness peaks—perhaps to the point that formerly discrete peaks are no longer separated by valleys. Indeed, many theoretical models (Dieckmann et al. 2004; Gavrilets 2004) and some empirical studies (Svensson and Calsbeek 2012) show that intense competition can reduce the heights of fitness peaks. To identify how variation in precipitation shapes evolutionary dynamics, we construct temporally variable fitness functions for a natural population of Darwin's finches.

2.2.1 Study system

The adaptive radiation of Darwin's finches is thought to have been driven largely by the availability of different food types, which is in turn influenced by spatial and temporal variation in climatic conditions (Grant and Grant 1993; Lack 1947). Accordingly, beak sizes of finches on different islands match the food types most readily available on those islands (Schluter and Grant 1984). Moreover, closely related species show exaggerated beak size divergence when inhabiting the same island, suggesting that competition enhances divergence through character displacement (Schluter and Grant 1984; Grant 1999). Thus, different finch species are thought to have evolved phenotypes that correspond to different fitness peaks separated by fitness valleys that are jointly shaped by local resource distributions and local interspecific competition.

Several observations suggest that Darwin's finches' fitness functions could be highly variable through time, potentially influencing their adaptive radiation. In particular, stochastic climatic

events—especially El Niño and La Niña—that shape rainfall in the Galápagos are known to strongly modify plant reproduction, and hence, the abundance and distribution of seeds available for granivorous ground finches (Abbott et al. 1977; De León et al. 2014). In drought years, with little rainfall during the wet season, the production of seeds is very low; whereas in wet years, with high rainfall during the wet season, seeds are usually produced in abundance (Grant and Grant 1981, 1989). Additionally, the dry seasons can vary from moderate amounts of rain to severe droughts with severe effects on the seed production. Inter-annual differences in seed production are known to have large effects on ground finches, which—during droughts—show high mortality (Grant and Grant 2011), greater niche differentiation (De León et al. 2014) and larger estimated directional coefficients (Grant 1985; Grant and Grant 2002). Hence, estimating selection from fitness functions in multiple years could be used to explore how temporal environmental variation shapes disruptive selection and, thus, acts to drive or impede adaptive radiation.

Although natural selection in Darwin's finches surely influences multiple traits (Grant and Grant 1993), much of the focus has been—for the seed-eating ground finches (*Geospiza* spp.)—on beak size and shape. Beak size (usually indexed as a linear combination of length, depth and width measurements) is highly heritable (Boag 1983; Boag and Grant 1978; Grant and Grant 1993, 1997, 2002) and is clearly polygenic, including associations with several candidate genes (Chaves et al. 2016; Lamichhaney et al. 2016). Beak size functions in both food processing and species recognition (Grant and Grant 1997; Huber et al. 2007), and hence represents a putative magic trait (Gavrilets 2004) that is under disruptive selection and influences reproductive isolation. Beak size correlates with diet (Abbott et al. 1977), bite force (Herrel et al. 2005), song features (Podos 2001), mate choice (Ratcliffe and Grant 1983) and selection (Grant and Grant 1993). Importantly, all of these effects and patterns are evident not only between species but also in the earliest stages of diversification within species (De León et al. 2012).

Of particular interest are sympatric beak size morphotypes within the medium ground finch (*Geospiza fortis*), observed currently at El Garrapatero and formerly at Academy Bay on Santa Cruz Island (De León et al. 2012). The smaller morph is similar in size to *G. fortis* on many other

islands (Lack 1947), including Daphne Major (Grant 1999). The larger morph is not found in many other locations and, in fact, verges on the size of the large ground finch (*Geospiza magnirostris*) on at least some other islands; whereas *G. magnirostris* on Santa Cruz Island are larger still (Lack 1947). Overall, the differences between sympatric morphotypes of *G. fortis* on Santa Cruz mirror among-species differences in diet, bite force, song features, mate choice, allelic variants in candidate beak genes (Chaves et al. 2016) and selection (Grant 1999; Hendry et al. 2006, 2009; Huber et al. 2007). Thus, the two *G. fortis* beak size morphotypes provide an excellent system for studying how selection can shape the early stages of diversification.

We used a 9-year dataset to identify associations among beak size, fitness and climate. Our primary focus was on the putative selective disadvantage of birds with beak sizes that are intermediate between the small and large morphotypes in the well-studied bimodal population of *G. fortis* at El Garrapatero (Grant 1999; Grant et al. 1976; Hendry et al. 2009; Lack 1947). Our first objective was to identify whether observable disruptive selection between the small and large morphotypes was evident across the 9 years—as was the case in an earlier study (Hendry et al. 2009) of a 2-year period in the same population.

Confirming that disruptive selection is indeed present, we determined the intensity of disruptive selection across years. Finding that the pattern of selection was variable, we next asked whether temporal variation in rainfall in dry or wet seasons predicted temporal variation in disruptive selection. Finally, we used this analysis to evaluate alternative ideas for how variation in precipitation might influence fitness functions.

2.3 Material and methods

2.3.1 Data collection and field study site

We captured individual birds of the medium ground finch (*G. fortis*) annually between 2003 and 2011 at El Garrapatero ($0^{\circ}41'22.9''$ S, $90^{\circ}13'19.7''$ W), an arid zone site on Santa Cruz Island in Galápagos, Ecuador (figure 2.1a,b). Captures took place between January and April, which generally corresponds to the wet season—although the amount of rainfall during this season varied among

years (dry season rainfall showing in figure 2.1c). The birds were captured in mist-nets placed across an area of about 20 hectares (figure 2.1b), with specific net locations determined by logistics and bird abundance. Captured birds were processed according to standard protocols (see supplemental material on page 198; De León et al. 2012; Grant 1999). We then measured, with digital callipers (precision ± 0.02 mm), each bird's beak length, depth and width. Three separate measurements were taken for each dimension on each bird and repeatability from our data, estimated with a type II ANOVA, has a mean of 92.8% (trait repeatability is as follows: width 96.5%, length 89.5% and depth 92.4%; Sokal and Rohlf 1995). We further increased precision and accuracy by using the median of the three measurements for subsequent analyses (De León et al. 2012).

We first pooled *G. fortis* across all years (supplemental material, table B.1) for principal component analysis (PCA) of the three beak traits (length, depth and width; figure 2.2; supplemental material, figure B.1) based on the covariance matrix because all beak traits were on the same scale (mm) and this ordination technique is consistent with previous work on Darwin's finches (Grant 1999). A correlation biplot is represented in figure 2.2. The first axis of variation (PC1) reflected overall beak size, as in previous work (see supplemental material; De León et al. 2012; Hendry et al. 2009). Subsequent analyses focused on this axis as our research questions were specifically related to beak size (see 2.2 Introduction on page 67).

We estimated annual dry-season rainfall (total amount of rain in millimetres from June through December; figure 2.1c) and wet-season rainfall (from January to May) at El Garrapatero using data from rain gauges at the town of Puerto Ayora 11 km to the southwest (Charles Darwin Foundation 2019). Rainfall was our focal climate variable because it is the main factor that affects plant reproduction and, hence, the abundance of food resources for ground finches (Grant 1999). Over the time frame of our study, the mean rainfall was 185.4 mm during the wet season (January through May) versus 96.37 mm during the dry season (June through December), with El Niño conditions present in 2004–2005, 2006–2007 and 2009–2010.

2.3.2 Statistical model to estimate selection coefficients

We calculated apparent survival (Gilroy et al. 2012) for individual birds between pairs of years, assuming perfect detection (Kellner and Swihart 2014). We did not account for variation in recapture rates (Kellner and Swihart 2014) because we did not want to overfit our models. Apparent survival between two specific years was specified as a bird being recaptured in the latter or any subsequent year. Thus, some of the birds inferred to have died might simply have remained uncaptured or might have emigrated (Kingsolver and Smith 1995; Pradel et al. 1997). Although mortality and emigration are different biological processes, emigrating birds are nevertheless permanent losses to the local population and, hence, have the same consequences for selection within a generation. As with most other such studies, we also assume that recapture probability is constant and not affected by the phenotypes in question, and that prior-capture history does not affect survival and recapture probabilities.

To describe the overall primary contributors to variation in fitness (apparent fitness, as above), we first calculated a generalized linear model (GLM) with apparent fitness as a function of the explanatory variables beak size (PC1) and dry season rainfall across all years. The model included both linear and quadratic terms for beak size (PC1), as well as an interaction between these terms and total rainfall in the previous year (supplemental material, tables B.2 and B.3). To capture flexible shapes in the fitness function, we next characterized the fitness function in each year individually without imposing an *a priori* mode of selection. Hence, we used a generalized additive model (*gam* in the MGCV R package), which is a generalized linear model with the addition of smoothing functions of covariates (using a penalized smoothing of a thin plate regression spline; figure 2.3; Hendry et al. 2009; R Core Team 2019; Schluter 1988; Wood 2017). The GAM is here intended as a heuristic (we do not focus on p-values) for inferring whether the fitness function has a convex shape consistent with disruptive selection against intermediate phenotypes. Details about the choice of smoothing parameter of the GAM can be found in the supplemental material, figure B.2 and table B.4.

The fitness functions estimated from splines revealed at least two peaks in each year,

consistent with an ongoing process of disruptive selection (figure 2.3). We next used a custom script (available on GitHub: https://github.com/beausoleilmo/temporal_fitness_landscape; Beausoleil et al. 2019) to extract the phenotypic values between the two maxima identified in each year. Using these between-peak trait values, we calculated nonlinear selection coefficients in order to estimate statistical significance specifically for the putative disruptive part of the fitness function (as in Hendry et al. 2009). Note that these selection estimates potentially include indirect selection caused by correlated traits; especially body size, given its high correlation with beak size (in our data, the Pearson correlation of mass (g) versus PC1 was r = 0.789). Fortunately, our hypotheses relate to total selection acting on beak size, which includes any indirect selection. The resulting estimates of disruptive selection were obtained via logistic regression (GLM) with a linear and a quadratic term to model both linear and nonlinear selection in each year (Janzen and Stern 1998; Kingsolver and Smith 1995). In these logistic regressions, the subset (between-peak) of PC1 values used was first standardized to a mean of 0 and standard deviation of 1. The selection coefficient was standardized by dividing absolute fitness by mean fitness as in Janzen and Stern (1998).

Because the logistic models represent only a subset of the phenotypic distribution, whereas the GAM represents a more comprehensive fitness function across morphospace, we kept only the logistic models that showed similar fits to the functions obtained from the spline models (this criterion led to the exclusion of the logistic coefficient for 2007). A Wald test was used to assess the significance of the raw logistic regression parameters. Given that we expected the quadratic term to be positive (meaning that the curve deflects upward, which is the pattern expected for disruptive selection), we halved the p-value to get a one-tailed test (Hendry et al. 2009). Our focal interest is the association between environmental variation and the effect size of the selection coefficient; these coefficients are generally weak and often non-significant for disruptive selection (Kingsolver et al. 2001). Quadratic coefficients from the logistic model were then converted to their linear equivalents according to Janzen and Stern (1998) and were then doubled (Lande and Arnold 1983; Stinchcombe et al. 2008). To assess logistic model fits, we report the pseudo- R^2 (table 2.1) and the goodness of fit results from the Hosmer–Lemeshow tests (Hosmer Jr et al. 2013).

Finally, we related the between-peak quadratic coefficients to climate data, and thereby tested for correlations between environmental variation and disruptive selection between the peaks. Here, we modelled a weighted $(1/SE^2)$ linear regression between peak quadratic coefficients as predicted by the standardized mean = 0 and standard deviation = 1 across years. We identified three non-exclusive hypotheses regarding which period of rainfall would be most relevant to disruptive selection in a given year. First, wet season rainfall might be most important because low precipitation in the wet season would mean a protracted period of drought when combined with the dry season, thus potentially amplifying the strength of disruptive selection. Second, dry season rainfall might be most important if particularly severe dry seasons exacerbate fitness differences during the most strenuous time of year, again amplifying disruptive selection. Third, dry or wet season rainfall during the previous year might better predict the strength of selection than rainfall during the focal year, as rainfall in the previous year might influence the number of seeds in the seed bank during the subsequent year, as well as the number of birds competing for those seeds (Grant and Grant 2002). Hence, we performed four separate analyses, relating disruptive selection in a given year to wet season or dry season rainfall in that year (no lag) or in the previous year (1-year lag). We assessed the significance of each regression at $\alpha = 0.05$; however, we emphasize that this climate association analysis is exploratory and hence our primary objective was to generate hypotheses for future formal testing as opposed to performing definitive tests of these hypotheses.

2.4 Results

We captured and measured 1073 *G. fortis* from 2003 to 2011 at El Garrapatero (supplemental material, table B.1). The first principal component (PC1) explained 90.67% of the total variation (figure 2.2) and represented variation in beak size—as in previous analyses (Grant 1999; Huber and Podos 2006). A consistent feature of the fitness functions inferred from the splines was the presence of two fitness peaks for *G. fortis* beak size (figure 2.3; solid black lines)—a pattern strongly implying disruptive selection between the peaks. The fitness maxima generally corresponded to peaks of the phenotypic distributions of the two beak size morphotypes—a finding also consistent

with a hypothesis of disruptive selection (figure 2.3 and tables 2.2 and 2.3). However, the strength of disruptive selection between the peaks varied considerably among years (figure 2.3). We therefore next focused on birds with beak sizes between the two fitness maxima in each year. One year (2007–2008) was excluded owing to a low sample size for these intermediate birds (n = 13, with only four surviving individuals) that also led to inconsistency between the splines and the logistic estimates. The Hosmer-Lemeshow goodness of fit tests indicated that the GLM model was a good fit for the data in years except 2006–2007 (table 2.1). The quadratic term from the GLM was strong and significant in three years (2004–2005, 2005–2006 and 2009–2010; tables 2.1 and 2.2), but weak and not significant in the other three years. Similar results were obtained based on classic logistic regression approaches (table 2.2).

We detected an association between disruptive selection and climate (figure 2.4). A GLM including all years with sufficient data (2005, 2006, 2008, 2009, 2010, 2011) revealed a negative relationship between overall survival and cumulative dry-season rainfall the year before selection occurred (z-value = -1.97, p-value = 0.049; supplemental material, table B.3). That is, greater dry season rainfall led to higher overall finch mortality. The weighted linear regression revealed a positive association between quadratic selection coefficients and cumulative rainfall over the previous dry season. Thus, we can infer that greater dry season rainfall generated stronger disruptive selection between the beak size morphotypes, although the association is weak and only marginally significant (slope = 0.27, $R^2 = 0.67$, p-value = 0.048; figure 2.4b and table 2.3). No other periods of rainfall were predictive of disruptive selection (figure 2.4a,c,d).

2.5 Discussion

High variability in beak size for *G. fortis* on Santa Cruz Island has been repeatedly noted by researchers for nearly a century (Lack 1947), with recent investigators specifically noting bimodal distributions of beak size measures (Hendry et al. 2006). A persistent question is how the two beak morphotypes have been maintained without having either fused back together or diverged into distinct species. Our approach here was to use a long-term mark-recapture dataset to investigate

how changes in the consistency of disruptive selection might influence the degree of divergence at El Garrapatero, a relatively undisturbed site on Santa Cruz Island. We also explored one possible mechanism for changes in the strength of disruptive selection over time: variation in rainfall. Our analysis revealed temporally variable disruptive selection, with half of the years showing significant disruptive selection between fitness peaks (reduced fitness of birds with intermediate beak size) and half of the years showing non-significant disruptive selection. Additionally, interannual variation in selection was partly associated with the extent of rainfall in the previous year's dry season, with increased rainfall leading to greater overall finch mortality and stronger disruptive selection.

2.5.1 Temporal variation and its causes

Many studies have reported inter-annual variation in selection, especially for directional selection (Siepielski et al. 2009). By contrast, few have investigated temporal variation in disruptive selection between fitness peaks in natural populations (but see Morrissey and Hadfield 2012). Variation in this form of selection is expected to be crucial in the early stages of adaptive divergence, ecological speciation and adaptive radiation (Nosil 2012; Schluter 2000). To gain some additional insight into the importance of disruptive selection between fitness peaks, we calculated the lowest predicted fitness (apparent survival) between peaks in relation to the predicted fitness of birds on the two phenotypic optima. From this estimate, the depth of the fitness valley was greatest between years 2009-2010, where fitness in the valley bottom was 10.0% lower than fitness of the small-morph peak and 50.0% lower than fitness of the large-morph peak, as inferred from the splines in figure 2.3. This pattern differs most markedly from the fitness estimates for 2006–2007, where fitness in the valley bottom was 4.4% lower than fitness on the small-morph peak and 11.3% lower than fitness on the large-morph peak. These extreme alternatives for valley depth exceed the range of the few estimates that have been recorded for other sympatric morphotypes (or young species) in natural settings. For instance, comparative values for other systems are 6.6–30.7% for pupfish (figure 2, durophage-generalist major axis in Martin and Wainwright (2013)) and 8.3-44.1% and for juvenile African seedcrackers (figure 1, lower mandible length (mm) in Smith (1993)).

Our exploratory analysis suggests that climate may be a possible driver of the pronounced temporal variation in selection on G. fortis at El Garrapatero, with disruptive selection strongest in years with relatively high rainfall during the previous dry season. At first glance, this might seem to contradict previous work showing that selection on Darwin's finches is strongest during drought periods—as documented on Daphne Major (Grant and Grant 1993, 2014, 2002). However, the previous work focused on directional selection in a unimodal population, whereas we focused on disruptive selection in a bimodal population; hence, the different outcomes are not necessarily contradictory. Yet, two aspects of this outcome remain unanswered: (i) why does higher (rather than lower) rainfall generate strong disruptive selection, and (ii) why is this effect delayed by a 1-year lag? For the first question, we hypothesize that drier conditions could increase intraspecific competition among similar phenotypes, and hence more dramatically reduce the survival of common phenotypes at the phenotypic modes (Bolnick 2004a). That is, drier conditions could shrink the peaks more than the valleys, hence generating weaker disruptive selection. For the second question, we hypothesize that higher dry season rainfall in a given year will lead to higher reproduction and higher offspring survival in that year, hence making competition more severe during the next year's dry season (Grant and Grant 2002). These are hypotheses emerging after analysis; yet, they suggest the value of reconsidering several standard assumptions of the factors that favour diversification in this classic system for studying adaptive radiation.

We recognize that our results are particular to the specific range of climate conditions that took place during our study, and thus might not translate to even more extreme conditions. For instance, the maximum dry season rainfall at El Garrapatero during our study was 110.1 mm (2004) and the minimum was 56.6 mm (2010). These levels are far from the extremes observed at other time periods or at other locations. Dry-season rainfall at our study site has previously been as high as 968.0 mm (1983) and as low as 23.8 mm (1980). Similarly, dry season rainfall is estimated to have been near zero during the key periods of strong selection on Daphne Major (Grant and Grant 1993, 2014, 2002). Additional years of sampling that span such extremes will be needed to see if our main result, that disruptive selection is stronger when conditions are less harsh in the previous

year, holds (or is perhaps amplified) under even more extreme conditions.

2.5.2 Consequences of temporal dynamics in disruptive selection

Disruptive selection is one mechanism that can maintain phenotypic and genetic variation (Bolnick 2004b; Dieckmann and Doebeli 1999; Rueffler et al. 2006). Hence, persistent disruptive selection provides a reasonable hypothesis for the maintenance of divergent beak size in Santa Cruz *G. fortis*. Other mechanisms likely contributing to intraspecific variation for finches in general, and perhaps Santa Cruz *G. fortis* in particular, include hybridization between species and spatial variation in selection coupled with gene flow within species (Vagvolgyi and Vagvolgyi 1990). These processes have not been explicitly quantified for our study population but, overall, gene flow among islands is relatively low in relation to the size of resident populations (Grant 1999; Lawson et al. 2019) and movement within an island is also somewhat restricted. For instance, our long-term data include only one individual out of 8417 birds (0.01%) that moved between our two study sites separated by only 10 km. It has been argued that disruptive selection on a resource polymorphism is a key contributor to speciation and adaptive radiation (Skúlason and Smith 1995). It may be that El Garrapatero finches represents an ongoing analogue of this situation that likely drove the adaptive radiation of Darwin's finches in the first place (De León et al. 2012).

What might be the influence of temporal variation in strength of disruptive selection? Generally, it has been argued that temporal variation in directional selection will maintain variation within populations (Sasaki and Ellner 1997). However, the basic logic applied in studies of directional selection might not apply to temporal variation in disruptive selection. Instead, consistently strong disruptive selection would be expected to maintain variation more robustly than would a temporal mix of strong and weak disruptive selection, given that the latter would promote fusion. In the arid coastal zones of the Galápagos, the climate is typically harsh, with prolonged dry seasons resulting in strong selection. In an El Niño year, rain is expected to release disruptive selection in that year but perhaps, as shown here, enhance it in a subsequent year. Hence, temporal variation in selection could be a critical factor in the process of adaptive radiation.

We were interested not just in variation in selection but also in the degree to which it generates and maintains alternative morphs: reasonably discrete large and small beak size morphs with relatively few intermediates. To exemplify the difference in these two inferences, consider a comparison of two populations on Santa Cruz Island: the El Garrapatero *G. fortis* population that is the focus of this study, and the Academy Bay *G. fortis* population located approximately 10 km to the southwest. Both are highly variable in beak size (Hendry et al. 2006), but only the former is currently bimodal, meaning that it is characterized by a statistically defensible dip in the beak size frequency distribution between large and small beak size morphs (Hendry et al. 2006). The reason for this difference between sites seems to be that recent human influences at Academy Bay have modified what finches feed on (De León et al. 2018)—and thereby reduced or eliminated disruptive selection. Available data do not allow estimates of disruptive selection can be strong even at relatively undisturbed sites. Perhaps this variation, especially the periods of weak disruptive selection, explains the fact that the two morphs do not appear to be progressing towards the status of separate species—even at the relatively undisturbed El Garrapatero site.

2.6 Whither now?

Few studies have quantified temporal variation in disruptive selection in natural populations, and we are not aware of any that have done so for bimodal populations diverging intra-specifically on the same axes as the adaptive radiation of which they are a part. A main finding of our study is that such selection is, in fact, variable in strength—leading to questions about its influence on adaptive radiation. An important next stage seems to be a theoretical one. We need to determine how the mean strength of disruptive selection, as well as the effect of temporal variation in that selection, should shape adaptive radiations. Consistently strong disruptive selection is likely to promote divergence (Schluter 2000), but the influence of temporal variation around that mean is uncertain. A first question might be the extent to which symmetrical variation around that mean should enhance or degrade divergence. In short, does a given high value contribute more or less
to divergence than a correspondingly low value. Other important parameters might be the specific distribution of symmetrical variation around the mean (e.g. does a skewed distribution enhance or degrade divergence) and the nature of autocorrelation (do runs of similar deviations from the mean enhance or degrade divergence). Finally, asymmetry about the mean might be critical: that is, do extreme high levels of disruptive selection have a stronger effect on promoting divergence than similarly extreme low levels of disruptive selection on constraining divergence. Future studies that investigate temporal variation in fitness surfaces of multiple morphotypes or species will help to answer these questions, and thus improve our understanding of the potential for ecological speciation and adaptive radiation.

2.7 Figures



Figure 2.1: Map of the major Galápagos Island. (a) Puerto Ayora, Santa Cruz Island and El Garrapatero (black dots). (b) Santa Cruz island (black dot is El Garrapatero). Inset: the polygon includes the sampling site at El Garrapatero. Maps from Google Maps (2017; Web Mercator projection, datum WGS84). (c) Climatic data from Puerto Ayora, located 10 km from El Garrapatero (Charles Darwin Foundation 2019). The y-axis corresponds to the cumulative dry season rainfall per year (June through December). Data from OpenStreetMap, http://osm2.carto. com/viz/feeaae54-9e89-11e4-ba3a-0e853d047bba/public_map (accessed 8 October 2019).



Figure 2.2: Correlation biplot of the PCA based on beak dimensions (length, width and depth) for *G. fortis.* The first axis of variation (PC1) represents variation in beak size (bigger beaks have higher scores) and PC2 represents variation in beak shape (pointer beaks have higher scores). The grey axes (top and right) are scaled for the trait vectors (light grey), whereas the black axes (bottom and left) are scaled for the points. The black ellipses refer to the 95% expectation-maximization algorithm for mixtures of univariate normal (Benaglia et al. 2009). Illustrations of heads of finches are reproduced from (Schluter 2000).



Figure 2.3: Fitness functions for *G. fortis* at El Garrapatero across 6 years of data (larger-beaked birds have $PC1 \ge 0.2$). Solid black lines show the generalized additive model (GAM) results (dashed black line represents 1 *SE*). Solid blue lines (and dotted blue lines, quadratic functions that open upward) show quadratic logistic models (GLM) computed between the fitness function's peaks. Black and blue dots represent individual birds. Solid grey shades (right y-axes) represent the density distribution of phenotypes. The blue dotted line is the GLM function beyond the data used to run the models.



Figure 2.4: Between-peak quadratic coefficients as a function of cumulative rainfall. Valley quadratic coefficients obtained from fitness functions of the logistic regression. Rainfall is standardized across years to a mean = 0 and standard deviation = 1. (a,b) The weighted $(1/SE^2)$ linear relationship between dry season's precipitation and valley quadratic coefficients without a lag (a) and a 1-year lag (b), respectively. Weighted linear relationship between precipitation in the wet season and valley quadratic coefficients without a lag (c) and a 1-year lag (d), respectively. Each point is labelled with the year in which precipitation was calculated from, for a selection interval. The error bars are selection coefficient standard error in table 2.2. Line with a significant slope is shown.

2.8 Tables

Table 2.1: Estimates from the logistic models and Hosmer–Lemeshow goodness-of-fit tests (HL GOF). The estimates correspond to the GLM models in figure 2.3. The numbers in square brackets are the confidence interval calculated for 1 *SD* The range data PC1 column refers to the interval of the PC1 scores between the two fitness peaks. Asterisk indicates significance at p < 0.05.

	HL GOF		Estimates					Deviance				
Year	χ^2	p- val.	Int.†	p- val.	Linear term (x)	p- value	Non- linear term (x^2)	p-val.	Model	Null	Pseudo- R ²	Range PC1
2005- 2006	3.83	0.87	-1.83 [-2.48; -1.18]	0.00*	$ \begin{array}{c} -0.51 \\ [-1.07; \\ 0.04] \end{array} $	0.13	0.44 [0.01; 0.87]	0.04*	110.15	113.27	0.03	[0.06, 1.33]
2006- 2007	16.44	0.04	-2.74 [-3.42; -2.05]	0.00*	0.07 [-0.53; 0.67]	0.85	0.15 [-0.29; 0.58]	0.29	92.82	93.66	0.01	[-0.04, 1.62]
2008- 2009	11.81	0.16	-1.83 [-2.82; -0.85]	0.00*	-0.51 [-1.27; 0.25]	0.27	0.29 [-0.44; 1.01]	0.26	50.92	52.16	0.02	[0.25, 1.51]
2009- 2010	4.45	0.81	-2.57 [-3.26 ; -1.88]	0.00*	-0.42 [-1.00; 0.15]	0.23	0.70 [0.28; 1.12]	0.00*	100.09	112.29	0.11	[0.10, 1.85]
2010- 2011	8.60	0.38	-2.09 [-2.74 ; -1.45]	0.00*	-0.23 [-0.66; 0.21]	0.39	0.25 [-0.09; 0.59]	0.11	78.13	80.38	0.03	[-0.35, 0.57]

[†] Int.: Intercept

Table 2.2: Yearly between peak quadratic coefficients (GLM) estimated for birds between the two fitness peaks previously estimated by the GAM (figure 2.3). β and γ are the linear and quadratic standardized between peak quadratic coefficients. The 95% confidence interval (CI) is calculated for a one-tailed test (p-values were divided in two). N0 and N1 are the sample sizes for apparent mortality (0) and apparent survival (1). N is the total sample size. Asterisk indicates significance at p <0.05.

Year	β average [95% CI]	β SE	β p-value	γ average [95% CI]	γSE	γ p-value	N0	N1	\mathbf{N}^{\dagger}
2004-2005	-0.15 [-0.46; 0.16]	0.19	0.21	0.87 [0.07; 1.68]	0.49	0.04*	50	20	70
2005-2006	-0.39 [-0.82; 0.03]	0.26	0.07	0.68 [0.02; 1.34]	0.40	0.05*	88	23	111
2006-2007	0.06 [-0.49; 0.62]	0.34	0.43	0.27 [-0.54; 1.08]	0.49	0.29	172	13	185
2008-2009	-0.41 [-1.02; 0.20]	0.37	0.14	0.46 [-0.70; 1.62]	0.70	0.26	44	11	55
2009-2010	-0.32 [-0.75; 0.11]	0.26	0.12	1.04 [0.42; 1.67]	0.38	0.01*	114	20	134
2010-2011	-0.19 [-0.55; 0.17]	0.22	0.20	0.42 [-0.14; 0.99]	0.34	0.11	84	14	98

[†] Sample size of individuals between the fitness peaks from figure 2.3 (blue points only).

Table 2.3: Coefficients of linear regressions of the amount of rain and between peak quadratic coefficients for the same years as the between peak quadratic coefficients (2004, 2005, 2006, 2008, 2009 and 2010) and with a 1-year lag (2003, 2004, 2005, 2007, 2008 and 2009). The regressions are shown in figure 2.4. Asterisk indicates significance at p < 0.05.

		Intercept [95% CI]	SE	p- value	Quadratic coefficients [95% CI]	SE	p- value	<i>R</i> ²	N	DF [†]
Dry	Same year	0.66 [0.39; 0.93]	0.14	0.01*	0.04 [-0.25; 0.33]	0.15	0.792	0.02		
season	1 year lag	0.61 [0.45; 0.77]	0.08	0.00*	0.27 [0.09; 0.44]	0.09	0.048*	0.67	6	4
Wet season	Same year 1 year lag	0.64 [0.40; 0.88] 0.63 [0.43; 0.83]	0.12 0.10	0.01* 0.00*	-0.16 [-0.47; 0.15] 0.19 [-0.01; 0.39]	0.16 0.10	0.37 0.132	0.20 0.47		

[†] DF: Degrees of freedom

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Linking Statement 2

In chapter 2, using long term capture-mark-recapture data, I quantified the relationship between beak size and fitness in a single species (*G. fortis*) to extract nonlinear selection coefficients in different pairs of years. As an exploratory analysis, I then used the selection estimates and found an association with precipitation patterns. I found that the fitness landscapes are dynamic from year to year. Moreover, stronger selection was associated with more rainfall in the previous year's dry season. It can also be hypothesized that competition within or between species can have an impact on the heights of fitness peaks which could impact the strength of selection. This study sheds light on the factors that are involved in the maintenance of species divergence. However, this was done using only one species. Since Darwin's finches are currently speciating, hybridizing, and competing with each other, to fully understand the forces governing their evolutionary change it is necessary to characterize a fitness landscape that includes all of the related species in this community.

For chapter 3, I constructed and characterized the beak phenotypic fitness and adaptive landscapes of a community of ground finches found at the study site El Garrapatero on Santa Cruz Island. This difficult endeavor has never been achieved in natural populations, in particular not in a scenario where there is an almost uninterrupted gradient of trait morphologies between currently diverging species. Here, I test the hypothesis that fitness and adaptive landscapes are expected to be rugged, i.e., with multiple peaks and valleys, due to divergent natural selection. These landscapes are constructed when phenotypic variation is associated with fitness at the individual level or averaged at the population level. I estimated a global fitness landscape with apparent survival calculated from a 17-year dataset of individually marked, captured, and recaptured Darwin's finches. I also used population genetics to characterize the fitness landscape of this community of finches and developed a new metric called 'prospective selection' to explore potential evolutionary constraints that could impede movement across the landscape towards adaptive peaks. "The machine model for life has led biologists to ignore one of the common characteristics of many physical systems, their dependence on initial conditions. [...] All species that exist are the result of a unique historical process from the origins of life, a process that might have taken many paths other than the one it actually took. Evolution is not an unfolding but an historically contingent wandering pathway through the space of possibilities."

> Richard C. Lewontin, 2000 The triple helix

Chapter 3

The fitness landscape of a community of Darwin's finches

This chapter is republished from the article: M.-O. Beausoleil¹, P. L. Carrión¹, J. Podos², C. Camacho³, J. Rabadán-González⁴, R. Richard¹, K. Lalla⁵, J. A. M. Raeymaekers⁶, S. A. Knutie⁷, L. F. De León⁸, J. A. Chaves^{9,10}, D. H. Clayton¹¹, J. A. H. Koop¹², D. M. T. Sharpe¹³, K. M. Gotanda^{1, 14, 15, 16}, S. K. Huber¹⁷, A. P. Hendry¹ and R. D. H. Barrett¹. 2023. The fitness landscape of a community of Darwin's finches. *Evolution* 77(12):2533-2546, licensed under Attribution 4.0 International (CC BY 4.0)

Author affiliations:

- ¹ Redpath Museum and Department of Biology, McGill University, Montréal, QC. Canada
- ² Department of Biology, University of Massachusetts Amherst, MA, United States
- ³ Department of Ecology and Evolution, Estación Biológica de Doñana—CSIC, Sevilla, Spain

⁴ Observation.org Spain, Almensilla, Seville, Spain

- ⁶ Faculty of Biosciences and Aquaculture, Nord University, Bodø, Norway
- ⁷ Department of Ecology and Evolutionary Biology, Institute for Systems Genomics, University of

⁵ Department of Natural Resource Sciences, McGill University, Sainte-Anne-de-Bellevue, QC. Canada

Connecticut, Storrs, CT, United States

⁸ Department of Biology, University of Massachusetts Boston, Boston, MA, United States

⁹ Department of Biology, San Francisco State University, San Francisco, CA, United States

¹⁰ Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito, Quito, Ecuador

¹¹ School of Biological Sciences, University of Utah, Salt Lake City, UT, United States

¹² Department of Biological Sciences, Northern Illinois University, DeKalb, IL, United States

¹³ Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, United States

¹⁴ Department of Biological Sciences, Brock University, St. Catharines, On. Canada

¹⁵ Department of Zoology, University of Cambridge, Cambridge, United Kingdom

¹⁶ Département de biologie, Université de Sherbrooke, Qc. Canada

¹⁷ Virginia Institute of Marine Science, William and Mary, Gloucester Point, VA, United States

3.1 Abstract

Divergent natural selection should lead to adaptive radiation—that is, the rapid evolution of phenotypic and ecological diversity originating from a single clade. The drivers of adaptive radiation have often been conceptualized through the concept of 'adaptive landscapes'; yet formal empirical estimates of adaptive landscapes for natural adaptive radiations have proven elusive. Here we use a 17-year dataset of Darwin's ground finches (*Geospiza* spp.) at an intensively-studied site on Santa Cruz (Galápagos) to estimate individual apparent lifespan in relation to beak traits. We use these estimates to model a multi-species fitness landscape, which we also convert to a formal adaptive landscapes. We then assess correspondence between estimated fitness peaks and observed phenotypes for each of five phenotypic modes (*G. fuliginosa*, *G. fortis* [small and large morphotypes], *G. magnirostris*, and *G. scandens*). The fitness and adaptive landscapes show five and four peaks, respectively, and, as expected, the adaptive landscape was smoother than the fitness landscape. Each of the five phenotypic modes appeared reasonably close to the corresponding

fitness peak, yet interesting deviations were also documented and examined. By estimating adaptive landscapes in an ongoing adaptive radiation, our study demonstrates their utility as a quantitative tool for exploring and predicting adaptive radiation.

3.2 Introduction

The concept of adaptive landscapes has been conceptually compelling yet empirically elusive. The phenotypic version of these landscapes (as opposed to their genetic counterpart developed by Wright [1932]) depicts multivariate relationships between mean population fitness and mean phenotype, which then—in conjunction with additive genetic (co)variances—can predict the progress and outcome of adaptive radiations (Simpson 1944; Lande 1976; Schluter 2000; Arnold et al. 2001; Hendry 2017). Adaptive landscapes are generally expected to be 'rugged'—with multiple peaks of high fitness separated by valleys of lower fitness (Schluter 2000). Adaptive radiation is often fueled by ecological speciation, which occurs when divergent natural selection splits an ancestral species occupying one fitness peak into new populations that bridge fitness valleys and occupy new fitness peaks (Schluter 2000; Nosil 2012; Hendry 2017). Partly as a consequence of this adaptive divergence, reproductive isolation then evolves among the descendent populations (Schluter 2000). This process then repeats to generate a larger adaptive radiation composed of multiple reproductively isolated species each occupying a different fitness peak on the adaptive landscape (Schluter 2000; Nosil 2012).

It has proven difficult to characterize adaptive landscapes in wild populations, and we therefore have a limited understanding of the fitness peaks and valleys expected to shape adaptive radiation (Fear and Price 1998; Gavrilets 2004; Svensson and Calsbeek 2012a). In principle, data are required on individual fitnesses for the full range of phenotypes characterizing the existing species—as well as any phenotypic 'gaps' between them that might not be occupied by existing phenotypes. The resulting individual 'fitness landscape' then needs to be converted to a formal 'adaptive landscape' by calculating mean fitness across an expected distribution of phenotypes for populations (conceptually) centered at every possible location on the individual fitness landscape

(Schluter 2000; Arnold et al. 2001). The conversion between these two landscape types is needed because theory has shown that the evolution of mean phenotypes should proceed in the direction of the steepest increase in the *population mean fitness*, with an attendant bias dictated by the structure of the genetic covariance matrix (Lande 1979; Fear and Price 1998). Therefore, to predict the dynamics of adaptive radiation, it is necessary to describe not just the individual fitness landscape but also the surface of mean phenotypes and mean fitness: that is, the adaptive landscape. Accomplishing these tasks is such a tall order that a formal adaptive landscape has never been estimated for an adaptive radiation in its natural environment.

Lacking formal estimates of adaptive landscapes, several proxies have been developed (Schluter 2000; Hendry 2017). For instance, estimates of phenotypic selection in natural populations can be used—with numerous assumptions—to infer the location of fitness peaks and curvature of the adaptive landscape in the vicinity of existing phenotypes (Smith 1993; Estes and Arnold 2007; Beausoleil et al. 2019). Furthermore, expected fitness for phenotypes in the gaps between existing populations can be inferred by generating 'missing' phenotypes through simulated morphologies (Raup 1967; McGhee Jr. 2006; Tseng 2013), phenotypic manipulations (Sinervo et al. 1992), hybridization (Martin and Wainwright 2013; Arnegard et al. 2014), or reciprocal transplants (Nagy 1997; Nagy and Rice 1997). Finally, performance-based expectations can be used to translate resource distributions into expected fitness functions across the range of phenotypes (Schluter and Grant 1984; Benkman 2003; see Stayton 2019 and Holzman et al. 2022 for performance surfaces). Studies using these proxies for adaptive landscapes have supported some expectations laid out in the ecological theory of adaptive radiation. In particular, the phenotypic distributions of at least some species pairs are centered on different fitness peaks and separated by fitness valleys that arise from different environments defined by resources, predators, parasites, or competitors (reviews: Schluter 2000; Hendry 2017).

Although studies using the above proxies have inferred rugged genotype or phenotype fitness landscapes (Schemske and Bradshaw 1999; Pfaender et al. 2016; Martin and Gould 2020), several uncertainties continue to surround the concept, interpretation, and application of adaptive

landscapes, and even the individual fitness landscapes that underpin them. First, key aspects of many fitness landscape estimates might be unrealistic because they were (a) generated in controlled experimental settings (Benkman 2003; Martin and Wainwright 2013; Arnegard et al. 2014; Martin and Gould 2020); (b) estimated at one location and then projected to other locations (Schluter and Grant 1984); or (c) based on only one species with multiple morphotypes, such as Red Crossbills (Loxia curvirostra; Benkman 1993, 2003) or Black-bellied Seedcrackers (Pyrenestes ostrinus; Smith 1990; Smith and Girman 2000). Second, fitness landscapes are rarely estimated over more than a single time frame (e.g., one season or one year) at any particular location, even though selection is expected to vary through time in accordance with changing conditions (Schluter 2000; Siepielski et al. 2009; Beausoleil et al. 2019). As a result, we still have only a rudimentary understanding not only of adaptive landscapes, but also their underlying individual fitness landscapes—especially for multiple species within natural adaptive radiations over multiple years (but see Martin and Gould 2020). Thus, our main goal in the present study is to estimate the fitness landscape thought to underlie the adaptive landscape for Darwin's ground finch species (*Geospiza* spp.) at a single location over nearly two decades (2003-2020). We then use the estimated fitness landscape to consider theoretical expectations and previous empirical assertions regarding the topology of fitness and adaptive landscapes.

3.2.1 Study system

Darwin's finches started to radiate on the Galápagos about 1.5 million years ago (Petren et al. 2005; Lamichhaney et al. 2015, 2016); however, radiation of the ground finch (*Geospiza*) group was more rapid and recent, perhaps starting between 100,000 and 400,000 years ago (Lamichhaney et al. 2015). The primary phenotypic driver of this radiation at all phylogenetic levels is thought to be variation in beak (and body) size and shape (Lack 1947; Bowman 1961; Grant 1999). In particular, beak dimensions are highly heritable (Boag 1983), are influenced by large effect genes (Chaves et al. 2016; Lamichhaney et al. 2016), are linked to resource consumption (Schluter and Grant 1984; De León et al. 2014), contribute to assortative mating (Ratcliffe and Grant 1983; Huber et al.

2007; Podos 2010), and show extensive variation linked to individual fitness (Grant and Grant 1995; Hendry et al. 2009; Beausoleil et al. 2019). Other traits are surely also involved in the radiation but work to date suggests that changes in beak dimensions have played a primary role.

Here we focus on an intensively-studied ground finch community at the relatively undisturbed location of El Garrapatero, Santa Cruz island, Galápagos. The four species of ground finch at this site—and at nearby sites on Santa Cruz—generally manifest five phenotypic modes (Lack 1947; Ford et al. 1973; Hendry et al. 2006; Foster et al. 2008; Beausoleil et al. 2019; figure C.1). First, the cactus finch (Geospiza scandens) has a long and pointy beak that it uses for consuming the nectar, pollen, and seeds of cactus plants in the genus Opuntia (Grant 1999). Second, the small ground finch (Geospiza fuliginosa) has a small and blunt (i.e., not elongated like G. scandens) beak that it uses for cracking small seeds of a diversity of plant species (De León et al. 2014). Third, the large ground finch (Geospiza magnirostris) has a large and blunt beak that it often uses for cracking large and hard seeds of a few key plant species (De León et al. 2014; Carvajal-Endara et al. 2020). Fourth, the medium ground finch (Geospiza fortis) manifests two beak size modes (small and large 'morphs') that fill out the distribution between G. fuliginosa and G. magnirostris (Hendry et al. 2006; Foster et al. 2008; De León et al. 2014; Beausoleil et al. 2019). These two morphs appear to partition the middle of the seed size and hardness distribution along the same diet and performance axis that separates them from their smaller and larger congeners (De León et al. 2010, 2011). The evolutionary origin of these two morphs is uncertain, but hybridization with G. magnirostris is probably involved (Chaves et al. 2016).

Our intensive work on the ground finch community at this location affords a rare opportunity to estimate fitness landscapes in a natural system. Specifically, although five peaks are evident in the beak size and shape distribution, the presence of birds with intermediate beaks produces a continuum of phenotypes, allowing us to infer a fitness landscape across nearly the entire range of trait variation. Furthermore, our 17-year (2003-2020) mark-recapture dataset allows us to integrate viability selection and inferences about lifespans across a wide range of environmental conditions, from very wet El Niño years to very dry La Niña years (Beausoleil et al. 2019; figure C.2).

3.2.2 Our goals

Using our long-term data set of the five phenotypic modes across four species of Darwin's ground finches at El Garrapatero, we examine (a) features of the fitness landscape, and (b) correspondence between those features and the phenotypic distribution.

Features of the fitness landscape

The basic dynamic underlying adaptive divergence is that different environments select for different combinations of trait values best suited for those environments (Darwin 1859; Simpson 1944; Lack 1947). Hence, the fitness landscape for finch beak traits is expected to have peaks separated by valleys or surrounded by 'moats' (Schluter 2000). That is, the fitness landscape should not be flat, nor should it be a simple plane or saddle that lacks defined peaks. Furthermore, the fitness landscapes underlying adaptive *radiations* should be 'rugged,' with multiple fitness peaks at different combinations of trait values (Schluter 2000). What remains uncertain, however, is just how many peaks are available to a given adaptive radiation (Schluter 2000; Nosil 2012; Hendry 2017). The typical expectation might be that as many peaks exist as do species (more about this below); yet it is also possible for multiple species to evolve on a single fitness 'ridge' (Schluter 2000). We here test the classic expectation by modeling a fitness landscape across the entire range of data and species.

Correspondence between fitness and phenotypes

Adaptation is expected to drive the evolution of populations and species such that their phenotypes become localized near peaks on the fitness landscape (Schluter and Nychka 1994; Schluter 2000; Arnold et al. 2001). However, how many peaks are 'occupied' by species (see the above expectation), and how close those species' phenotypes are to the peaks, is typically uncertain (Schluter 2000; Estes and Arnold 2007; Hendry 2017). With regard to the second uncertainty, it has been variously argued that phenotypic distributions should closely match fitness landscapes (Schluter 2000; Estes and Arnold 2007) or that various constraints (e.g., gene flow, genetic correlations, environmental change) cause substantial maladaptation such that mean phenotypes will often be

'far' from fitness peaks (reviews: Brady et al. 2019a,b). We here address these uncertainties by estimating various measures of the distance between phenotypic modes and different peaks on the fitness landscape.

Our previous work on natural selection in this study system sets the stage for the present expanded effort. First, Hendry et al. (2009) showed that, in drought years (2004 to 2006), viability selection disfavored individuals between the two *G. fortis* beak size modes (i.e., they recorded disruptive selection between the modes). This viability selection also disfavored the largest and smallest individuals of that species, thus suggesting stabilizing selection around each beak size mode within this species. Second, Beausoleil et al. (2019) analyzed additional years of data and showed that disruptive selection between the *G. fortis* beak size modes varied through time in a manner that was partly predictable based on the amount of rainfall in the preceding year. Both of those studies took a single-species approach to the fitness landscape, thus limiting inferences about adaptive radiation of the ground finch community as a whole. Here we use an even longer time series and a multi-species approach to estimate the fitness landscape and thus inform our understanding of the process of adaptive radiation.

3.3 Methods

3.3.1 Long term data

From 2003 to 2020, we used mist nets to capture ground finches at El Garrapatero (Santa Cruz, Galápagos, Ecuador; $(0^{\circ}41'22.9'' \text{ S}, 90^{\circ}13'19.7'' \text{ W};$ figure C.3A). The specific net locations were chosen for accessibility; that is, they were situated in relatively open areas within a larger 0.43 km² study site (figure C.3B). Sampling took place in the typical finch breeding season (January–April), with year-to-year variation in the dates and duration of sampling (figure C.4; table C.1) that reflected logistical constraints. In most years, effort was directed at ensuring that all ground finch species were a part of the study; however, in the earliest years (2003-2009), effort was primarily focused on *G. fortis*. Hence, the relative numbers of captured birds of the different species do not necessarily reflect variation in natural patterns of relative abundance.

Captured finches were fitted with individually-numbered aluminum or Monel metal leg bands. Each bird was then measured for beak length, depth, and width (the classic measurements used to infer variation in this radiation; Grant 1999)—always with calipers having a precision of 0.01 mm (further details appear in De León et al. 2012). In many cases, each measurement was taken three times and the median value was used for subsequent analyses—thus reducing measurement error. The mean repeatability (intra-class correlation coefficient) of beak trait measurements (length, depth, and width) based on the same birds captured at different times was 0.92. Repeatability was calculated from birds with three measurements by the same observer using a random effect of bird band number in the rptR package (Stoffel et al. 2017; version 0.9.22). Only individuals for which we obtained all three beak measurements (length, depth, and width) were retained for subsequent analyses (n = 3428; table C.2).

The four recognized species (*G. fuliginosa*, *G. fortis*, *G. magnirostris*, and *G. scandens*) were identified based on classic visual assessment (Grant 1999), which we have confirmed to be very reliable (Foster et al. 2008). To further assign birds of the medium ground finch (*G. fortis*) to one of the two 'morphs' or 'modes' (Hendry et al. 2006), we used an expectation-maximization algorithm model from the mixtools R package based on the first principal component (beak size) calculated from the three beak traits of all species (Benaglia et al. 2009; version 1.2.0; see Beausoleil et al. 2019). Note, however, that the phenotypic distribution is continuous, and so birds in the valley between the two modes could not be reliably assigned to one or the other 'morph'. Furthermore, although the distributions for small *G. fortis* versus *G. fuliginosa* are relatively discrete (i.e., a small gap exists between them; figure C.1; figure C.5), the distribution for large *G. fortis* grades continuously into *G. magnirostris*, again indicating that intermediate birds could not be reliably assigned to one or the other species. However, these ambiguities do not impact our analyses as we are considering the entire phenotypic distribution across all species.

3.3.2 Converting capture history into a fitness metric

We estimated the individual fitness for each bird from its capture history. One approach here could have been a year-by-year survival estimate—as indeed we have employed in previous work that focused on the species (G. fortis) over a subset of the years (2003-2011) that had by far the largest sample sizes (Beausoleil et al. 2019). Here, however, we needed the best possible survival-based fitness surrogate across all species, some of which had low sample sizes in any given year. Thus, to achieve our community-wide fitness landscape, we here instead used the 'apparent lifespan' of a bird as the best obtainable surrogate for fitness; and, indeed, lifespan is known to be a major determinant of fitness variation in Geospiza (Grant and Grant 2000, 2011). We estimated apparent lifespan as the last year a bird was captured minus the first year that bird was captured. Only captures of adult birds were included; 28 individuals were first caught as juveniles, but later became adults and were then analyzed as adults. This apparent lifespan estimate is thus a minimum (when rounded to number of years) of the true lifespan of a bird; that is, most birds would have been alive for at least one year before their first capture and would continue living for an unknown period of time after their last capture. Note that our fitness surrogate thus does not discriminate between mortality and emigration but, fortunately, both processes are functionally equivalent at the level of the population: that is, both represent the loss of individuals from the local area. We focused our fitness landscape estimates on two traits: beak length and beak depth. The reasons were twofold. First, we could retain the original trait values in the analysis, which allows representation of the fitness landscape using raw trait values that also correspond to published estimates of additive genetic (co)variances (See section 'Prospective selection' below on page 109; Boag 1983). Second, these two traits have been identified as key targets of selection in finches (Boag and Grant 1984; Price et al. 1984; Schluter 2000). Beak width was not analyzed because the Pearson correlation between beak depth and beak width was very high (r = 0.97, p < 0.001). By contrast, the correlation between beak length and depth was much lower (Pearson correlation r = 0.74, p < 0.01)—and therefore both traits (and their combination) were informative.

We note, however, that many papers analyze all three traits based on their re-orientation into

two primary principal component analysis (PCA) axes. Indeed, many of our previous papers on this system have taken that approach (Hendry et al. 2006, 2009; Chaves et al. 2016; Beausoleil et al. 2019). Therefore, as a supplement, we also estimated the fitness landscape for the two first principal components describing beak size and shape (respectively) based on the combination of beak length, depth, and width. We used the vegan package (Oksanen et al. 2022; version 2.6-4) to calculate the principal components on the three beak dimensions across all birds included in the analysis. The thin plate spline generalized additive models (GAM) generated the fitness landscape ($f(\mathbf{z})$), with apparent lifespan against beak size (PC1) and beak shape (PC2) as previously described in the main text except for the thin plate regression spline, which had 4 and 19 dimensions for the bases (k) of the smooth function and the interaction smooth function, respectively.

3.3.3 Fitness landscape model

We decided to estimate a single fitness landscape that integrates information from all birds across all years—as opposed to year-specific or climate-specific surfaces. The reasons were threefold. First, evolutionary differences on the relevant scale of inference (i.e., the distribution of beak traits in a community of finches) is a function of the long-term 'average' surface, as opposed to year-specific surfaces. Second, by leveraging all of our data into a single fitness landscape estimate, we hoped to obtain a comprehensive long-term 'best' estimate of the surface—as opposed to less precise year-specific estimates. Finally, our fitness measure is an estimate of lifespan, which necessarily spans multiple years for many birds, and so cannot be parsed into subsets of those years. For year-specific estimates based on annual survival for part of this fitness landscape (*G. fortis* for the years 2004-2011), we refer the reader to Beausoleil et al. (2019).

To generate the single integrated fitness landscape $(f(\mathbf{z}))$, we plotted apparent lifespan (W, expected fitness, estimated as above) against individual beak length and beak depth (\mathbf{z}) . We started with a model-free estimate by calculating the natural-logarithm of mean fitness by mean phenotype in phenotypic 'windows' (bins) of 0.14 mm (figure 3.1A). Binning of individual fitness values smooths the landscape from the raw data and makes it possible to diagnose some key features.

Second, we used the individual fitness estimates and beak traits in thin plate spline generalized additive models (GAM) with a Poisson response variable, applying the smooth function *s* as an interaction between traits and the *gam* function in the mgcv package (version 1.8-39; Wood 2003; Wood et al. 2013, 2016; R Core Team 2023). Note that GAMs are a modern flexible approach to studying complex fitness landscapes (Martin and Gould 2020; Patton et al. 2022) that have largely replaced the formerly favored projection pursuit regressions (Schluter and Nychka 1994; figure C.6), with the latter technique also being more focused on dimension reduction which was not necessary here given our focus on only two traits. The curvature of the function was estimated using smoothing parameters determined by restricted maximum likelihood (REML), with an extra term to allow a penalty of 0 (removing this option did not change the results; figure C.7) in a thin plate regression spline with 4 and 27 dimensions for the bases (*k*) of the smooth function and the interaction smooth function, respectively.

To then examine correspondence between the fitness landscape peaks and the five phenotypic modes, we developed a function to locate the fitness peaks, which then could be compared to the finch modes as mean trait values. Specifically, we calculated phenotypic Euclidean distances between the fitness peak and the phenotypic mean of each mode, as well as the angle of each Euclidean distance vector counterclockwise from the positive side of the x-axis, representing beak length. These Euclidean distances represent the shortest distances in two-dimensional phenotypic space between the fitness peaks and the phenotypic means.

3.3.4 Adaptive landscape estimate

Adaptive landscape estimation requires the conversion of an individual fitness landscape (as above) to a landscape of mean fitnesses (\overline{W}) for a population with a given phenotypic mean (\overline{z}) and variance (Fear and Price 1998; Schluter 2000). To make this conversion, we simulated—across the entire phenotypic range—a hypothetical population with a bivariate normal distribution with a mean (standard deviation) beak length and beak depth across species of 12.42 mm (0.67 mm) and 11.02 mm (0.69 mm), respectively and a correlation of r = 0.39 (mean coefficients of variation [standard deviation divided by mean] of 5.4% and 6.2% for beak length and beak depth). We used *rnorm_multi* function from the faux package (DeBruine 2021; version 1.2.0; note that when we used the phenotypic distribution of the small morphotype of *G. fortis*, it did not significantly change the adaptive landscape compared to the one with simulated data, see figure C.8). We generated a 90x90 point-grid (the distance between each point of the grid was 0.13 mm (beak length) and 0.17 mm (beak depth)) covering the phenotypic space of each trait. We then centered the hypothetical population at the mean of the two phenotypic distributions (\bar{z}) on each point on the grid (Schluter 2000). Finally, we calculated the mean fitness values (\bar{W}) based on their expected fitness f(z) from the fitness landscape (spline model) on the transformed (link) scale for each point on the grid (see Animation S1 online and figure C.12).

3.3.5 Prospective selection

An evolutionarily-informed estimate of the distance between population phenotypes and adaptive peaks can be calculated as the amount of selection that would be required to complete an adaptive shift to that peak. We performed this calculation using the multivariate equation of evolutionary phenotypic change, where the vector of changes in mean trait values ($\Delta \bar{z}$) is a product of the additive genetic variance-covariance matrix (G) for those traits and the vector of selection gradients (β) acting on those traits. That is, $\Delta \bar{z} = G\beta$ (Lande 1979; Schluter 1984, 2000). Rearranging this equation for species in an existing adaptive radiation gives what Schluter (1984) called 'retrospective selection' ($\Delta \beta = G^{-1} \bar{z}_b - G^{-1} \bar{z}_a$), where the subscripts 'b' and 'a' represent the phenotypic values of different populations. Using this approach, Schluter (1984, 2000) estimated the amount of selection that would have been required in the past (hence 'retrospective') to generate the phenotypic differences that currently exist among species in the finch radiation. In our case, we used the approach to estimate the amount of selection that would be required for each phenotypic mode to reach its nearest adaptive peak (hence 'prospective' which we note as β_p). In our cases, ($\Delta \bar{z}$) was the distance between the bivariate trait mean of each of the five phenotypic modes and the nearest bivariate phenotypic optimum on the individual fitness landscape. For G, we used the genetic variances and covariances for *G. fortis* estimated in Boag (1983)—the same values used by Schluter (1984, 2000). The resulting *G*-transformed beak trait differences in Euclidean space represent the net selection gradients that would be needed to bridge the distances between the current phenotypic means and their nearest fitness peaks on the individual fitness landscape. Note that this approach is simply a way of providing a genetic context for phenotypic distances and is not intended to estimate the actual selection that would occur during such evolution. In particular, the approach requires a number of restrictive assumptions, including constancy of the *G* matrix, that all relevant correlated traits are included, and that the difference in population means is genetically based. The code for the analyses is available at the Borealis dataverse (Beausoleil et al. 2023) https://doi.org/10.5683/SP3/0YIWSE and on GitHub https://github.com/beausoleilmo/adaptive.landscapes.finches.

3.4 Results

Of the 3428 individuals analyzed in our study, 3038 (88.6%) were captured only once, whereas 390 birds were captured across multiple years (fitness >0). Minimum lifespans of these birds ranged from 1 to 12 years (table C.2). The species with the highest proportion of recaptured individuals in the dataset was of the small morphotype of *G. fortis* (40.4%), whereas the lowest proportion of individuals were *G. magnirostris* (1.5%; table C.2).

The GAM-estimated individual-based fitness landscape is shown in figure 3.1B, and its standard error is shown in figure C.9. To select the appropriate topology for this landscape, we designed a model including a smoothing term for each trait and an interaction between the two traits. We started with the smallest dimension parameter (k, an arbitrary number chosen by the user to reflect the non-linearity in the data; it defines the number of basis functions used to calculate the smooth line in GAMs) for each smoothed function of the traits and incrementally increased this parameter until the model showed the simplest peaked landscape. We compared this model to a model without the interaction and to another model with only the intercept. The significant smoothing term in the model was the interaction between beak length and beak depth (p <<0.01; 20.27 effective degrees of freedom; table C.3). That is, the smoothed model was much better

supported than a similar model including only the intercept (the difference in AIC between the intercept model without smoothing and the smoothed model was $\Delta AIC = 192.04$, where a lower AIC (for the smoothed model) indicates a better-fit model; likelihood ratio tests with *p* <<0.01, difference in deviance = 238.65; table C.4). Therefore, the rest of the analyses used the model with the main effects and the interaction between the two beak traits.

3.4.1 Features of the fitness landscape

The individual fitness landscape estimated for beak length and depth revealed five peaks, each separated from adjacent fitness peaks by fitness valleys (figure 3.1B). In a number of cases, those valleys were deep. Consider, for instance, the fitness peak nearest to *G. scandens*. In a straight line (in Euclidean phenotypic space) from that peak to each of the other peaks (figure 3.2A; table C.5), fitness declined by 84.08% (minimum fitness toward the peak nearest *G. magnirostris* relative to the maximum fitness of *G. scandens*), 86.58% (toward the peak nearest the large morph of *G. fortis*), 47.74% (toward the peak nearest the small morph of *G. fortis*), and 71.13% (toward the peak nearest *G. fuliginosa*). The fitness valley was also especially deep between the two peaks nearest the *G. fortis* beak size morphs: wherein fitness declined by 60.64% moving from small *G. fortis* toward large *G. fortis*, and by 48.48% moving in the other direction. By contrast, the fitness valley was shallow—indeed, almost absent (17.04%)—between the peak nearest *G. fuliginosa* and the peak nearest the small morph of *G. fortis*.

The basic 'rugged' property of this individual fitness landscape was conserved in an alternative representation based on principal components of beak 'size' and 'shape' (figure C.10). In this supplementary analysis, PC1 can be interpreted as beak size (loadings in absolute values for beak length = 7.3, depth = 9.0, width = 6.9 and variance explained by the first axis being 88.3%), with greater values indicating larger beaks; and PC2 can be interpreted as beak shape (loadings in absolute values for beak length = 4.0, depth = 2.2, width = 1.4 and variance explained being 10.9%), with greater values indicating pointier beaks. Using these PCA scores, a fitness landscape with three major peaks was apparent (figure C.10). Finally, when converting the focal fitness landscape for

beak length and depth (based on individual phenotypes and fitnesses: figure 3.1B) to an adaptive landscape (based on simulated population mean phenotypes and predicted fitnesses), many of the same peaks remained evident, although relative differences between peak heights and valley depths were much reduced—as expected from such conversions (Schluter 2000). In short, all analyses support the expectation that fitness landscapes—and the adaptive landscapes they underpin—are characterized by multiple fitness peaks separated by fitness valleys of varying depth.

3.4.2 Correspondence between fitness and phenotypes

Mean trait values for the five phenotypic modes (i.e., the four species in which *G. fortis* separates in two distinct morphs) were situated reasonably close to their corresponding fitness peaks. For instance, the mean Euclidean distance between bivariate (beak length and depth) means (for the five modes) and their nearest peaks on the fitness landscape was 0.90 mm (range 0.64-1.62 mm; figure 3.1; table 3.1). By comparison, Euclidean distances among the various species phenotypic means averaged 5.69 mm (n = 10, range 2.94-10.94 mm; table C.6). Thus the *shortest* distances among phenotypic modes exceeded the *largest* distances between each mode and their nearest fitness peaks.

Analyses of 'prospective selection' ($\boldsymbol{\beta}_{P}$) that adjust phenotypic distances for the genetic (co)variances of traits yielded similar—but further nuanced—conclusions (figure 3.3). For instance, $\boldsymbol{\beta}_{P}$ values for the distance between the five modes and their nearest fitness peaks averaged 1.59 (range 0.50-3.50; table 3.1). By contrast, $\boldsymbol{\beta}_{P}$ values for the distance between means of the five modes averaged 3.27 (range 0.37-7.47; table C.6). In summary, each phenotypic mode was closer to its nearest peak than it was to the other phenotypic modes; but the differences in this comparison were diminished as we accounted for genetic correlations (figure 3.3).

Although fitness estimates required use of the entire data set across all years (see Methods on page 106), phenotypic means could be estimated for each year, thus allowing us to consider whether the above inferences about phenotype-to-fitness correspondence showed noticeable temporal variation. We find that trait mean values for each of the five modes were reasonably similar

across years—such that year-specific estimates were always oriented (in phenotypic space) in a similar direction and to a similar distance from the nearest fitness peak (figure 3.4). Variation across years was highest for *G. magnirostris*, presumably due—at least in part—to its small sample size.

3.5 Discussion

3.5.1 Features of the fitness landscape

As expected from the ecological theory of adaptive radiation (Schluter 2000; Nosil 2012), the individual fitness landscape that we estimated for a community of ground finches showed a number of distinct peaks separated by fitness valleys. Depending on how the traits were represented, the number of estimated peaks varied from five (beak length vs. beak depth; figure 3.1) to three (PC1 vs. PC2; figure C.10). For the rest of this discussion, we focus on the five-peaked landscape because selection presumably acts more directly on the original traits (beak length and depth) than on statistically-generated linear combinations of traits (PCs). However, we acknowledge that some of the more detailed inferences that follow are sensitive to the ways in which traits are represented. The general inferences, however, are robust to such variation. When reading the following, bear in mind that the inferences we present do not depend on which modes are considered to be separate 'species' (we use the traditional designations), nor the specific manner in which those modes originated (e.g., via fission from a single ancestral source or fusion via hybridization between ancestral sources).

We also converted the above fitness landscape estimated for individual traits and fitnesses to an adaptive landscape for mean traits and fitnesses (figure 3.1). Again as expected from theory (Schluter 2000; Arnold et al. 2001), the adaptive landscape was smoother than its underlying fitness landscape. The reason is that adaptive landscapes average individual fitnesses across a range of phenotypes—and so, relative to the fitness landscape, the peaks sink (because they include lower fitness values from either side of the peak) and the valleys rise (because they include higher fitness values from either side of the valley). This smoothing of the adaptive landscape tends to obscure some features of the fitness landscape, and is perhaps why previous analyses of adaptive radiations in vertebrates have not converted fitness landscapes to adaptive landscapes (Benkman 1993; Smith 1993; but see Schluter 2000) or have instead generated resource-based adaptive landscapes (Schluter 1984). In our case, conversion of the individual fitness landscape to the adaptive landscape eliminated the valley between the large morph of *G. fortis* and *G. magnirostris* (more about this later) but retained the rest of the topology. Thus, our analysis shows that most key features of the fitness landscape are retained in the adaptive landscape, providing support for the empirical quantification of a function (the phenotypic adaptive landscape) that has thus far been mostly theoretical, heuristic, or aspirational for field studies of adaptive radiations (Schluter 2000; Arnold et al. 2001; Hendry 2017).

3.5.2 Correspondence between fitness and phenotypes

We found that phenotypic modes of the *Geospiza* are close to, but not directly on, their respective fitness peaks (figure 3.1). The first part of this conclusion (i.e., 'close to') supports the basic premise of the ecological theory of adaptive radiation that different resources (here different seed types) generate multiple phenotypic fitness peaks that promote diversification into different species (Schluter 1984; Grant 1999; Schluter 2000; Arnold et al. 2001; Nosil 2012; Hendry 2017). The second part of the conclusion (i.e., 'not directly on') also is not unexpected (Brady et al. 2019a,b), and affords an opportunity to discuss the reasons why adaptation (and adaptive radiation) might be constrained in various ways. Some such constraints can be considered with our current analysis and by reference to previous studies within our study system.

First, introgression among species can constrain divergence from reaching the species' respective optima and, indeed, interbreeding and introgression are known to occur between *G. fortis* and each of the other *Geospiza* species as well as between the two *G. fortis* morphs (Grant and Grant 1992; Grant 1993, 1999; De León et al. 2010; Lamichhaney et al. 2015; Grant and Grant 2021). This potential constraint predicts that species means will be displaced from fitness optima in the direction of the species from which introgression occurs. Such a pattern was not evident in our data for *G. fuliginosa*, *G. scandens*, or *G. magnirostris* (figure 3.1B). By contrast, phenotypic modes for the *G. fortis* morphs did deviate from their fitness peaks in the direction of groups with which they

hybridize (the large morph of *G. fortis* toward the small morph of *G. fortis*, and the small morph of *G. fortis* toward *G. scandens*)—but these deviations were among the smallest observed (figure 3.1B). Introgression therefore seems unlikely to explain why the phenotypic modes were displaced to one side of their fitness peaks. Indeed, an increasing body of work argues that introgression is a creative rather than constraining force in adaptive radiation in general (Grant and Grant 2019) and in Darwin's finches specifically (Lamichhaney et al. 2015).

Second, as with introgression (above), gene flow across populations within species can bias adaptation away from local optima (Hendry and Taylor 2004; Bolnick and Nosil 2007; Garant et al. 2007). Indeed, we expect considerable immigration and emigration for our 'open' study site. (Note that emigration and mortality are functionally equivalent at the level of a population and so both are relevant to selection at that level.) Supporting this point, previous analyses have shown high levels of gene flow and connectivity across the island of Santa Cruz, at least for *G. fortis* (Petren et al. 2005; De León et al. 2010; Galligan et al. 2012). It seems unlikely, however, that movement of birds across sites could be a primary driver of the deviations we observed between phenotypic modes and fitness peaks. In particular, the deviations we observed were not generally in the direction of another known population of each species (Kleindorfer et al. 2006; Foster et al. 2008; Carrión et al. 2022; See supplemental material on page 215 and figure C.11).

Third, genetic constraints can cause trait means to deviate from adaptive optima (Arnold et al. 2001; Svensson and Calsbeek 2012a). For instance, ground finches generally show a positive genetic correlation between beak length and depth (Boag 1983; Price et al. 1984; Grant and Grant 1994), which could constrain evolution along orthogonal axes. We do not favor this possibility as an explanation for the deviations we observed between phenotypic modes and their estimated fitness optima. Consider our analysis of 'prospective selection' (figure 3.3), which scales trait differences by genetic correlations. In particular, when ignoring such correlations (i.e., Euclidean distances), the phenotypic distance between each phenotypic mode and the nearest optima (peak) was much smaller than phenotypic distances across modes. However, when including such correlations (i.e., estimates of 'prospective selection'), the same type of comparison yielded a much smaller contrast. In other
words, accounting for genetic correlations 'shrinks' the distance among different phenotypic modes more than it shrinks the distance between each mode and its nearest fitness peak. This result suggests that diversification across the species was not strongly constrained by genetic (co)variances, except perhaps for *G. scandens*, which lies off the main axis of variation in having evolved long but shallow beaks (Grant 1999); and yet *G. scandens* did, in fact, evolve. As such, it seems unlikely that genetic (co)variances constrain each of the species from reaching their respective fitness peaks.

Although each of the above constraints could contribute to the observed offsets between phenotypic modes and fitness peaks, none are likely an important causal factor. Instead, we suggest that the primary cause of observed deviations from fitness peaks is merely methodological. This suggestion comes from our observation that all displacements of mean phenotypes from fitness peaks in our analyses always fell in the same direction, an outcome that implies some sort of methodological bias (figure 3.4). One possible bias is that adaptive radiation can be strongly influenced by rare events (De León et al. 2012; Grant and Grant 2014), in which case fitness peaks estimated in some years might not reflect the fitness peaks that drove adaptive radiation in the first place. However, our dataset was long term (17 years) and integrated across very diverse ecological conditions (figure C.2). Another possibility is that our fitness surrogate was biased in capturing only one of several key fitness components. For instance, we only used longevity, whereas fitness is also determined by reproductive success, which perhaps favors different trait values. It would take an entirely new and different set of data to address this possibility. Beyond this possible bias, some imprecision is also present in our estimates, owing principally to low sample sizes (especially for G. magnirostris) and low recapture rates (see supplemental material; figure C.4 and figure C.9). Resulting imprecision adds noise to our estimates of the fitness landscape, such that the true landscape might be much more refined than the one our data captures.

3.5.3 Future research and prospectus

The structure of fitness and adaptive landscapes depends on features of the environment, such as local resources and competition (Schluter 2000) that vary dramatically across space. Hence,

it would be informative, using similar techniques to those applied here, to construct fitness and adaptive landscapes for finch communities on other islands. Daphne Major is an obvious candidate as previous work has estimated lifetime fitness for finches at that site, which differs dramatically in environment and phenotype from our study site (Grant and Grant 2002, 2011, 2014; Carrión et al. 2022). Another informative situation would be the community of ground finches at Academy Bay, Santa Cruz, where human influences have been inferred to strongly alter resources, selection, and adaptation (Hendry et al. 2006; De León et al. 2011, 2018). These formal landscapes then also could be compared to the resource based landscape presented by Schluter (1984). Similar analyses could be applied to data for other adaptive radiations of birds and other organisms. A major limiting factor is likely to be the large effort and time required to do so with any degree of confidence, at least in the case of long-lived organisms such as finches.

Environmental features shaping adaptive radiation can also vary through time (Merrell 1994); such effects could be examined by considering temporal variation in landscape estimates. Such an analysis was not possible in our case because our fitness surrogate (lifespan) required integration across the entire data set. However, our previous analysis of annual survival in *G. fortis* (the species with the largest sample size and best recapture rates) over 9 years at this site revealed notable associations between selection and environmental conditions (Beausoleil et al. 2019). Such variation is likely common given evidence not only of temporal environmental fluctuations, but also of temporal variation in selection coefficients acting on phenotypic traits (Siepielski et al. 2009, 2017). Accordingly, a goal for future work could be to compare, in natural populations, long term estimates of adaptive landscapes to patterns of temporal variation in key environmental factors.

The ultimate promise of adaptive landscapes, as an analytic tool, is to link genetic architecture to selection and adaptive radiation (Schluter 2000; Arnold et al. 2001; Hendry 2017). Making these connections should in theory allow insight into the genetic constraints or opportunities that impede or facilitate the occupation of adaptive landscape peaks, shifts between them, and—thus—speciation and diversification (Patton et al. 2022; and reference therein). At present, however, estimates of the *G* matrix are extremely limited in the traits examined, the environments in which they are quantified,

and the number of species in either case. Future G matrix estimations for species in adaptive radiations in their natural environments will be greatly facilitated through recent applications of genomic data to relatedness estimates, as used in 'animal model' estimates (Kruuk 2004; Wilson et al. 2010).

Is the 'landscape concept' still useful today? It has been argued by a number of authors that the concept of the adaptive landscape has so many assumptions as to be unhelpful at best and misleading at worst (Kaplan 2008; Pigliucci 2008). Yet, at the same time, other authors have argued that the adaptive landscape concept remains a useful tool in a variety of fields, including population genetics, evolutionary ecology, conservation biology, and speciation (Gavrilets 2004; Svensson and Calsbeek 2012b). It is our view that adaptive landscapes are useful and informative, even if we still hold a poor understanding of many of their features such as their spatio-temporal dynamics, their sensitivity to assumptions (e.g., multivariate normality), their modification by density and frequency dependence, and many other subtle and not-so-subtle nuances (Svensson and Calsbeek 2012a). Perhaps most daunting thus far, however, has been the inability of practicing biologists to actually generate empirically-based adaptive landscapes for natural adaptive radiations.

Our analysis addresses this last criticism (of practicality) by showing that multi-species fitness landscapes can be used not just as a metaphorical concept, but also as a quantitative tool for exploring the factors contributing to adaptive radiation. Our adaptive landscape for beak traits of *Geospiza* spp. unveiled the expected number of fitness peaks, with the phenotypes of four species (and two intra-specific 'morphs') near, but not directly on, the inferred fitness maxima. Admittedly, this system is optimal for adaptive landscape estimation in some respects: only a few species are involved, they are all (here) sympatric, the important traits are clear, and the phenotypic distribution is nearly continuous. At the same time, however, other aspects of the system are decidedly suboptimal for estimating adaptive landscapes: lifespans are long, only some fitness components can be reliably measured, long-term data are necessary, recapture rates are relatively low, and the populations are 'open.' Given that other study systems are at least as suitable as ours, even if for different reasons, we anticipate considerable value in applying similar methods to a great

diversity of biological communities. Once such data accumulates, perhaps the promise of the theory of adaptive landscapes will finally be realized.



3.6 Figures

Figure 3.1: Fitness and adaptive landscape of Geospiza spp. at El Garrapatero (Santa Cruz Island). (A) fitness Ln-transformed mean for bins of phenotypes without model by increments of 0.14 mm. The ellipses are 95% multivariate t-distributions based on the individual beak phenotypes of each species. (B) Individual-based fitness landscape from the spline model. Note there are more contour lines compared to the legend to more clearly show the peaks. (C) the adaptive landscape is obtained by 'moving' simulated population for each а phenotypic mean and mean predicted fitness. The fitness landscape spline model predicted the fitness values of the simulated population to generate the adaptive landscape (Schluter 2000). The color scale is scaled to be comparable between the figures. The triangles are the local fitness peak maximum and the large points are the population G. magnirostris phenotypic means for the various modes of ground finches (smaller transparent points are the data for each bird). Distances between fitness peaks (triangles) and population means (larger points) were calculated using Euclidean distances. The standard error of the fitness landscape can be found in the supplemental material (figure C.9).



Figure 3.2: Fitness landscape with lines (in green) connecting the fitness peaks of (panel A) all *Geospiza* spp. and (panel B) from fitness peak-mean phenotypes of each species. The down-pointing purple triangle represents the minimum on that line. Note that the minimum fitness in panel B is at the phenotypic mean for each species (the triangle overlaps the point for a population phenotypic mean).



Figure 3.3: Prospective selection assuming finch populations would evolve towards their fitness landscape peaks. In panel A, coloured points represent species means from our data, the points in gray with the corresponding shape for each species, are the positions of the fitness landscape peaks (figure 3.1B). The vertical and horizontal bars are one standard deviation for the phenotypic traits. In panel B, the *G*-transformed beak phenotypes (calculated via the genetic variance-covariance matrix (*G*-matrix) from a population of *G. fortis*, Boag 1983) gives an idea of how much selection is required to make a population evolve in a certain direction. The distance between two points represents the net selection gradient required to move from one point to the other. In both panels, the dashed lines approximately represent the axes of beak size and shape for the raw traits.



Figure 3.4: Fitness landscape with black lines connecting the fitness peaks of a species (triangles) to its phenotypic mean (large coloured dots). The coloured segments (starting from purple to yellow) represent all the phenotypic means in all years (small dots).

3.7 Tables

Species	BL [sd; CV] [†]	BD [sd; CV] [†]	Pk pos. BL [‡]	Pk pos. BD [‡]	ΔBL; ΔBD crd. [§]	Dist. <i>P</i> - pk _{fit} ¶	Dist. <i>P̄s</i> - pk _{fit} ¶	Angle (°) of vector [∥]	Dist. $m{G}_{ar{P}}^-$ $m{G}_{pk}^{\dagger\dagger}$	$oldsymbol{eta}_P^{\ddagger\ddagger} \ [oldsymbol{G}_{BL}, \ oldsymbol{G}_{BD}]$
G. fuliginosa	8.57 [0.49; 5.69]	7.10 [0.38; 5.29]	8.21	8.67	0.51; 2.08	1.62	4.26	102.70	3.50	[-2.77, 2.14]
<i>G. fortis</i> small	11.37 [0.60; 5.27]	10.45 [0.68; 6.53]	10.81	10.77	0.55; 0.37	0.64	1.04	149.71	1.36	[-1.11, 0.78]
<i>G. fortis</i> large	13.01 [0.67; 5.12]	12.89 [0.85; 6.63]	13.13	13.56	0.13; 0.67	0.68	0.81	76.33	0.50	[-0.38, 0.33]
G. magnirostris	14.90 [0.71; 4.76]	16.02 [0.93; 5.81]	15.52	15.43	0.65; 0.64	0.85	1.08	316.27	1.28	[1.04, -0.74]
G. scandens	14.25 [0.86; 6.01]	8.63 [0.54; 6.26]	13.98	9.27	0.27; 0.64	0.69	1.22	103.11	1.32	[-1.05, 0.80]
Mean	-	-				0.90	1.68	152.22	1.59	

Table 3.1: Euclidean distances of population mean to the position of the peaks on the fitness landscape

[†] BL: Beak length (mm), BD: Beak depth (mm), sd: standard deviation, CV: coefficient of variation

[‡] Peak pos.: Position of peak for beak length (BL; mm) and beak depth (BD; mm)

[§] ΔBL: delta beak length (mm), ΔBD: delta beak depth (mm), crd.: coordinate, difference (Δ) in phenotypic space between the fitness peak and the population mean

^I Dist. \bar{P} -pk_{fit}: Euclidean distance between phenotypic mean (\bar{P}) and fitness peak (pk_{fit}). For mean scaled traits (\bar{P}_S), in standard deviation units

^{$\|$} The angle is taken counterclockwise from the positive side of the x-axis, so that a 90° angle is pointing straight up in the y-axis.

^{††} Dist. $G_{\bar{P}} - G_{pk}$: Euclidean distance between *G*-transformed phenotypic mean (\bar{P}) and *G*-transformed fitness peak (pk) ^{‡‡} Distance $\Delta \boldsymbol{\beta} = \boldsymbol{G}^{-1}(\bar{\boldsymbol{z}}_b) - \boldsymbol{G}^{-1}(\bar{\boldsymbol{z}}_a)$ between the fitness peak and the population mean phenotypic traits (see

figure 3.1B). The values represent the G-transformed beak traits (length and depth respectively.).

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Linking Statement 3

The fitness landscape in chapter 3 was revealed to be composed of mountains of high fitness near each finch morphotype and valleys between each morphotype. I determined the topology of the fitness landscape and found that the populations were close, but not directly on their adaptive peaks. This might be due to evolutionary constraints from genetic covariance between traits, and/or gene exchange between populations or species. As expected from theory, the adaptive landscape was smoother compared to the fitness landscape and had only four peaks instead of the five found on the fitness landscape. Together, this chapter demonstrates how fitness and adaptive landscapes are useful for uncovering the causes of phenotypic and genetic divergence during adaptive radiation. However, the phenotypic adaptive landscape does not shed light on the specific loci involved in species divergence. Constructing genetic adaptive landscapes based on loci associated with beak morphology, or other traits targeted by selection, could be useful to help answer questions about the relationship between phenotypic and genetic adaptive landscapes, the shape of the adaptive landscapes in various environments, its temporal dynamics and the genomic basis of adaptation in Darwin's finches. This might be achieved by quantifying the topology of landscapes from loci that are found at different frequencies among species.

The fourth chapter links genotypes, phenotypes, and fitness together by constructing adaptive landscapes based on population allele frequencies. I used whole genome low-depth sequencing on individuals of small, medium, and large ground finches (*G. fuliginosa*, *G. fortis*, and *G. magnirostris*) on Santa Cruz Island to find the loci associated with beak length. From the long-term dataset used in previous chapters, I used the apparent survival of each individual to calculate the fitness of

genotypes, which provides the base of the genetic adaptive landscape. Each combination of genetic markers associated with beak phenotype is then characterized to identify the adaptive peaks and their distance from the current population allele frequency of each species. These adaptive landscapes can be compared to genetic markers that are not putatively associated with beak morphologies to uncover other loci that might be linked to another phenotype that might be targeted by selection. In particular, there could be other genomic positions that have high association with fitness that might not be related to beak morphology. Exploring higher dimensions of the genetic adaptive landscapes is an exciting avenue of research to help connect genetic and phenotypic adaptive landscapes. This chapter demonstrates that genetic adaptive landscapes are a powerful tool for uncovering the putative loci involved in adaptive radiation.

"The really fundamental questions in evolution may be answerable only by regarding each gene as ultimately in conflict with every other gene, even those at other loci in the same cell. A really valid theory of natural selection must be based ultimately on selfish replicators, genes and all other entities capable of the biased accumulation of different variant forms."

G. C. Williams, 1979 The question of adaptive sex ratio in outcrossed vertebrates

Chapter 4

Exploring genetic adaptive landscapes in Darwin's finches

M.-O. Beausoleil¹, I. Schulz^{2, 3}, X. Wietlisbach^{2, 3}, L. P. Singer^{2, 3}, P. L. Carrión¹, J. Podos⁴, C. Camacho⁵, J. Rabadán-González⁶, R. Richard¹, K. Lalla⁷, J. A. M. Raeymaekers⁸, S. A. Knutie⁹, L. F. De León¹⁰, J. A. Chaves^{11,12}, D. H. Clayton¹³, J. A. H. Koop¹⁴, D. M. T. Sharpe¹⁵, K. M. Gotanda^{1, 16, 17, 18}, S. K. Huber¹⁹, A. P. Hendry¹, D. Wegmann^{2, 3}, and R. D. H. Barrett¹ *Author affiliations*:

¹ Redpath Museum and Department of Biology, McGill University, Montréal, QC. Canada

² Department of Biology, University of Fribourg, 1700 Fribourg, Switzerland

³ Swiss Institute of Bioinformatics, 1700 Fribourg, Switzerland

- ⁴ Department of Biology, University of Massachusetts Amherst, MA, United States
- ⁵ Department of Ecology and Evolution, Estación Biológica de Doñana—CSIC, Sevilla, Spain
- ⁶ Observation.org Spain, Almensilla, Seville, Spain

⁷ Department of Natural Resource Sciences, McGill University, Sainte-Anne-de-Bellevue, QC. Canada

⁸ Faculty of Biosciences and Aquaculture, Nord University, Bodø, Norway

⁹ Department of Ecology and Evolutionary Biology, Institute for Systems Genomics, University of Connecticut, Storrs, CT, United States

¹⁰ Department of Biology, University of Massachusetts Boston, Boston, MA, United States
¹¹ Department of Biology, San Francisco State University, San Francisco, CA, United States
¹² Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito, Quito, Ecuador

¹³ School of Biological Sciences, University of Utah, Salt Lake City, UT, United States
¹⁴ Department of Biological Sciences, Northern Illinois University, DeKalb, IL, United States
¹⁵ Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, United States

¹⁶ Department of Biological Sciences, Brock University, St. Catharines, On. Canada

¹⁷ Department of Zoology, University of Cambridge, Cambridge, United Kingdom

¹⁸ Département de biologie, Université de Sherbrooke, Qc. Canada

¹⁹ Virginia Institute of Marine Science, William and Mary, Gloucester Point, VA, United States

4.1 Abstract

Connecting genotypes, phenotypes, and fitness is a foundational pursuit of evolutionary biology. The metaphor of adaptive landscapes, as in its original formulation at the beginning of the 20th century, provides a link from genotypes to fitness. Natural selection shapes these adaptive landscapes which are expected to be composed of mountains of high fitness and valleys of low fitness. At the genetic levels, estimating adaptive landscapes based on allele frequencies requires information on the agent and target of selection as well as the link between genotypes and phenotypes, which makes them challenging to estimate in natural populations. We constructed empirical adaptive landscapes using apparent lifespan as a proxy for fitness and low-coverage whole genome sequencing of 482 Darwin's ground finches in four phenotypic modes (*G. fuliginosa*, *G. fortis* small and large morphotypes, and *G. magnirostris*) on Santa Cruz Island (Galápagos) at the site Academy Bay, near an urban center, and the natural site El Garrapatero to compare the topology of adaptive landscapes from beak loci. These landscapes are calculated from genotype fitness matrices using population allele frequencies at pairs of loci that are either associated with

beak morphology or are not. To determine if the loci are adaptive, we then compared the Euclidean distance from location of the population (based on current population allele frequency at each pair of loci) to the highest adaptive peak on each species' adaptive landscape. At the relatively natural El Garrapatero site, the location of the populations on the adaptive landscape was significantly closer to their adaptive peak when calculated using beak-associated loci versus non-beak loci, suggesting that selection is driving allele frequency at these loci towards the peak. In contrast, we found no significant difference in the distance to the adaptive peak when calculating location using beak-associated versus random loci at the urbanized Academy Bay site. The variability and abundance of food resources near urban centers might relax natural selection on beak morphology, rendering similar performance regardless of the beak morphology therefore changing the allele frequency of beak loci. This study provides the first characterization of an empirical genetic adaptive landscape in nature, and in doing so helps to shed light on the role that natural selection plays in shaping genome evolution through its impacts on phenotypic variation.

4.2 Introduction

Central to our understanding of the evolution of organisms is to find links between genotypes, phenotypes and fitness in particular environments (Barrett and Hoekstra 2011). Identifying genes in part responsible for phenotypic variation and uncovering the genetic basis of local adaptations and speciation can answer questions about the number of genes involved, their interactions, their history, the link with reproductive isolation and their change through time (Bell 2010; Kautt et al. 2020; Nelson et al. 2019; Waples et al. 2022). Different approaches are used to find how genotypes, phenotypes, and fitness are connected such as in silico exploration of genotype-phenotype-fitness maps (Greenbury et al. 2022), genomic analysis of individuals in field experiments (Patton et al. 2022), and following allele frequency changes in natural populations with fitness recorded for each individual (Barrett et al. 2019; Enbody et al. 2023). In addition, ecological and genetic data have been used in conjunction with many study systems to make direct connections between an ecological trait and its underlying genetic architecture which allowed researchers to uncover the

genetic basis of adaptation. One famous example is in threespine stickleback fish (*Gasteroseus aculeatus*), where an allele at a locus in the *Ectodysplasin* (*Eda*) gene is associated with the number of lateral amour plates which is higher in marine compared to freshwater fish (reviewed in Reid et al. 2021). Moreover, this association was explained by an ecologically induced change: a derived *Eda* allele is fixed in Stickleback populations that colonized freshwater environments from the sea (Bell et al. 2009). In plants, an example of local adaptive divergence was studied regarding salt stress in coastal areas compared to inland ecotypes of the yellow monkeyflower (*Mimulus guttatus*; Lowry et al. 2009). Five genetic markers were associated with salt tolerance and leaf sodium concentrations in coastal plants and interestingly, reciprocal transplant experiments showed that there was no evidence of genetic trade-offs for the loci. These studies show that the adaptive traits studied have a genetic basis with few genomic markers involved and that there is a correlation with fitness values. However, few attempts have been made to construct genetic adaptive landscapes using genomic data and fitness at the individual level. Hence, there is little information about the features of genetic adaptive landscapes and their role in speciation.

4.2.1 Genetic adaptive landscapes

One of the tools available to connect genotype-phenotype-fitness are genetic adaptive landscapes which is a graphical representation of gene combinations or genetic space (Wright 1932; review of genotype-fitness maps in de Visser and Krug 2014). Although the adaptive landscape metaphor has been developed for nearly a century, most of the discussion is theoretical and few empirical adaptive landscapes have been developed using wild organisms (see Patton et al. 2022). However, adaptive landscapes using sequence space (Maynard Smith 1970; Nowak 2006) can become exponentially large when studying all sequences differing in base pairs (in DNA), codons (in RNA; Fontana and Schuster 1987; Fontana et al. 1993) or amino acid (in proteins; Firnberg et al. 2014; Maynard Smith 1970, 1962; Perelson and Macken 1995). This is a challenge when studying continuous phenotypes, which are assumed to be polygenic (Barton et al. 2017; Barton 2022), because fitness landscapes based on genotypes or loci combinations are potentially large and discrete: the order of the genotypes is arbitrary changing the 'shape' of the fitness landscape (as in Wright 1932; but see Weinreich et al. 2006 and Mira et al. 2015 for mutational molecular landscapes). One way to alleviate this problem is to construct adaptive landscapes using mean allele frequencies of large effect loci instead of using mean phenotypes with mean fitness (Schluter 2000; Svensson and Calsbeek 2012). These empirical *genetic* or *genomic adaptive landscape* can show peaks and valleys on continuous axes constructed from a genotype fitness matrix as in Lewontin and White (1960) studying chromosomal inversion in *Moraba scurra* (Dietrich and Skipper Jr 2012; but see Gavrilets 2004). Increasing evidence is showing that adaptive traits in natural populations might be explained by a couple of large effect loci (Enbody et al. 2023; Jensen et al. 2022; Jones et al. 2018; Lamichhaney et al. 2016; Waples et al. 2022). Genetic adaptive landscapes could be used in order to verify if these loci are close to adaptive peaks compared to loci that are putatively not involved in species divergence.

4.2.2 Study system

Low dimensional adaptive landscapes are possible to be calculated from study organisms that have a trait which was demonstrated to have a link with fitness and that is oligogenic meaning that few genes have a major effect on phenotypic variation. On the Galápagos Islands, Darwin's finches have diversified into about 18 species and a group of ground finches (*Geospiza*) have recently diverged from 100,000 to 400,000 years ago (Lamichhaney et al. 2015, 2016). The diversity of beak morphologies (size and shape) in Darwin's finches is an ecological trait linked with the specialized diet each species has. This private diet becomes especially relevant in moments of food scarcity due to natural selection because the beaks are heritable (Boag 1983) and linked to fitness differences between individuals (Grant and Grant 2002, 2014). For ground finches, smaller beaked finches are better at eating small seeds compared to larger beaked finches that are more efficient at eating bigger and harder seeds (Grant 1999). However, beak is not the only relevant trait for the consumption of resources: muscle size and body size are also probably involved (Boag 1983). In addition to resource consumption, recent investigations showed that beak traits are associated with large effect loci

which makes it a candidate for the construction of genetic adaptive landscapes (Chaves et al. 2016; Enbody et al. 2023; Lamichhaney et al. 2016; Rubin et al. 2022). For example, Chaves et al. (2016) and Lamichhaney et al. (2016) found genes near loci putatively associated with beak size (*HMGA2*, *MSRB3*, *LEMD3*, and *WIF1*; see also Enbody et al. 2023; Rubin et al. 2022). Lamichhaney et al. (2015) found the gene *ALX1* to be putatively associated with beak shape.

In this study, we focus on a sympatric community of Darwin's finches on Santa Cruz island which shows signs of ecologically driven divergence of beak morphology and in some populations, potential convergence of beak size near an urban center (Hendry et al. 2006, 2009; Lack 1947). More specifically our long-term study of the finches uses two locations: one, called Academy Bay, close to the largest city in the Galápagos Archipelago and, separated by about ~ 10 kilometers, the other called El Garrapatero which is a relatively undisturbed site. Both sites, situated in the arid coastal zone, are home to ground dwelling finches with blunted small (Geospiza fuliginosa), medium (Geospiza fortis), large (Geospiza magnirostris), and elongated pointy (Geospiza scandens) beaks. However, at the El Garrapatero sampling site, G. fortis is bimodal for beak size distribution (which are referred as the small and large morphs of the medium ground finch) consuming seeds of intermediate size and hardness (Beausoleil et al. 2023, 2019; De León et al. 2011; De León 2010; Ford et al. 1973; Foster et al. 2008; Hendry et al. 2006; Lack 1947). On the other hand, it has been proposed that human activity at Academy Bay, close to an urban center, might affect the adaptive landscape by reducing natural selection between the two morphotypes of G. fortis slowing down or stopping diversification of this population (Hendry et al. 2006). Therefore, comparing the topologies of the adaptive landscape or how distant each population is to their adaptive peak between the two sites could reveal differences in selection due to the contrasting ecology. The long term aspect of the project, which focuses on individual variation, allows quantifying fitness from the capture-mark-recapture data (Beausoleil et al. 2023). The generation time is on the order of 3 to 5 years and finches can live up to 15 years which means that a cohort can experience multiple selective events depending on the environmental variability (Grant and Grant 1992a, 2002; Grant 1999). This makes it then possible, with the morphological and genomic data collected, from blood

samples, to make associations between genotypes, phenotypes and fitness to construct genetic adaptive landscapes.

In order to characterize genetic adaptive landscapes, we leveraged our genetic and phenotypic long-term survey on Santa Cruz Island from wild populations of Darwin's finches. The core questions we address here are: What is the topology of genetic adaptive landscapes for different species of ground finches? Are loci associated with beak morphologies closer to adaptive peaks compared to markers that are not putatively related to the beak of the finches? Are beak loci closer to their adaptive peaks in the natural site El Garrapatero compared to the site Academy Bay which is near an urban area? To our knowledge only one example of adaptive landscapes using allele frequencies as genetic information was published (Lewontin and White 1960). This work constitutes an exploration and an extension of the idea of genetic adaptive landscapes to reveal how it can be used to find loci contributing to a current adaptive radiation. We build upon previous phenotypic studies to bring a genomic perspective of the adaptive landscape (Beausoleil et al. 2023; Hendry et al. 2009). In addition, this work will allow deeper understanding of the ecological opportunities or mechanisms that contribute to the generation and maintenance of biodiversity (De León et al. 2011; Moritz 2002).

4.3 Materials and Methods

4.3.1 Captures and sampling

We used samples of Darwin's finches (*Geospiza fuliginosa*, *Geospiza fortis* (small and large morphs), and *Geospiza magnirostris*) collected on the island of Santa Cruz, Galápagos, Ecuador, in 2010, 2011, 2017, 2018, and 2019 as part of a long-term study. All birds were sampled using mist nets in the breeding season between January to April (with an average of 68 days, range 53 to 93 days; Beausoleil et al. 2023, 2019; De León et al. 2011; Hendry et al. 2009; Knutie et al. 2019; Podos 2007). Each species is categorized based on visual cues and also confirmed through multivariate analysis of their phenotypes (Grant 1999). We also used an expectation-maximization algorithm to assign the small and large morphs of the medium ground finch (*G. fortis*) with the

mixtools R package (Benaglia et al. 2009; V 1.2.0), as in Beausoleil et al. (2023, 2019). As might be expected in an ongoing adaptive radiation, the variation in beak and body size is continuous, with some individuals falling between the distribution of two species. We chose two sampling sites based on their proximity of the city Puerto Ayora: Academy Bay (AB; 0°44'20.836'' S, 90°18'6.628'' W) and El Garrapatero (EG; 0°41'22.9'' S, 90°13'19.7'' W), which are ~1 km and ~11 km away from the city, respectively (figure 4.1). For each bird captured, we fitted a marked aluminum or Monel metal leg band. We then measured morphological traits including beak length, depth, and width (±0.02 mm, digital caliper, each measurement taken three times with the median value used for analyses), metatarsal length (±0.02 mm, digital caliper), body mass (±0.1 g, digital scale), wing chord (±0.1 mm), and noted sex based on plumage colouration (Grant 1999; Price 1984; also detailed in De León et al. 2012 and Beausoleil et al. 2023). We also took blood for genetic samples, taken from the brachial vein and blotted on Flinders Technology Associates (FTATM) WhatmanTM blood cards (GE Healthcare, Life Sciences, Piscataway, New Jersey) sprayed with ethylenediamine tetraacetic acid (EDTA, 0.5 M, pH 8.0).

The years selected represent two distinct time points (2010-2011 and 2017-2019) with ecological differences between them (cumulative rainfall corresponding to the breeding wet season between January until the end of April was 437.6 mm during 2010-2011 and 50.4 mm for 2017-2019 (difference 387.2 mm); figure D.1). We focused on 3 species (*n*: total number of birds): *G. fuliginosa* (*n* = 291), *G. fortis* (small (*n* = 332) and large morphs (*n* = 238)), and *G. magnirostris* (*n* = 32) in two environments (the natural site El Garrapatero and the urbanized site Academy Bay). Our sample size was 482 males and 411 females (table 4.1). We restricted our genomic analyses to males due to a strong signal of sex in population structure and an increase in expected heterozygosity in females (data not shown). We used this strong signal of sex in a genomic PCA (PCAngsd; Meisner and Albrechtsen 2018) to impute missing or corrected sex information in the dataset (108 males and 24 females had missing information on sex). From the genomic analysis of males we then used all individuals, including females, in the computation of adaptive landscapes. All individuals had beak phenotypes, but some had missing body trait measurements. We imputed 10 missing

individual values for mass with the predictions of a linear model using beak length, tarsus length and species (mass \sim beak length + tarsus + species; adjusted $R^2 = 0.90$). For the individuals missing both mass and tarsus length (n = 1), we used another linear model (mass \sim beak length + species; adjusted $R^2 = 0.89$). We analyzed the data in R (R Core Team 2023; R V 4.3.1, Beagle Scouts). As a measure of fitness, we used the individual apparent lifespan from Beausoleil et al. (2023) which was inferred from capture history as the last year of capture minus the first (figure 4.2). By using the entire collection of the dataset, we have a fitness surrogate that can be used for all species including those with low sample sizes (see Beausoleil et al. 2023). Although this fitness measure does not discriminate between mortality and emigration, functionally equivalent, they represent the loss of individuals (Grant and Grant 1992a).

4.3.2 Genetic material and Library preparation

DNA was extracted at the McGill Genome Centre using a modified Chemagen extraction protocol for dry avian blood on FTATM cards (see protocol 'Chemagen extraction' on page 281). Library preparation was conducted at the Genomic Diversity Center at ETH Zurich (Switzerland). To prepare the low-coverage libraries, we used a custom NEXTERA low-coverage library (See protocol 'NEXTERA low coverage library' on page 284), adapted from Baym et al. (2015), using the Illumina Tagment DNA Enzyme and Buffer kits containing the Tagment DNA Enzyme (TDE1) and Tagment DNA Buffer (TD Buffer). The libraries were indexed using the Nextera XT Index Kit v2 Set A and D, leading to 384 index combinations used. We verified library quality using a Bioanalyzer or Tapestation. We normalized library pool concentrations, as measured by Qubit. Sequencing was conducted at the University of Bern (Switzerland) for low-depth whole genome sequencing on a NovaSeq 6000 S4 (Illumina, CA), which produced 150 base pair (bp) paired-end reads. To reach our desired read coverage (average depth of coverage $\sim 3.00X \pm 2.50$ SD), we conducted four sequencing runs (with a total of 13 S4 lanes).

4.3.3 Preprocessing pipeline of raw reads

Individual samples were processed using the Analysis tools for Low-depth and Ancient Samples (ATLAS) automated pipeline available on Bitbucket (Marchi et al. 2022; Pipeline wiki accessible here (Atlas Wiki): https://atlaswiki.netlify.app/getting-started.html) and the ATLAS program (at this link: https://bitbucket.org/wegmannlab/atlas/src/master/; Link et al. 2017: The Wegmann Lab 2023; figure D.2; V 0.91, alpha branch). We aligned the reads with BWA (genome alignment and mapping, using MEM algorithm for local alignment, Li and Durbin 2009, V 0.7.17) and samtools view (Li et al. 2009, V 1.9), using the Camarhynchus parvulus reference genome (GCA_902806625.1 V1.1; total length 1.1Gbp; 30 chromosomes, 1756 unplaced scaffolds; Enbody et al. 2023; Rubin et al. 2022). Rubin et al. (2022) have argued that this genome provides a suitable reference across the phylogeny of Darwin's finches due to the low interspecific absolute genetic divergence (Han et al. 2017). Any reads with a mapping quality under 30 were filtered out. Because we sequenced the majority of samples multiple times (64% of the samples), we used the splitMerge subroutine in ATLAS for the multiple sequencing run libraries to generate the Binary Alignment Map file (BAM) for downstream analysis. We used ATLAS to estimate genotype likelihood (Genotype Likelihood Format or GLF) with the GLF task (ATLAS V 0.91; Link et al. 2017). We generated the VCF (Variant Call Format) file with task majorMinor (parameter -minMAF 0.01 for minimum minor allele frequency; parameter -minSamplesWithData set to 50%, and activated options -phredLik and -method Skotte) and task convertVCF to output a BEAGLE format. The BEAGLE file was imputed using the BEAGLE program (V 3.3.2; note that although there is a more recent version of the program, version 3.3.2 was required by other programs, such as ANGSD; Browning and Browning 2009, 2007).

4.3.4 Downstream analyses of genetic samples

Genome-wide Association study of beak morphology

To evaluate which markers are associated with beak length, we fitted a Bayesian sparse linear mixed model (BSLMM, which combines the benefits of both linear mixed models and sparse regression model) using GEMMA, which accounts for population structure with a relatedness matrix as a covariate (Zhou et al. 2013; Zhou and Stephens 2012). To prepare the input for GEMMA, we used PLINK (-make-bed; Chang et al. 2015; V 2.00a2LM AVX2 Intel) with the VCF file from the ATLAS pipeline which outputs a *fam* file in which the phenotypic information is added. For the trait, we used the residuals of a linear model for beak length (mm) in relation to mass (g), which will be referred to as beak length henceforth. We calculated a centered relatedness matrix using GEMMA and a mean genotype file from the bcf2bbgeno.pl script (Available on GitHub at visoca/ popgenomworkshop-gwas_gemma, accessed 25 November 2023). We ran the BSLMM model ten independent times with 100,000 burn-in iterations and 200,000 sampling iterations and averaged the hyperparameters and parameters across the runs (Comeault et al. 2016, 2015). We selected a stringent posterior inclusion probability (PIP) threshold of 0.05 to determine the top SNPs (see Chaves et al. 2016). To find the genes putatively associated with the beak length SNPs, we searched in an annotation file with a window size totalling 525,000 bp based on linkage disequilibrium (LD; figure D.3), similar to Chaves et al. (2016). Since there is no annotation for the reference genome for C. parvulus, we used the python package liftoff (V 1.6.3; Shumate and Salzberg 2020) to convert the annotation file sequences from G. fortis' annotated genome (GCA_000277835.1; Chaves et al. 2016; Lamichhaney et al. 2015). Using an imputed BEAGLE file, we calculated per site Fst between each pair of species from the site allele frequency (SAF) and the folded two dimensional site frequency spectrum with realSFS (-fold 1 and realSFS fst index; Korneliussen et al. 2014; Reynolds et al. 1983, from ANGSD V 0.939) was calculated. We divided the alpha and beta from the output of realSFS fst print commands to get the per site Fst. Most of the commands ran in parallel with GNU parallel (Tange 2022) or the SLURM array feature (Yoo et al. 2009).

4.3.5 Genetic adaptive landscape

To extract individual genotypes for the top SNPs from the GWAS, we used the BEAGLE (V 3.3.2) phased file. Following Lewontin and White (1960), we selected pairs of loci and constructed a 3X3 genotype matrix using mean apparent survival (as defined in Beausoleil et al. 2023) for each genotype as a measure of fitness, as calculated within species and sampling site. Unobserved genotypes were assigned a fitness of 0. Adaptive landscapes are population landscapes representing mean fitness (($\bar{W} = \sum Z_i W_i$), where Z_i is the frequency of ith genotype, fitness is W_i and the mean adaptive value is \overline{W}) for any combination of allele (and genotype) frequencies. The genetic adaptive landscapes are constructed from the allele frequencies of two loci and form a two-dimensional plot where each point on the lattice represents a fitness value. For each locus, we calculated the expected genotype frequencies for a given allele frequency (p, between 0 and 1 at increments of 0.01 giving a 101x101 grid or 10201 points lattice) assuming Hardy-Weinberg $(p^2+2pq+q^2=1)$ and independence of the sites (i.e., no linkage disequilibrium). Here we concentrate on only two dimensions, but it is mathematically possible to include more loci in the calculation at the cost of losing the visual representation of the landscape. We then multiplied these genotype frequencies by the apparent fitness values to give the expected fitness value for a given allele frequency at each locus (as in Lewontin and White 1960). To assess the fit between genotype and fitness, for each combination of loci, we estimated the Euclidean distance between the location of the population based on current allele frequencies to the location of the fitness maximum on the adaptive landscape. We developed an iterative algorithm to find the trajectory to the greatest fitness increase (gradient) for the population's current allele frequencies (initial conditions). The trajectory was calculated by drawing a circle with fixed radius (0.01) around the starting allele frequencies, and finding allele frequency coordinates that maximized fitness on the circle. We repeated the operation until a maximum was found. Note that this maximum might not be the global maximum of the landscape. To assess if natural selection on beak length has shifted beak loci towards adaptive peaks, we compared the relative distance to the fitness maximum for pairs of loci that either were or were not associated with beak length (i.e. high versus low PIP values in the GEMMA analysis). The

top beak loci based on their high PIP values (n = 15, range PIP = [0.055, 0.860], median 0.090), were selected by multiplying the median proportion of variants with non-zero effects by the total number of SNPs analyzed (279,311). The loci with a PIP strictly less than 0.01 were considered not associated with beak morphology (n = 383, range PIP = [0, 0.006], median = 0). We used a nonparametric one sided Wilcoxon rank sum test to find if the beak loci were associated with smaller Euclidean distances compared to the non-beak loci. For a fitness scan (relating each genotype at a locus to individual fitness) of beak-related loci, we used a Kruskal-Wallis rank sum test for each species (R Core Team 2023; R V 4.3.1, Beagle Scouts).

4.4 Results

4.4.1 GWAS and genetic adaptive landscape

From our low-coverage whole genome sequencing, we analyzed 645,200 SNPs. To determine which loci are putatively associated with beak length, we conducted a genome-wide association study (GWAS) using males, as explained in the methods, of 3 species (G. fuliginosa, G. fortis (small and large morphs), G. magnirostris, total = 482) that cover the beak size gradient from small to large in both of our study sites (figure 4.2). With the residuals of a linear model with beak length as a function of mass (for the focal species, adjusted- $R^2 = 0.84$, p-value << 0.05), we computed the relatedness matrix using GEMMA. Almost all variation in beak length was explained by 279,311 SNPs PVE_{Beak.length} = 97.1% [87.0%, 99.8%] (PVE: proportion of variance explained; median [Equal-Tailed Interval (ETI) of posterior 2.5%, 97.5%]), with the majority explained by 37 large effect SNPs (PVE_{Beak.length} = 50.0% [39.6%, 63.5%]; table D.1). To identify SNPs within annotated genes, we next pruned the dataset to only SNPs located on assembled chromosomes, which resulted in 15 SNPs on 11 chromosomes (figure 4.3). The positions found on the same chromosome (n = 7)were separated by a minimum of 850 bp to a maximum of 8758 bp (mean = 4973 bp). The mean PIP for the 15 beak-associated SNPs was 0.22 with a minimum of 0.06 and a maximum of 0.86. The annotation file from liftoff included 539,817 features, 322 unmapped features from the liftoff program. Genes (WIF1, LEMD3, MSRB3, and HMGA2) that have also been associated with beak

length in other studies were found inside or astride a window with a total length of 525,000 bp centered at each locus of major effect (figure 4.4 for chromosome 1A positions 786,507,733 and 786,508,583; Chaves et al. 2016; Enbody et al. 2023; Lamichhaney et al. 2015; Rubin et al. 2022).

Using the genetic adaptive landscape constructed from population allele frequencies for pairs of major effect loci ($n_{loci} = 15$), we calculated the Euclidean distance between the location of each population relative to their adaptive peak (total number of combinations = 105; see figure 4.5 for an example using chromosome 1A at positions 786,507,733 and 786,508,583; genomic positions are calculated from the beginning of the genome). We also calculated these distances for adaptive landscapes constructed using loci that our GWAS did not find to be in association with the beak morphology ($n_{loci.rdm} = 383$; number of combinations = 206). The Wilcoxon rank sum test on Euclidean distances was significant at the El Garrapatero site (W = 160576, p-value = 0.02; figure 4.6 and figure D.4). In contrast, we found no significant difference between the beak loci and the non-beak loci at the Academy Bay site (W = 181472, p-value = 0.92). A fitness scan with Kruskal-Wallis rank sum test, to find the association between each genotype at a locus and fitness, revealed a significant association for three beak loci with fitness (*G. fuliginosa* chr11:682,097,235 and chr18:845,098,737, *G. fortis* small chr2:209,969,308, p-values = 0.024, 0.025, 0.023 respectively; figure 4.7).

Although genome wide Fst values are low between the species (figure D.5; table D.2), some loci found by the GWAS were also close to regions of high Fst between *G. fuliginosa* and the small morphotype of *G. fortis*. We chose this pair of species because it showed intermediate patterns of genome-wide differentiation when comparing all pairs of species (figure D.5). In particular, using a window size of 10,000 bp, putative beak loci found on three chromosomes have elevated Fst values (chromosome 1A, 11 and 18 with mean Fst of 0.061, 0.012, and 0.011 respectively; number of sites included in the windows 332, 190, and 591 respectively; figure D.6, table D.3).

4.5 Discussion

4.5.1 Linking genetic adaptive landscapes and phenotypic adaptive landscapes

Genetic adaptive landscapes constructed from pairs of loci are quantitative tools that can help uncover the loci involved in species divergence. Compared to phenotypic adaptive landscapes (Beausoleil et al. 2023), genetic adaptive landscapes are limited in the number of peaks that can be visualized, when constructed from pairs of loci (Lewontin and White 1960; McCandlish 2011; Phillips and Arnold 1989). Since phenotypes are the result of all genes interacting, phenotypic adaptive landscapes are in essence a highly dimensional genetic adaptive landscape. However, it is possible to have genetic adaptive landscapes with more dimensions (i.e., more loci) which would allow an increase in the number of peaks, but this would prevent visualization with the approach used in the study. As recognized early in the construction of multidimensional adaptive landscapes, the computation becomes exponential as we add more loci studied, which also come as a computational cost (Dietrich and Skipper Jr 2012; Wright 1932). The aim of this study was to explore the construction of genetic adaptive landscapes using loci related to beak morphology as a way to zoom in on specific loci that are putatively involved in the speciation of Darwin's finches. We found that the positions associated with putative major beak loci were closer to adaptive peaks compared to non-beak loci at the site El Garrapatero. The shape of genetic adaptive landscapes is determined by the fitness of genotypes. However, we are aware that the adaptive landscapes based on allele frequencies have their own limitations. In multi-locus systems, the mean fitness of populations is usually not explained by allele frequencies when fitness is not additive and that there is linkage disequilibrium among the loci (Gavrilets 2004). Therefore, a 'genotype' fitness landscape might be more appropriate for more complex interactions between loci and their effect on fitness.

4.5.2 Factors shaping the adaptive landscapes

Peaks are formed when genotypes, which relate to an ecological trait, with high fitness are observed, but valleys can be formed in at least two ways: first they can result from a low fitness
genotype or, second, they are not observed in the sampling of individuals. However, the type of fitness component measured can change the topography (which can be composed of adaptive peaks, low fitness valleys or unstable saddles) of the genetic adaptive landscape (Dietrich and Skipper Jr 2012; Lewontin and White 1960; Lewontin 1974; Turner 1972). It should be noted that the fitness contribution of a particular genotype is confounded for complex organisms because it is in interaction with all the other loci. A robust way to test for the fitness contribution of a genotype would be to have individuals that have known genotypes at a locus, but a random genomic composition at any other loci. This is difficult to obtain in nature, but could be achievable for small organisms such as bacteria or viruses (Rokyta et al. 2005; Weinreich et al. 2006). Therefore, the distribution of genotype fitness effects could be interpreted. Our analysis compares the combination of loci pairs (one locus is found in multiple pairs) and genotypes are calculated based on *expected* genotype frequencies assuming Hardy-Weinberg. This assumption would need to be verified by looking at the linkage disequilibrium between the markers (and haplotypes) although our results don't show strong patterns to be present (table D.4). Enbody et al. (2023) found that there is increased linkage disequilibrium in the same region where we found two putative beak loci chromosome 1A (see G03 haplotypes composed of four genes which are thought to be epistatic for beak size and body size). In addition, the genotype-phenotype map is formed with many interactions among other genes and environmental effects that lead to the development of a phenotype. Reciprocal transplant experiments with Mendelian crosses and wild fitness assays could disentangle the genetic and environmental effects and help characterize the adaptive landscape (Arnold 2023; Rundle and Whitlock 2001). Beak morphology in Darwin's finches is polygenic (including 15 loci uncovered in this study; Bosse et al. 2017; Chaves et al. 2016; Enbody et al. 2023; Lamichhaney et al. 2016; Lundregan et al. 2018; Rubin et al. 2022), epistatic (such as the G03 haplotypes), and pleiotropic (i.e., loci affecting more than one trait, such as body size and beak size). Another mechanism that can change the shape of adaptive landscapes is the patterns of introgressive hybridization. The movement of alleles among species can change the population allele frequencies which could displace a population from an adaptive peak. In Darwin's finches, the hybrids can sometimes have

higher fitness than the parental species (Grant and Grant 1993; Grant 1993; Grant and Grant 1992b). However, previous study at our sites could not conclude if introgression has played a role in a displacement from an adaptive peak (Beausoleil et al. 2023).

4.5.3 Genetic differentiation among species

Previous analysis of the genomics of beak variation found markers near the same genes (figure 4.4; Chaves et al. 2016; Enbody et al. 2023; Lamichhaney et al. 2016; Rubin et al. 2022). Furthermore, the positions found in this study have for certain pairs of species an increase in the genetic differentiation (Fst). Most notably, the pair G. fuliginosa and G. fortis small or G. fortis large have among the largest Fst values near the beak-related loci. This can be explained by selection acting on these loci in these populations or species. It has been shown that when an island is home to only one smaller beaked species (e.g., G. fuliginosa), a larger beak evolves from the lack of competition for food resources to larger beaked birds (e.g., G. fortis) which makes them able to exploit abundant resources (Boag and Grant 1984; Lack 1947; Schluter et al. 1985). The high Fst values for the loci in proximity of the beak genomic positions between the pair G. fortis small and G. fortis large also match what is expected from analysis of phenotypic selection against the intermediates situated between these two phenotypic modes (Beausoleil et al. 2019, 2023). Interestingly, the Fst for the pair of G. magnirostris to either of the G. fortis morphotypes is small compared to the pair of G. fuliginosa to either of the G. fortis morphotypes probably indicating a relaxation of selection for beak length (figure D.6). This might be due to the relatively low number of G. magnirostris found at El Garrapatero which might not increase competition for food resources with G. fortis.

4.5.4 Future exploration of adaptive landscapes

Adaptive landscapes constructed from loci in association with a trait which are themselves related to fitness can help connect genotypes, phenotypes and fitness. The characterization of the adaptive landscape, in other words, determining the number of peaks, the position of populations on the landscape, and the closeness to the adaptive peaks, could be used to verify if populations are evolving towards adaptive peaks. To find the genetic positions to be used in an adaptive landscape, we suggest finding the loci that overlap three different approaches. First, a GWAS can get the set of loci that are associated with phenotypes (genotype-phenotype). Second, an Fst scan can uncover the set of genetic positions that are under selection between populations or species (genotype-fitness). Third, we advocate for a fitness scan: that is finding the genotypes that are associated with individual fitness values (genotype-fitness). A consistent change in population allele frequencies and fitness through time towards an adaptive peak could be an indication of selection on loci related to a heritable trait. This has the potential of finding other loci that might contribute to species divergence since some loci might not be associated with a phenotype of interest, but still be associated with fitness. This may facilitate the discovery of new loci that are involved in the speciation of wild organisms.

4.6 Conclusion

Adaptive landscapes, whether they are based on phenotypes of genotypes, have inspired generations of evolutionary biologists. They can help explore the link between genotype, phenotype, fitness. In the case of this study, more exploration of the genomic architecture underlying beak morphologies is needed to uncover the shape and dynamics of genetic adaptive landscapes. Rather than using the community of ground finches in the GWAS, a species approach might be needed to find the specific positions that are associated with beak morphology (Enbody et al. 2023).

The extent to which spatial variation affects the shape of the genetic adaptive landscape is unknown. Future studies could concentrate on the potential evolutionary impact of urbanization by comparing Darwin's finches living in Puerto Ayora and the ones living in natural environments (such as El Garrapatero), but also the finches living in an agricultural setting. Understanding geneticphenotype-fitness maps could help recognize how populations evolve in the future in response to the impact of anthropogenically altered environments (Pelletier and Coltman 2018; Sanderson et al. 2021).

Further, we lack a temporal perspective regarding variation of the topology of genetic

adaptive landscape, but also how allele frequency changes in a species in order to 'track' its adaptive peak. We currently have a poor view of the importance of a stable compared to a constantly moving adaptive peak on the adaptive landscapes to maintain or foster population divergence. However, the advances in genomic technologies make it possible and easier to explore these adaptive landscapes, so that perhaps, one day, they will reveal their secrets.

4.7 Figures



Figure 4.1: Map of Santa Cruz Island in the Galápagos Archipelago showing the city Puerto Ayora, and the two sampling sites Academy Bay and El Garrapatero. All sites are situated in the arid coastal zone. Santa Cruz Island (SC) in the inset is filled black.



Figure 4.2: Phenotypic fitness landscape with ground finches (n = 482) using apparent lifespan. Each square has 0.14 mm sides and are colored based on the ln-transformed mean fitness values for bins of phenotypes without model. The rug-marks on the left and bottom represent the position of each individual on the fitness landscape. The species are highlighted with the 95% multivariate beak phenotypes t-distributions ellipses.



Figure 4.3: Manhattan plot for each position in the genome of males *Geospiza* species. GWAS was calculated using GEMMA (Zhou et al. 2013; Zhou and Stephens 2012) using residuals of beak length on mass. The alternating shading shows the 30 chromosomes (identified at the top of the plot) in the reference genome. The red dashed line shows 0.1 PIP threshold. The Fst values plotted at the bottom are genome-wide per site comparisons between *G. fuliginosa* and the small morphotype of *G. fortis*.



Figure 4.4: Genes on chromosome 1A around two putative beak loci with highest PIP from the GWAS in Manhattan plot (same data as in figure 4.3, zoom of $7x10^5$ bp showing the positions 786,507,733 and 786,508,583 [large point on top]). The genes inside or astride a window (length of window totalling 525,000 bp, coloured pale blue) are highlighted in purple for genes whereas genes outside the window are coloured turquoise. We used the program liftoff with the annotated *G. fortis* genome on the *C. parvulus* reference genome to identify the genes and their positions in the genome.



Figure 4.5: Genetic adaptive landscapes for chromosome 1A at position 786,507,733 (x-axis) and chromosome 1A at position 786,508,583 (y-axis). Each panel represents a species (including males and females in all years) at El Garrapatero. The maximum fitness value (adaptive peak) is shown as a large translucent black triangle and the location of the population based on current allele frequencies at each locus is shown as a large blue point. The blue path is the gradient ascent to an adaptive peak and the green line is the Euclidean distance between the population allele frequency and the adaptive peak on the landscape. Sample size for panel A: n = 186, B: n = 218, C: n = 154, D: n = 18.



Figure 4.6: Distribution of Euclidean distances in Violin plots for putative beak loci uncovered from the GWAS analysis compared to loci not in association with beak loci. Data shown for El Garrapatero (panel A) and Academy Bay (panel B). Wilcoxon rank sum between types of loci (panel A: W = 160576, p-value = 0.019; panel B: W = 181472, p-value = 0.920). The marginal plot on the right superimposes the two distributions for comparison.



Species • G. fuliginosa • G. fortis small • G. fortis large • G. magnirostris

Figure 4.7: Fitness scan for genotype from major beak related loci where each point represents the p-value extracted from a Kruskal-Wallis rank sum test of genotypes in relation to fitness for each species. The points are displaced horizontally to provide better clarity of their vertical position. The red dashed line corresponds to a p-value of 0.05.

4.8 Tables

		Sites		
Sex [†]	Species	Academy Bay	El Garrapatero	Total
Females	G. fuliginosa	46	83	129
	G. fortis small	50	116	166
	G. fortis large	38	65	103
	G. magnirostris	6	7	13
	Sub-total	140	271	411
Males	G. fuliginosa	59	103	162
	G. fortis small	64	102	166
	G. fortis large	48	87	135
	G. magnirostris	8	11	19
	Sub-total	179	303	482
	Total	319	574	893

Table 4.1: Number of individuals of each species per site, and sex.

[†] Sex was determined from the first genetic principal component from PCAngsd.

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General Discussion and Conclusion

My thesis tested predictions made by the ecological theory of adaptive radiation, especially regarding the role of divergent natural selection in shaping fitness and adaptive landscapes in wild populations. At the heart of each chapter are questions about the ways in which ecology and evolution interact to form new species. Next, I review each chapter and propose ideas on how to further our knowledge of adaptive radiation with the methods developed in the thesis.

In the first chapter, I explored the feasibility of using telemetry on Darwin's finches and calculated the home range size of medium ground finches. The home range of Darwin's finches was larger than anticipated. This will help inform future analysis of the finch populations, but is also a valuable starting point to make comparisons of space use in a relatively undisturbed environment compared to urbanized sites such as the one in the city Puerto Ayora, which is the most populous town in the Galápagos Islands. Current studies comparing urban and non-urban sites could benefit from using spatial information to learn about the specific effect of landscape on the ecology and evolution of finches (McNew et al. 2017; De León et al. 2018; Harvey et al. 2021; Rivkin et al. 2021; Solomon et al. 2023). My results showed that the behaviour of finches was associated with differential use of the landscape. This highlights the need for more studies on movement patterns over longer periods of time and with more species. Prior work has only described general movement patterns in ground Darwin's finches, such as when they flock in dryer conditions and opportunistically breed when precipitation increases the food availability for nestlings (Grant 1999). Ecological factors such as precipitation patterns, the availability of nosting sites, the number of nesting sites

as well as nestling dispersal might all be contributors to the movement and space use variability in the finches. Unanswered questions remain about the relative importance of each ecological factor and their evolutionary importance in species divergence. Further, the movement patterns of Darwin's finches could be informative for conservation biologists. Darwin's finches could disperse seeds of native and invasive plant species (Camacho et al. 2018). Therefore, the finches could be ecological gardeners maintaining the plant community or altering its composition if invasive plants enter their diets. In the movement study conducted in this thesis, I also used an index of preference in a habitat selection analysis to find which environment the finches tended to be found most often in relation to their behaviour. I also explored the possibility of using telemetry to gain more information about the global movement patterns on large islands in these iconic birds. This information is crucial to understand the ecology, evolution, and conservation of animals and can answer unresolved questions about habitat preference which can play a role in speciation. It is not known if there might be fitness trade-offs that would lead to selection against habitat switching or if there are information-processing costs influencing preference for particular environments, especially due to environmental variation (Egan and Funk 2006; Nosil 2012).

The focus of the second chapter was on how disruptive selection is temporally varying in a population of medium ground finches (*G. fortis*) with small and large beak size morphotypes. Specifically, I explored the association of the selection coefficients with precipitation patterns at the study site. I showed that disruptive selection on the intermediate phenotypes was variable through time. A future avenue of research would be to test whether different fitness components (survival, mating success, and fecundity; Siepielski et al. 2011) show different patterns of selection in the population. In addition, a longer temporal dataset would make it possible to generate a distribution of selection coefficients. Questions remain about the shape of the distribution of disruptive selection coefficients and the effect of specific selection episodes in maintaining divergence between species. For example, does one large disruptive selection coefficient impact a population more than several small consecutive selective events (even if the sum of the selection coefficients are equal in both cases)? Is there a specific distribution of disruptive selection coefficients required to maintain

species divergence? How does this distribution of selection vary through space? Different locations might have different selection regimes, due to the environmental heterogeneity, which could be reflected in the shape of the distribution of selection coefficient through time. For the population of Darwin's finches studied here, it appeared that selection was stronger when precipitation was higher in the previous year's dry season. Precipitation is a proxy for other ecological variables such as availability of diverse food types, but it might not be the only selective agent. Thus, finding the relative contribution of additional environmental factors, including human disturbances, in relation to disruptive selection would bring a clearer picture of the actors contributing to speciation. Together, this study raises new questions about the timing and strength of divergent natural selection in promoting divergence of species.

For the third chapter, I examined the expectation that during adaptive radiation, divergent natural selection sculpts the fitness and adaptive landscapes, which are expected to have a topology that includes mountains of high fitness and valleys of low fitness. Using a wild community of Darwin's finches, associations between individual beak phenotypes and fitness revealed a rugged fitness landscape with five adaptive peaks and fitness valleys between the species. The different species of finches were not located directly on their adaptive peaks, which could be explained by introgression between species or hybridization between different locally adapted populations, although the prior work argues against this idea because in Darwin's finches, hybrids can form and have high fitness (Grant 1999). Thus it is unknown how hybrids are contributing to the topology of fitness landscapes. Also, future analyses of fitness and adaptive landscapes should consider what makes them vary through time and space. These could then be dissected with 'fitness transects' to extract the selection gradients (Stroud et al. 2023), which could then be related to ecological variables. Another avenue of research would be to characterize how similar (or different) fitness landscapes are when they are constructed with different fitness components such as survival, mating success, and fecundity. This would help to determine if a phenotype is positively selected with regard to a fitness component or negatively selected when considering another fitness component (Price 1984; Grant 1999). This study demonstrates how divergent natural selection is an important

mechanism shaping fitness and adaptive landscapes. Further, it illuminates how the fitness landscape metaphor is a tool that has still much to offer. In conjunction with population genetics, it can give information on the potential constraints for evolving a particular phenotype (Schluter 2000; Arnold 2023).

In the fourth chapter, I connected genotypes, phenotypes, and fitness from Darwin's finch individuals to understand the genomic architecture of adaptive landscapes. I first tested the association of beak length with genotype. I next investigated the evidence for selection on beak-associated loci using individual fitness estimates to characterize regions of the genome with signatures of past selection. Using population mean allele frequencies, I showed that putative beak genomic markers are closer to their adaptive peaks compared to random (not beak-related) markers in the genome. This is the first study that uses genomic data to construct an adaptive landscape in a wild population. Although multiple studies found signatures of selection at the genomic level (Anderson et al. 2011; Jones et al. 2012; Barrett et al. 2019), the architecture of genetic adaptive landscapes are generally unknown and more studies are needed to make connections between phenotypic and genetic adaptive landscapes (Patton et al. 2022). Further, questions about how many and which loci drive divergence between species is a central problem in speciation (Nosil 2012). Although beak morphology is recognized as important in the speciation of Darwin's finches, other traits experience selection as well (Grant 1999). One productive avenue of future research would be to find the relative overlap between the loci that are associated with beak morphology (through a genome wide association study), the loci showing evidence of genetic differentiation between species (e.g., using Fst), and the loci that are associated with fitness (e.g., using a genome-wide 'fitness scan' where genotypes at each loci is related to fitness). This kind of analysis could first focus on the beak loci that are hypothesized to make a large contribution in the speciation of Darwin's finches. Also, these techniques could help find if there are other sites that are contributing to differentiation between the species that are not beak related. Importantly, if loci are under strong selection, the alleles explaining a certain phenotype might be fixed when looking within species, but variable when considering multiple species currently under speciation. Finding the overlap between

the loci that relate genotypes, phenotypes, and fitness could help find the loci that contribute to the adaptive divergence between species and their effect size. Complementary to this analysis, understanding how diet interacts with the associations between genotype, phenotype, and fitness might help to understand the genomic basis of adaptation. Often, when handling the finches, they release feces that could be used with metabarcoding to determine the diverse plants that individual finches ate. This 'environmental' genome wide association study could then be linked with the genomics of the finches, especially the beak-related loci. It would be interesting to find if particular genetic compositions could be associated with particular diets. Overall, this chapter shows how the genetic adaptive landscape can be a useful tool for understanding the drivers of ecological speciation.

Tracking how species are continuously forming is a spatial and temporal endeavor. Longterm studies, especially in the wild, covering the ecology, evolution and development of organisms are of importance to learn about the role of selection as an agent of change, but also how it also interacts with evolutionary processes such as mutation, gene flow, genetic drift, and mating patterns (Clutton-Brock and Sheldon 2010; Hughes et al. 2017; Kuebbing et al. 2018; Reinke et al. 2019; Sheldon et al. 2022). This thesis leveraged a long-term dataset that was started in 1999 and benefitted from long-term studies carried out on other populations of Darwin's finches (Enbody et al. 2023; Grant and Grant 2014; Grant 1999). It provided detailed quantitative information regarding selection in a community of Darwin's finches, especially the peculiar population of small and large morphotypes of the medium ground finch (Lack 1947). Especially for long-lived organisms, long-term data allows us to test hypotheses about the reciprocal interactions between ecological and evolutionary processes over time. Global environmental changes are affecting the evolution of organisms and having a detrimental impact on biodiversity (Palumbi 2001), making it imperative that we understand these dynamics.

Conclusion

Living organisms exist in a fragile balance with their environment. It is recognized that the diverse interactions that biotic organisms have with their environments generate services forged by eco-evolutionnary dynamics (ecosystem and evosystem services; see Faith et al. 2010; IPBES 2019) that are sometimes essential for certain organisms including humans. Like other living organisms, humans are interacting with and shaping the environments to suit their needs (Lewontin 2000). One of the most striking examples of this is the domestication of crops and animals to sustain human populations (Doebley et al. 2006; Frantz et al. 2020; Greenspoon et al. 2023; Ramos-Madrigal et al. 2016). However, humans are now modifying the environment at an unprecedented scale and rate that is threatening biodiversity with rapid extinctions (Palumbi 2001; Rosenberg et al. 2019; Wienhues 2020; Ceballos and Ehrlich 2023), but also generating new opportunities for natural selection to shape populations (Otto 2018; Fugère and Hendry 2018; Wood et al. 2021). Such anthropogenic activities include modifications of the landscape (Alberti et al. 2017), the introduction of invasive species (Colautti et al. 2017), hunting and harvesting (Van de Walle et al. 2021), use of drugs generating antibiotic resistance (Hiltunen et al. 2017; Andersson et al. 2020), virus resistance (Foll et al. 2014; N'Guessan et al. 2023), drug-resistant cancer cells (DeGregori 2018), and climate change (Hendry et al. 2017; Baltazar-Soares et al. 2021). Therefore, understanding and planning for the evolutionary consequences of environmental change is important for the conservation of biodiversity and for the wellbeing of society (Sarrazin and Lecomte 2016; Rivkin et al. 2018). Although we now face multiple global challenges, including the loss of biodiversity and climate change, we are building towards a better understanding of the many ways in which evolution plays a role in the biological responses of living systems (Sanderson et al. 2021), and can hopefully harness this knowledge in the creation of solutions.

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Appendix

Supplemental Material for Chapter 1

Supplemental material for: Where did the finch go? Insights from radio telemetry of the medium ground finch (*Geospiza fortis*)

A.1 Supplemental figures

All appendix analysis and figures were produced in R (R Core Team 2021)



Figure A.1: Attached radio transmitters on *Geospiza fortis* band number (a) LF1233 and (b) LF1234. Mounting process of the radio-transmitter backpack on individual JP4645 (c-d-e-f).



Figure A.2: Density of sampling effort across time of the day at El Garrapatero. The points at the bottom were y-jittered to better see the amount of sampling at a particular time of the day. The sunrise (0606 h) and sunset (1814 h) on the first day of March 2019 is shown as the dotted vertical lines.


Figure A.3: Bearing estimation from razimuth package (shown for only 4 points of individual KGSK2033 as an example; Gerber et al. 2018). The points behind the transmitter estimate and posterior mode are the MCMC iterations (50,000).



Figure A.4: Diagnostic plot for razimuth model outputs for the individual JP4645.



Figure A.5: Differences between habitats at El Garrapatero. The arid natural zone of El Garrapatero (dry-forest, a-c-e) and the beach transitional zone more utilized by tourists (b-d-f). The photo (b) was taken at the beach, and (d-f) were taken at the site referred to as "inland water" which was considered the edge of the manzanillo forest. The same site can be seen at El Garrapatero (a and c), but (a) is in a wetter season in 2019 than (c) in 2018.



Figure A.6: Minimum convex polygon rarefaction curve for each finch (a-e). We used the function mcp (100%) from the adehabitatHR package to calculate the polygons (Calenge 2006). All the points are ordered based on their sampling date. The blue line represents a Nonlinear Least Squares calculated with the function nlsLM from the minpack.lm package (Elzhov et al. 2016).



Figure A.7: Bearing estimation from razimuth package (Gerber et al. 2018) quantifying the error location of the VHF emitters. The points not shown in the legend (the colour scale from yellow to purple) are the MCMC iterations (50,000).



Figure A.8: Average distances travelled by finches from their nest during the diurnal and nocturnal activities.



Figure A.9: Estimation of nest location with the centroid of all diurnal activity locations of each finch. The yellow triangle is the known location of the nest of a bird. The black dot represents the centroid of all diurnal activity locations and the area around it is a buffer of 36.6 m determined by the upper limit of the 95% confidence interval of the distance between the nest and the centroid of all diurnal activity locations. Note that for female JP4645, the roosting points at the bottom of the map are from 2019-02-28 and 2019-03-01, before incubation started. From then on, this female remained on the nesting territory at night, as indicated by the three additional roosting points recorded during the incubation period, on 2019-03-04, 05, and 13. For the incubating female LF1234, the estimated location of the nest and that of nocturnal roosts are relatively close to each other, suggesting that this female also did not abandon the nesting territory during the night.

A.2 Supplemental tables

	Lake side			Shoreline	side		Total
Time	Entering	Leaving	Difference	Entering	Leaving	Difference	Balance
17:40-17:56	25	6	19	41	8	33	52
17:56-18:03	40	1	39	49	6	43	82
18:03-18:13	100	4	96	140	5	225	320
18:13-18:22	82	1	81	158	4	154	235
18:22-18:30	20	5	15	57	3	54	69
Subtotal	267	17	250	445	26	419	669

Table A.1: Roost count data.

Table A.2: JP4645 (female) roosting behaviour and clutch state.

Date	Time	Point name	Roosting place	Clutch state	Presumed stage
2019-02-28	5:42	R17	Manzanillo forest	Unknown	Unknown
2019-03-01	5:39	R21	Manzanillo forest	Unknown	Laying eggs
2019-03-02	-	-	Unknown	Unknown	Laying eggs
2019-03-03	9:45	Nest4	Unknown	3 eggs or more	Laying eggs
2019-03-04	5:28	R29	Nest (Opuntia)	Unknown	Incubating

	Home ra	Home range								
Band	JP4645	KGSK2033	LF0216	LF1233	LF1234	Average				
JP4645	-	65.85	38.94	75.62	68.03	62.11				
KGSK2033	17.15	-	14.50	34.07	45.52	27.81				
LF0216	19.85	28.39	-	77.15	41.24	41.66				
LF1233	23.19	40.11	46.41	-	60.43	42.53				
LF1234	19.47	50.03	23.15	56.40	-	37.26				
Average	19.92	46.09	30.75	60.81	53.80					
				00101						
8-	Core are	a								
JP4645	Core are	a0	0	61.01	0	15.25				
JP4645 KGSK2033	Core are	a 0 -	0 0	61.01 0	0 6.02	15.25 1.55				
JP4645 KGSK2033 LF0216	Core are - 0 0	a 0 - 0	0 0 -	61.01 0 43.42	0 6.02 0	15.25 1.55 10.86				
JP4645 KGSK2033 LF0216 LF1233	Core are - 0 0 17.32	a 0 - 0 0	0 0 - 20.03	61.01 0 43.42	0 6.02 0 18.30	15.25 1.55 10.86 13.91				
JP4645 KGSK2033 LF0216 LF1233 LF1234	Core are - 0 0 17.32 0	a 0 - 0 0 5.98	0 0 - 20.03 0	61.01 0 43.42 - 11.44	0 6.02 0 18.30	15.25 1.55 10.86 13.91 4.36				

Table A.3: Spatial interaction between the birds. Proportion (in percentage) of the 95% home range and 50% core area of one bird covered by the home range of another bird.

Read the table as a row bird ID is overlapped with a certain area given in proportion of the bird in a corresponding column.

Table A.4: Average proportion of home range and core area and number of individual bird locations in each habitat type.

	Proportion of finches' space	f habitat in e use $(\%)^{\dagger}$	Number of points in each habitat for each bird							
Habitat type	Home range	Core area	JP4645	KGSK2033	LF0216	LF1233	LF1234	Total		
Beach	6.93	2.37	1	5	0	0	0	6		
Inland water	0.95	0	0	0	0	0	0	0		
Manzanillo forest	35.54	33.67	1	15	4	5	5	30		
Dry-forest	55.20	61.80	28	3	27	24	23	105		
Road paved	1.39	2.15	0	0	0	0	2	3		
Total	100.01 [‡]	99.99 [‡]	30	23	31	29	30	143		

[†] Calculated from the habitat polygon divided by the union of all birds' home ranges (total area of home ranges)

[‡] Rounding imprecision

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Supplemental Material for Chapter 2

Supplemental material for: Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*)

B.1 Methodological details

In our long-term study of Darwin's finches, we captured individual birds of four ground finch species (*Geospiza magnirostris*, *G. fortis*, *G. fuliginosa*, and *G. scandens*) annually between 2003 and 2011 at El Garrapatero, an arid zone site on Santa Cruz Island in Galápagos, Ecuador (figure B.1). Table B.1 shows additional information about the number of individuals captured in the years the study was conducted. Although the analysis in the paper concerns *G. fortis*, we provide some capture information about the other ground finch species. We also conducted a supplementary principal component analysis of four ground finch species present in the area in order to characterize the major component axes with respect to known relationships between interspecific trait variation and diet. We first pooled all individuals of all species (*G. fuliginosa*, *G. fortis*, *G. magnirostris*, and *G. scandens*) across all years (table B.1) for principal component analysis (PCA) of the three beak traits (length, depth, and width; figure B.1). Beak morphologies all loaded positively on the first principal component (B.1). The beak trait that has the highest loading on PC1 is beak depth (with a score of 7.7), while beak width and length have similar loadings (5.7 for both). We then performed a similar analysis for *G. fortis* only (shown in the article)—the species on which subsequent analyses

were focused. We compared the interpretation of the axes of the PCA with all the species of ground finches versus the PCA of only *G. fortis* to ensure they retained similar biological interpretation. Consistent with previous work on Darwin's finches, the covariance matrix principal component analyses were calculated because all beak traits were on the same scale (mm) (De León et al. 2012; Grant 1999; Grant and Schluter 1984). Both PCAs were visualized with a correlation biplot (scaling 2), preserving the Mahalanobis distances among the objects in the matrix and taking into account collinearity of the traits (Legendre and Legendre 2012; Mahalanobis 1936). The three granivorous *Geospiza* species (i.e., excluding *G. scandens*) separated clearly along PC1, apart from a few intermediate individuals—again as in previous analyses (Hendry et al. 2009). The primary axis of morphological variation was similar (i.e., beak size) when restricting the analysis to *G. fortis* only (figure 2.2, in the article)—echoing previous work in finding that the primary axis of variation in *G. fortis* parallels the primary axis of variation for *Geospiza* as a group.

We identified and measured finches following previously established methods used in previous studies (De León et al. 2012; Grant 1999). We measured beak length from the anterior edge of nares to anterior tip of the upper mandible, beak depth at the nares and beak with at the base of the lower mandible. These measurements are plotted in figure B.1. We estimated the sex and age of each bird by examining beak and feather colour (Grant 1999), as well as the presence of a brood patch or cloacal protuberance characteristic of breeding birds. Additional information on our measurement methods can be found in the main article.

B.2 Generalized linear model selection

A generalized linear model was carried out to find if there is a general pattern throughout the years regarding survival and climatic conditions (table B.2 and B.3). The most explanatory models, based on AIC in table B.2, include a quadratic explanatory variable for beak size. It should be noted that the samples are not totally independent since some birds in multiple years can be found multiple times. Our goal here is not to infer selection in this model, but rather to inform of potential survival effect of beak size depending on climate (correlational selection) and beak size having a nonlinear on survival.

B.3 Generalized additive models: consistent smoothing across years

To standardize for variation in the smoothing across models, we estimated a mean smoothing parameter by calculating all possible GAMs without constraint regarding their smoothing parameter (λ) and then taking the mean of λ across all models. This mean λ ($ln(\lambda) = 4.58$) was near a local minimum of the validation score in all individual (year-specific) models. We then constrained the thin plate splines in each year to this mean λ to evaluate differences between years for a constant smoothing parameter. We conducted a visual check of the generalized cross-validation (GCV; figure B.2) across multiple λ values to ensure the model was not overfitting the data. The model fit of the splines can be found in the appendix (table B.4).



B.4 Supplemental figures

Figure B.1: Correlation biplot of the principal component analysis based on three beak dimensions (length, width, and depth) for all ground. The first axis of variation (PC1) represents variation in beak size (bigger beaks have higher scores) and PC2 represents variation in beak shape (pointer beaks have higher scores). The grey axes (top and right) are scaled for the trait vectors (in light grey), whereas the black axes (bottom and left) are scaled for the points.



Figure B.2: Minimization of the generalized cross-validation (GCV) score of the generalized additive model (GAM) in pairs of years. The x-axis shows different values of smoothing parameter (λ) that were tested and the corresponding GCV score (y-axis). Although, the λ is common to all the GAM (vertical dashed line), the GCV is generally minimized.

B.5 Supplemental tables

Table B.1: Number of birds captured and capture effort per year at El Garrapatero. These birds were used for the principal component analysis to compute the phenotypic space across all species and within *G. fortis* (figure B.1).

	2003	2004	2005	2006	2007	2008	2009	2010	2011	Total
G. fortis	45	92	148	185	36	76	149	147	195	1073
G. fuliginosa	5	6	9	1	1	0	57	136	189	404
G. magnirostris	1	0	8	8	4	0	2	4	10	37
G. scandens	5	3	0	7	1	0	8	21	35	80
Capture effort (hours)	36	140	212	120	52	56	132	300	128	1176
Bird per hour	1.6	0.7	0.8	1.7	0.8	1.4	1.6	1	3.4	1.44^{\dagger}

[†] This value is the mean across all years.

Table B.2: Model ranking of all GLMs using the mark-recapture data across all year. All the models that have a delta Akaike information criterion corrected for small sample size (AICc) less than 2 contain the nonlinear coefficient. py (or Precip. p.yr) is the total precipitation in the previous year, x and x2 are the raw and squared beak size PCA scores respectively.

		Precip.			Precip	. inter. [§]					
Models	Int. [†]	p. yr‡	PC1	$PC1^2$	PC1	$PC1^2$	DF	logLik	AICc	delta	Weight
y ~ py+ x2+											
py:x2+1	-1.21	-1.3e-3		0.77		0.02	4	-226.75	461.58	0.00	0.19
$y \sim py + x + x2 +$											
py:x2+ 1	-1.29	-1.2e-3	-1.67	6.07		0.02	5	-225.93	461.99	0.41	0.16
$y \sim py + x + x2 +$											
py:x+											
py:x2+ 1	-1.23	-1.4e-3	1.17	-3.22	-0.01	0.06	6	-224.93	462.03	0.46	0.15
y ~ py+ x2+ 1	-1.40	-7e-04		8.66			3	-228.36	462.77	1.19	0.11
$y \sim x + x2 + 1$	-1.70		-1.91	14.67			3	-228.36	462.78	1.20	0.11
y ~ x2+ 1	-1.64			8.58			2	-229.45	462.92	1.35	0.10
$y \sim py + x +$											
x2+ 1	-1.48	-6e-04	-1.69	14.05			4	-227.51	463.11	1.53	0.09
$y \sim py + x +$											
x2+ py:x+ 1	-1.40	-9e-04	-2.53	13.04	0		5	-227.07	464.27	2.69	0.05
y ~ py+ 1	-1.22	-7e-04					2	-231.83	467.68	6.10	0.01
y ~ 1	-1.45						1	-232.89	467.78	6.20	0.01
$y \sim py + x +$											
py:x + 1	-1.15	-1.1e-3	-0.57		0.01		4	-230.02	468.13	6.55	0.01
$y \sim py + x + 1$	-1.25	-7e-04	1.06				3	-231.06	468.16	6.59	0.01
y ~ x + 1	-1.49		0.97				2	-232.24	468.51	6.93	0.01

[†] Intercept

[‡] total precipitation in the previous year

[§] Precipitation interaction noted py:x or py:x2 in the *Models* columns

Table B.3: Estimates of the various models in table B.1 for the years 2005, 2006, 2008, 2009, 2010, and 2011. *py* is the raw precipitation (mm) in the previous year, x and x2 are the raw and squared beak size PCA scores respectively.

Model	Estimate	Standard Error	Z value	p-value	Variable
$y \sim py + x + x^2 + py:x^2 + 1$	-1.288	0.243	-5.30	<0.05*	Intercept
	-1.668	1.296	-1.29	0.2	PC1
	6.074	6.905	0.88	0.38	$PC1^2$
	-0.001	0.001	-1.97	0.049*	ру
	0.022	0.013	1.74	0.08	py:PC1 ²

Table B.4: Output of the generalized additive model (GAM) for each pair of years. Each spline is calculated over a pair of years. The Chi square (χ^2) statistics are calculated to assess significance of model smooth terms, N is the sample size of each pair of years, Int. p-value is the intercept p-value, Eff. DF is the effective degrees of freedom, and App. p-value is the approximate p-value smoothing.

Years	Intercept ± S.E.	Int. p-value	Eff. DF	χ^2	App. p-value	Adjusted R^2	N
2004-2005 2005-2006 2006-2007	-1.03 ± 0.22 -1.40 ± 0.19 2.40 ± 0.24	<0.001 <0.001	5.49 4.25	4.16 4.06	0.72 0.6	0 0.01	110 185
2006-2007 2007-2008	-2.40 ± 0.24 -1.15 ± 0.32	<0.001 <0.001	3.89 3.69	2.1 3.98	0.81	0.02	233 61
2008-2009 2009-2010 2010-2011	-1.46 ± 0.24 -1.82 ± 0.21 -2.13 ± 0.27	<0.001 <0.001 <0.001	3.96 4.83 4.58	4.17 12.23 5.87	0.52 0.05 0.44	0.02 0.07 0.02	127 196 175

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Supplemental Material for Chapter 3

Supplemental material for: The fitness landscape of a community of Darwin's finches

C.1 Supplemental figures



Figure C.1: (A) Density of the individuals from the 5 modes of ground finches. The medium ground finch (*G. fortis*) is separated by the two morphs. (B) PCA from beak length and depth with density of the points. The contour lines are not comparable between the two panels. The function $stat_density_2d$ from the package ggplot2 (Wickham 2016) produced the density of the points.



Figure C.2: Amount of rain (mm) per month through all the sampling years at Puerto Ayora, which is 10.78 km south-west of the field site. The red and blue portion of the line corresponds to El Niño and La Niña years respectively determined by the threshold of ± 0.5 °C for the Oceanic Niño Index (ONI) for Niño region 3.4. (Data: Charles Darwin Foundation 2022 and NOAA / National Weather Service, Extended Reconstructed Sea Surface Temperature version 5; Huang et al. 2017).



Figure C.3: Maps of the Galápagos islands and sampling sites. In panel A, Santa Cruz is represented with the position of El Garrapatero. The inset in panel A shows the archipelago with Santa Cruz island in black. Sampling sites are shown in panel B where each dot corresponds to the location of a net or a banding site for all the years the data were collected. The rounded polygon was estimated using the *kernelUD* function (area = 0.43 km^2) from the adehabitatHR package (Calenge 2006 version 0.4.19).

Our recapture rate was between 4.52% and 15.7% (estimated by the median time dependent model of encounter probability *p* of a capture-mark-recapture for each species computed from the marked package in R; marked version 1.2.6; Laake et al. 2013).



Figure C.4: Number of captures for ground finch species sampled at El Garrapatero (Santa Cruz) corrected for apparent observations. From 2003-2009, our mist netting sampling effort focused on the medium ground finch (*G. fortis*), but other species were collected opportunistically. All species were targeted equally from 2010 onward. Note the difference in the scale of the Y-axis across panels.



Figure C.5: Pearson correlation for morphological traits and principal component scores for the beak traits (length, depth, and width) and the body traits (mass, tarsus, and wing chord). The bottom triangle shows the scatter of the points coloured by species and morphotype, the diagonal is the density of the traits, the upper triangle is the Pearson correlation.



Figure C.6: Fitness landscape of *Geospiza* spp. at El Garrapatero (Santa Cruz Island) from a nonparametric projection pursuit regression (*ppr* function; R Core Team 2023) to analyze beak length and depth, interacting together, without species effect, using a spline smoothing method, 9 degrees of freedom and a maximum number of terms of 2. Like GAMs, the analysis reveals multiple peaks, with most of those peaks close to phenotypic modes. The GAM, however, is more precise, robust, and appropriate.



Figure C.7: Fitness landscapes using the penalty (left) and no penalty (right).



Figure C.8: Adaptive landscapes (as in figure 3.1) based on the simulated population (panel A) or based on the small morphotype of *G. fortis* (panel B). Panel C shows the distribution of the small morphotype of *G. fortis* with 50, 95, and 99% t-distribution dashed ellipses in black, dark gray and light gray respectively. The colours are the density levels.



Figure C.9: Error fitness landscape showing 2 standard errors lower (A) and higher (B) from the fitness landscape in figure 3.1B for median beak length and depth.



Figure C.10: Fitness landscapes with beak principal component scores for beak size (PC1), and beak shape (PC2). There are 3 peaks for the five finch modes. The small transparent points are each individual bird.

C.2 Introgression details

Kleindorfer et al. (2006) showed that Santa Cruz island's highlands populations of *G. fuliginosa* have longer beaks compared to the lowland populations, and Schluter (1984) and Grant (1999) report that the *G. fuliginosa* populations disperse from the lowlands to the highlands during dry seasons, and vice versa during wet seasons (Swash and Still 2005). Therefore, we might expect that in years with high precipitation, average *G. fuliginosa* beak length is increased via gene flow from longer beaked birds migrating from the highlands. In fact, we find that beak length increased in wetter years (figure C.11A) as smaller beak were missing. In seasons where the precipitation is greater than 300 mm, our lowland populations have longer beaks (Welch Two Sample t-test: t = 2.273, df = 13.47, p-value = 0.04, figure C.11B).



Figure C.11: Mean beak length (mm) of *G. fuliginosa* per year. (A) The vertical and horizontal dashed lines are the mean precipitation (between 2000 and 2020; range: 111-679 mm) and mean beak length across all sites (range: 7.98-8.87 mm) respectively. The vertical bars on each point are the standard error on the mean. From the legend, highlands and lowlands 'K06' are from Kleindorfer et al. (2006) whereas lowlands 'EG' refers to our El Garrapatero site. (B) boxplot of the 'Lowlands EG' data separated as low precipitation in a year (<300 mm) and high (>300 mm). (Data: figure 3 of Kleindorfer et al. 2006; Charles Darwin Foundation 2022).

C.3 Supplemental tables

			Species						
Year	Min data [†]	Max data [†]	G. fuliginosa	<i>G. f</i>	ortis	G. magnirostris	G. sandens	Total [‡]	
		Wax uale		Small	Large				
2003	02-25	03-17	6	22	16	1	6	51	
2004	01-28	03-27	8	77	41	2	7	135	
2005	01-15	04-28	15	138	56	10	2	221	
2006	01-26	03-07	4	102	50	8	10	174	
2007	02-14	03-03	4	66	25	7	4	106	
2008	02-07	04-15	3	90	30	3	3	129	
2009	01-20	04-27	41	106	32	5	13	197	
2010	01-20	04-22	144	124	66	6	23	363	
2011	01-27	03-21	166	149	40	7	39	401	
2012	02-03	04-01	143	147	51	5	35	381	
2013	03-04	04-16	207	171	63	4	52	497	
2014	01-16	03-05	86	100	43	4	32	265	
2015	01-07	02-03	37	36	17	0	15	105	
2016	03-05	04-01	91	96	25	1	9	222	
2017	02-26	04-25	71	84	32	0	30	217	
2018	01-06	03-08	99	117	57	2	41	316	
2019	02-19	04-16	121	185	76	3	33	418	
2020	02-06	03-13	56	76	33	1	46	212	
		Total	1302	1886	753	69	400	4410	
		Percent (%)	29.52	42.77	17.07	1.56	9.07	100	

Table C.1: Sampling effort for the ground finches studied with minimum and maximum date of visit and number of individual of each species captured.

[†] Date format MM-DD.

[‡] Total number of individuals for a given year, including within-year recaptured individuals.

Table C.2: Recapture data at El Garrapatero.

							1							
Species	1	2	3	4	5	6	7	8	9	10	11	12	Total	Percent (%)
G. fuliginosa	1015	37	13	13	3	8	3	2	0	0	2	0	1096	32.0
G. fortis small	1189	79	35	35	17	9	11	6	2	0	0	1	1384	40.4
G. fortis large	514	35	14	11	4	3	2	0	1	0	2	0	586	17.1
G. magnirostris	49	0	1	0	2	0	1	0	0	0	0	0	53	1.5
G. scandens	271	13	12	6	3	1	2	1	0	0	0	0	309	9.0
Total	3038	164	75	65	29	21	19	9	3	0	4	1	3428	100
Percent (%)	88.6	4.8	2.2	1.9	0.8	0.6	0.6	0.3	0.1	0	0.1	0	100	

Number of times individuals are captured in the population^{\dagger}

[†] For the model, we subtracted 1 from the data to generate the response variable as we want to see the contribution *from the first observation*. Within-year recaptures were removed.

Parameter type	Variable from model [†]	Estimate	Standard error	Z-value	p-value
Parametric coefficients	Intercept	-1.36	36 0.04 -38.49 ted DE Chi square		<< 0.01
		Estimated DF	Chi square		p-value
	s(bl)	0.001	0.001		0.318
Smooth tarms	s(bd)	0.25	0.350		0.159
Sillooui teriiis	s(bl, bd)	20.27	157.831		<<0.01
[†] y ~s(bl, bs = "tp", k	= 4) + s(bd, bs = "t"	p'', k = 4) + s	(mbl, mbd, bs =	"tp", k	= 27)

Table C.3: Parameters of spline models.

Table C.4: Anova table comparing different spline models

Models [†]	family(link)	Residuals DF	Residual deviance	DF	ΔDeviance	p-value	ΔAIC
y~1		3427.0	4741.8				
$y \sim bl$		3426.0	4721.0	1.0	20.7	<<0.01	18.7
$y \sim bl + bd$	noiscon(log)	3425.0	4694.7	1.0	26.4	<<0.01	24.4
y \sim bl * bd	poisson(log)	3424.0	4660.8	1.0	33.9	0.0001	31.9
$y \sim s(bl) + s(bd)$		3421.7	4642.0	2.3	18.9	<< 0.01	15.1
$y \sim s(bl) + s(bd)$							
+ s(bl, bd)		3400.9	4503.1	20.8	138.8	<<0.01	102.1

[†] All models use thin plate splines. k = 4 for all non-interaction smoothing functions and k = 27 for the interactions. 'y' is the last year of capture minus the first year of capture; bl is the average of median beak length for all recaptures of an individual; bd, same as bl but for beak depth. Visual inspection of a quasipoisson(log) model yielded a similar fitness landscape, but a negative binomial(log) wasn't.

Table C.5: Percentage	e fitness loss	from fitness	peak and fitness at	phenotypic mean.

Species 1	Species 2	Bl [†] (mm)	Bd [‡] (mm)	Fit. [§] peak sp1 [¶]	Fit. peak sp2 [¶]	Min. fitness value	Δfit. from peak to mini. sp1	Δfit. from peak to min. sp2	% of fit. drop from the peak sp1	% of fit. drop from the peak sp2
G. scandens	G. fortis large	13.52	11.59	0.55	0.5	0.07	0.47	0.42	86.58	85.13
	G. fortis small	12.26	10.08	0.55	0.65	0.29	0.26	0.36	47.74	55.77
	G. fuliginosa	10.78	8.94	0.55	0.37	0.16	0.39	0.22	71.13	57.61
	G. magnirostris	14.61	11.79	0.55	0.57	0.09	0.46	0.48	84.08	84.71
G. fortis large	G. fortis small	12.16	12.38	0.50	0.65	0.26	0.24	0.39	48.48	60.64
	G. fuliginosa	12.01	12.44	0.50	0.37	0.25	0.24	0.12	49.18	32.64
	G. magnirostris	14.10	14.32	0.50	0.57	0.37	0.12	0.20	24.37	34.45
G. fortis small	G. fuliginosa	9.45	9.67	0.65	0.37	0.31	0.34	0.06	52.19	17.04
	G. magnirostris	12.38	12.32	0.65	0.57	0.24	0.41	0.33	62.73	57.71
G. fuliginosa	G. magnirostris	12.20	12.36	0.37	0.57	0.25	0.12	0.32	32.01	55.54

[†] Bl: Beak length at minimum fitness value between species peaks (see figure 3.2).

[‡] Bd: Beak depth at minimum fitness value between species peaks.

¶ sp1: see column Species 1; sp2: see column Species 2

§ Fitness

Table C.6: Euclidean distance for all pairwise mean phenotypes of each mode (lower portion matrix, mean: 5.69 mm) and for all pairwise *G*-transformed mean phenotypes of each mode (upper portion matrix, mean: 3.27).

	G. fuliginosa	G. fortis small	G. fortis large	G. magnirostris	G. scandens
G. fuliginosa	-	0.56	0.80	1.15	7.08
G. fortis small	4.37	-	0.37	0.80	6.87
G. fortis large	7.30	2.94	-	0.44	7.12
G. magnirostris	10.94	6.59	3.66	-	7.47
G. scandens	5.89	3.41	4.44	7.42	-

Table C.7: Percentage fitness loss from fitness peak and fitness at phenotypic mean.

Species	Percentage of fitness loss from the fitness at a peak compared to the fitness at the mean phenotype (%)	Fitness at peak	Fitness at average phenotypes	Difference between fitness peak and fitness at average phenotype
G. fuliginosa	47.4	0.37	0.20	0.18
G. fortis small	29.4	0.65	0.46	0.19
G. fortis large	33.6	0.50	0.33	0.17
G. magnirostris	24.0	0.57	0.43	0.14
G. scandens	38.4	0.55	0.34	0.21
Mean	34.6	0.53	0.35	0.18

C.4 Supplemental animation



Figure C.12: Hypothetical one-phenotype fitness function $(f(z) = \hat{W}; \text{ red line})$ and population (z; black points) and its phenotypic distribution (dashed line) used to calculate an adaptive landscape $(\bar{W}_i; \text{ yellow points and turquoise line; see online animation})$ from the recentered mean phenotypes of the population $(\bar{z}_i; \text{ blue points})$. To calculate an adaptive landscape, we move the phenotypic distribution from the original population phenotypic mean (\bar{z}) covering the entire fitness function. Each time, the average fitness of the population is calculated at the mean phenotype of the population (\bar{z}_i) , generating the adaptive landscape $(f(\bar{z}) = \bar{W})$. See the online supplementary materials for the animated version.

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Supplemental Material for Chapter 4

Supplemental material for: Exploring genetic adaptive landscapes in Darwin's finches

D.1 Supplemental figures



Figure D.1: Sum of precipitation per month (mm) at Puerto Ayora 1.4 and 11.8 km south-west of the field site Academy Bay and El Garrapatero (figure 4.1). The dark-grey rectangles show the years of sampling of the samples. The segment is coloured based on El Niño (red) and La Niña (blue) years when outside a ± 0.5 °C threshold for the Oceanic Niño Index (ONI) of Niño region 3.4. (Data: Charles Darwin Foundation 2022 and NOAA / National Weather Service, Extended Reconstructed Sea Surface Temperature version 5; Huang et al. 2017).

Sequencing 1, 2, 3, and 4



Figure D.2: Atlas pipeline and production files for downstream analyses.



Figure D.3: Linkage disequilibrium decay for 30 aligned chromosomes in each species from ngsLD (with default parameters settings; Fox et al. 2019). We used a modified version of the fit_LDdecay.R script to calculate the decay model. The dashed line represents the average decay.


Figure D.4: Distribution of Euclidean distances in Violin plots for putative beak loci uncovered from the GWAS analysis compared to loci not in association with beak loci. Top row corresponds to El Garrapatero and the bottom row is for Academy Bay.



Figure D.5: Per site genome-wide Fst calculated with realSFS (fst index; fst stats; fst print) for each pair of species (Korneliussen et al. 2014). Negative values were changed to be 0.



(Panel B and caption on the next page)



Figure D.6: Fst per site around the center (dashed grey line) of a 10,000 bp-window from realSFS (Korneliussen et al. 2014). The labels at the top of the plot show the chromosome identifier. Species abbreviations on the right are ful: *Geospiza fuliginosa*, for.s: *Geospiza fortis* small morphotype, for.l: *G. fortis* large morphotype, mag: *Geospiza magnirostris*. Note that the y-axes change range for each plot. Panel A shows chromosomes 2, 3, 5, 10, 11, and 12, and panel B shows chromosomes 13, 1A, 18, 20, and Z.

D.2 Supplemental tables

Table D.1: Bayesian Sparse Linear Mixed Model (GEMMA) parameter estimates output averaged across 10 chains.

	Median (%)	Low 95%	Upper 95%
h	95.8	81.1	99.7
rho	35.1	22.4	50.6
PVE	97.1	87	99.8
PGE	50.0	39.6	63.5
n_gamma	0	0	0

Table D.2: Per site genome-wide Fst summary values for each pair of species with realSFS (Korneliussen et al. 2014).

		Fst									
Species 1	Species 2	Minimum	Median	Maximum	Mean	SD^\dagger	Unweighted [‡]				
G. fuliginosa	G. fortis small	0	0	0.301	0.003	0.008	0.001				
G. fuliginosa	G. fortis large	0	0	0.837	0.006	0.024	0.004				
G. fortis small	G. fortis large	0	0	0.433	0.005	0.014	0.002				
G. magnirostris	G. fuliginosa	0	0	0.718	0.002	0.012	0.003				
G. magnirostris	G. fortis small	0	0	0.493	0.006	0.017	0.001				
G. magnirostris	G. fortis large	0	0	0.926	0.009	0.031	0.000				

[†] Standard deviation.

[±] Unweighted Fst from realSFS fst stats estimate.

		Species ⁸										
Chr [†]	Count [‡]	<i>G. for.</i> s	G. ful	G. ful	G. mag	G. mag	G. mag					
Chr. Coul	Count	<i>G. for</i> . 1.	<i>G. for</i> . 1.	<i>G. for.</i> s.	<i>G. for</i> . 1.	<i>G. for.</i> s.	G. ful.					
1A	332	0.0083	0.084	0.0612	0.0051	0.0167	0.0811					
11	190	6E-04	0.0137	0.0117	0.001	0.0019	0.017					
18	591	0.001	0.0146	0.0109	0.0016	0.0025	0.0158					
10	298	0.0045	0.005	0.0026	0.0072	0.0038	0.005					
3	227	0.0035	0.0113	0.0023	0.0056	0.01	0.0194					
2	567	0.0012	0.0025	0.0015	0.0043	0.0052	0.0057					
5	76	0.0014	0.0012	0.0013	0.0014	0.0027	0.0038					
Ζ	417	0.0028	0.0023	0.001	0.0027	0.0073	0.0047					
20	451	3E-04	0.001	0.001	0.0067	0.0083	0.0091					
12	638	0.0015	0.0017	6E-04	0.0022	0.0036	0.0033					
13	425	7E-04	0.001	4E-04	0.0049	0.0038	0.0037					

Table D.3: Fst (unweighted) in 10,000 bp window near the major effect beak loci.

[†] Chromosome.

[‡] Count of the number of sites within the window centered on a major effect loci.

§ G. for. s.: G. fortis small; G. for. l.: G. fortis large; G. ful.: G. fuliginosa; G. mag.: G. magnirostris.

Table D.4: Linkage disequilibrium (LD) from ngsLD for the major effect loci from GEMMA using male ground finches (n = 482). Upper diagonal: D' (standardized D statistics), lower diagonal: r² (squared correlation coefficient); both statistics range from 0 to 1. Each r² and D' above 0.33 and 0.8 respectively are marked with an asterisk (*).

loc^{\dagger}	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
1		0.39	0.7	0.34	0.33	0.03	0.07	0.08	0.34	0.35	0.31	0.15	0.06	0.55	0.79	
2	0.04		0.37	0.11	0.24	0.14	1.00*	0.11	0.11	0	0.21	0.22	0.13	0.03	0.42	
3	0.39*	0.03		0.4	0.35	0.98*	0.4	0.13	0.5	0.64	0.36	0.24	0.1	0.71	0.81*	
4	0.02	0.01	0.02		0.66	0.4	0.07	0.28	0.25	0.1	0.42	0.09	0.05	0.1	0.47	
5	0.08	0.02	0.07	0		0.34	0.33	0.12	0.06	0.28	0.07	0.37	0.31	0.29	0.33	
6	0	0.01	0	0	0.09		0.23	0.22	0.12	0.1	0.03	0.57	0.55	0.04	0.13	
7	0	0	0.02	0	0.02	0.01		0.21	0.16	0.48	0.42	0.36	0	0.19	0.5	
8	0	0	0.01	0.02	0.01	0.04	0		0.27	0.17	0.17	0.26	0.28	0.02	0.08	D'
9	0.04	0.01	0.07	0.03	0	0.01	0.01	0.03		0.45	0.34	0.14	0.06	0.34	0.58	
10	0.04	0	0.1	0.01	0.03	0	0.1	0.01	0.18		0.45	0.07	0.08	0.46	0.79	
11	0.09	0.01	0.1	0.04	0	0	0.03	0.02	0.04	0.07		0.05	0.87*	0.25	0.46	
12	0.01	0.03	0.02	0	0.08	0.22	0.04	0.04	0.02	0	0		0.53	0.16	0.22	
13	0	0.01	0.01	0	0.09	0.27	0	0.07	0	0	0	0.17		0.07	0.11	
14	0.28	0	0.38*	0	0.07	0	0.01	0	0.05	0.07	0.06	0.01	0		0.8	
15	0.44*	0.03	0.57*	0.03	0.06	0	0.02	0	0.08	0.14	0.14	0.01	0	0.42*		
								r ²								

[†]loc: chromosomes:position; 1 chr2:209969308, 2 chr3:312229889, 3 chr5:488071042, 4 chr10:659792298, 5 chr11:682097235, 6 chr11:682105993, 7 chr12:684715809, 8 chr13:720499650, 9 chr1A:786507733, 10 chr1A:786508583, 11 chr18:845098737, 12 chr18:845099165, 13 chr18:845104049, 14 chr20:873735501, 15 chrZ:955258112

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Acronyms

W Expected fitness.

 $\Delta \bar{z}$ Change in mean trait values.

 \overline{W} Mean expected fitness.

 \bar{z} Mean phenotype.

 $\boldsymbol{\beta}_P$ Vector of prospective selection gradients.

 $\boldsymbol{\beta}$ Vector of selection gradients.

G Additive genetic variance-covariance matrix.

f(z) Fitness function with phenotype z.

k Number of dimensions of the smooth function in spline.

z Phenotypes.

 α Alpha; Significance level.

 β Beta; Linear selection gradient.

 χ^2 Chi square; Chi square value.

 γ Gamma; Quadratic selection gradient.

 κ Kappa; Parameter which controls the uncertainty in the ATM.

C. heliobates Camarhynchus heliobates, Mangrove finch.

C. parvulus Camarhynchus parvulus, Small tree finch.

G. fortis Geospiza fortis, Medium ground finch.

G. fuliginosa Geospiza fuliginosa, Small ground finch.

G. magnirostris Geospiza magnirostris, Large ground finch.

G. scandens Geospiza scandens, Common cactus finch.

AB Academy Bay.

AIC Akaike information criterion. Δ AIC for model comparison.

ANGSD Analysis of Next Generation Sequencing Data.

ATLAS Analysis tools for Low-depth and Ancient Samples.

ATM Azimuthal telemetry model.

BAM Binary Alignment Map.

bp Base pairs.

BSLMM Bayesian sparse linear mixed model.

BWA Burrows-Wheeler Aligner.

CDRS Charles Darwin Research Station. **chr** Chromosome. **CI** Confidance interval. CV Coefficient of variation.

df Degrees of freedom. **DNA** Deoxyribonucleic acid.

e.g. Exempli gratia, 'for example'.
EDTA Ethylenediamine tetraacetic acid.
EG El Garrapatero.
ETH Zurich Eidgenössische Technische Hochschule Zürich.
ETI Equal-Tailed Interval.

Fit. Fitness. FTA[™] card Flinders Technology Associates card.

GAM Generalized additive model.
GCV Generalized cross-validation.
GEMMA Genome-wide Efficient Mixed Model Association.
GLF Genotype Likelihood Format.
GLM Generalized linear model.
GPS Global positioning system.
GWAS Genome-wide association studies.

Hi-C High-throughput chromosome conformation capture technique.HL GOF Hosmer–Lemeshow goodness-of-fit.HR Home range.

i.e. Id est, 'that is'.

LD Linkage disequilibrium.Ln Natural logarithm.

MAF Minor allele frequency.MCMC Markov chain Monte Carlo.MCP Minimum convex polygons.Min. Minimum.

n Sample size. **NOAA** National Oceanic and Atmospheric Administration.

ONI Oceanic Niño Index.

PC1 First principal component.

PC2 Second principal component.

PCA Principal component analysis.

PIP Posterior inclusion probability.

ppm Pulse per minute.

PVE Proportion of variance explained.

QCBS Quebec Centre for Biodiversity Science.

REML Restricted maximum likelihood.

SAF Site allele frequency.
SC Santa Cruz Island.
SD Standard deviation.
SE Standard error on the mean.
SNP Single nucleotide polymorphism.
spp. species plurimae Latin for multiple species.
UD Utilization distribution.

UTM Universal Transverse Mercator.

VCF Variant Call Format.VHF Very-High Frequency.

WGS84 World Geodetic System 1984.

Glossary

- Adaptive landscape A smoother version of the fitness landscape obtained by calculating the mean fitness across an expected distribution of phenotypes (or allele frequencies) for a population centered at every possible location on the individual fitness landscape. xvi, 3–5, 7–9, 94, 98–101, 108, 112–114, 116–119, 134, 135, 138, 140–144, 148, 150–155, 158, 171, 173–175
- Adaptive radiation Rapid evolution of phenotypic and ecological diversity from a single ancestral species (Schluter 2000). Studies about adaptive radiations are focussing on the causes (here divergent selection) of phenotypic differentiation and ask how fit are the organisms in their environment. Note that nonadaptive radiation refer to only the speciation process, without divergent natural selection generating ecological differentiation, but could involve the evolution of secondary sexual traits that is not induced by the environment. The term was coined by Osborn (1902) and formalised by Simpson (1953). 1, 2, 4–11, 63, 66–69, 76–80, 98–101, 103, 104, 109, 113–118, 134, 135, 143, 144, 171, 173
- **Core area** A smaller portion of the home range. 31–33, 38, 40, 50
- **Disruptive selection** Existence of a fitness valley (or minimum) in the phenotypic range of a single population. Not to be confused with divergent natural selection where selection makes population means moving in different directions in phenotypic space. It should be noted that the difference between disruptive and divergent selection is fuzzy when populations are splitting in two. 63, 65–70, 72–80, 104
- **Divergent natural selection** Process where selection favors different phenotypic means and increasing the distance between them (therefore making intermediate phenotypes have a lower fitness). See note about disruptive selection. 1, 7, 10, 63, 94, 98, 99, 171, 173
- **Ecological speciation** Process where ecologically based divergent selection due to different environments promotes the evolution of reproductive isolation or provide a barrier to gene flow. See Nosil (2012) for a review on the subject. xvi, 10, 76, 80, 99, 175
- Ecological theory of adaptive radiation Schluter (2000) identifies three processes: 1. differential selection on heritable phenotypic variation between populations due to distinct environments, 2. resource competition causing further phenotypic divergence, and 3. ecological speciation or the emergence of reproductive isolation. 1, 100, 171
- **El Niño** Warm phase of the El Niño-Southern Oscillation (ENSO). In rainy years brought by El Niño, Darwin's finches benefit from an increase in plant (seeds, fruits, nectar, and pollen) and arthropod biomass and thus produce more offspring. 67, 69, 71, 78, 102
- Evolution Descent with modification. 31, 34, 41, 46, 98, 103, 110, 115, 139, 171, 172, 175, 176

Fitness Measure of the survival, reproduction or 'performance' of an individual for a particular

environment in which it is found. See Orr (2009) 'Fitness and its role in evolutionary genetics' or Dawkins (1982) 'The Extended Phenotype' for a discussion in depth of the concept. xv, xvi, 1–6, 8–10, 12, 13, 63, 66–70, 72–76, 80, 83–86, 94, 98–100, 134, 135, 138–143, 145, 148–154, 156, 158, 159, 171–175

- **Fitness landscape** Relationship between a variable trait with fitness (fitness function, when using a model to predict the expected fitness) which forms peaks and valleys of high and low fitness values respectively for each phenotypic combination. xvi, 2–4, 7, 8, 11, 12, 94, 95, 97–104, 106–114, 116, 118–123, 134, 140, 141, 151, 156, 173, 174
- **Habitat selection** Process where animals choose a habitat to perform certain behaviours or activities, see Stamps (1994) 'Territorial Behavior: Testing the Assumptions'. 31–34, 38, 39, 41–43
- Habitat use All the different ways an organism use biotic and abiotic in an environment, see Krausman (1999) 'Some basic principles of habitat use'. 31, 32, 41
- **Home range** Area traversed by an individual during its activities including foraging, mating, parental care, and other bahaviour as defined by Burt (1943) 'Territoriality and home range concepts as applied to mammals'). When an organism actively defends its home range, it is called a territory. 31–34, 38–46, 48, 50, 171
- La Niña Cold phase of the El Niño-Sourthern Oscillation (ENSO) with more or less opposite climate patterns to El Niño. 67, 69, 102
- **Mark-recapture** Method, where individuals are captured, marked and hopefully recaptured, used to estimate various parameters from a population such as population size, survival rate, movement, etc. Also known as capture-recapture or capture-mark-recapture. 33, 66, 75, 102
- **Natural selection** Process which can lead to adaptive evolution if a heritable phenotype is variable in a population and correlates with fitness causing certain individuals to survive and reproduce more effectively compared to other members of the population. In other words, it is a non-random population change due to differential reproduction of individuals with phenotypes that are advantageous (more fit) in a given environment. 31, 104
- **Prospective selection** Selection that would be required for a population mean phenotype to reach its nearest adaptive peak. 8, 95, 106, 112, 115
- **Retrospective selection** Amount of selection accumulated in the past since the separation of two species or populations from a common ancestor (used as an exploratory tool), assuming constant G since divergence, while included all genetically covarying traits under selection, and that differences between populations means are genetically based. 109
- **Spatial ecology** Field of study about how ecological dynamics are shaped by the spatial patterns of the landscape and organisms, populations, or species and by the interactions of biotic and abiotic factors. 31
- **Speciation** Process of species formation by the splitting of an evolutionary lineage. 31, 67, 78, 117, 118, 139, 140, 151, 154
- Territory Sociographical area in which an organism protects and defend. 32, 40, 41, 44–46

Protocols

Protocol 1 Chemagen Extraction: Dry Avian Blood on FTA card (Ioannis Ragoussis)

Objective.

Automated DNA extraction protocol developped by the McGill Innovation centre *Use*.

This protocol was used to extract the DNA samples.

Protocol

- 1. Safety Precautions:
 - 1.1. Turn on the blower in the Biological Safety Cabinet Class II (BSC_II) for 15 minutes before use.
 - 1.2. Spray down the full surface of the interior (side walls and instrumentation) of BSC_II using 70% ethanol.
 - 1.3. Wear protective clothing (lab coat, gloves and protective goggles) when working in the BSC.
 - 1.4. Prepare a biohazard bag inside the BSC_II for disposal of contaminated waste.
 - 1.5. Once work has been completed, seal disposable biohazard bag before removing and dispose of in a dedicated space for incineration.
 - 1.6. Clean all instruments with 70% ethanol and spray down BSC_II with 70% ethanol fully again.
 - 1.7. Turn off blower and turn on U.V. for 20 minutes.
- 2. Protocol:
 - 2.1. Under the BSC_II, punch out sample from FTA card using disposable Uni-Core punch straight into 2.0 mL Eppendorf tube OR cut out entire area containing sample into the tube. Disinfect scissors with a 1% sodium hypochlorite solution between each sample to avoid cross-contamination.
 - 2.2. While under the BSC_II add 1 mL CMG-756 Lysis Buffer 1 to the Eppendorf tubes containing the sample.
 - 2.3. Close the Eppendorf tubes before removing from the BSC_II for incubation.
 - 2.4. Incubate the sample Lysis Buffer mixture for 15 minutes at 98 °C.
 - 2.5. Remove the tubes from the heat block, let cool for 5 minutes at room temperature.
 - 2.6. Return sample to BSC_II and add 20 µL Protease K; mix well by vortex.
 - 2.7. Incubate the tubes for 10 min at room temperature.
 - 2.8. Spin down sample for 15-30 seconds in mini centrifuge in the BSC to remove droplets from lid.

- 2.9. Remove the lysate from the Eppendorf tube and transfer the 1 mL to a 50 mL Falcon tube.
- 2.10. Add 1 mL nuclease free water plus 240 μL CMG-756 magnetic beads per sample in the 50 mL tubes
- 2.11. Set up Chemagen deck as follows:
 - i. Position 1: Rack with Disposable Tips
 - ii. Position 2: 50 mL Tubes containing lysate with magnetic beadsA. Note: 4 mL Binding Buffer 2 (added automatically)
 - iii. Position 3: 50 mL Tubes_ 5 mL Wash Buffer 3 (added automatically)
 - iv. Position 4: 50 mL Tubes_ 5 mL Wash Buffer 4 (added automatically)
 - v. Position 5: 50 mL Tubes_ 10 mL Wash Buffer 5 (added automatically)
 - vi. Position 6: 50 mL Tubes prefilled with 10 mL Wash Buffer 6 (added automatically)
 - vii. Position 7: 4 mL Sarstedt Tubes prefilled with 200 µL-300 µL Elution Buffer 7
- 2.12. Check all plates for accurate orientation and fitting.
- 2.13. Close the cover and start the process by pressing the [Start] button for "chemagic DNA 2k prefilling H12 VD101111.che"
- 2.14. Once run is finished transfer rack containing elutes to the Janus Liquid handler (Perkin-Elmer) for sample clean up to remove any remaining beads (STEP1 in DWP) and transfer into Fluid-X 0.7 mL 2D barcoded storage tubes (STEP2).
- 3. Quality Control verification
 - 3.1. To verify sample integrity and fragment length run samples on a 1% agarose 96-well precast gel from Invitrogen
 - i. Prepare a 1 in 3 dilution of Invitrogen High Molecular weight DNA ladder
 - ii. Prepare 10 mL of 0.1X Rediload loading buffer from Invitrogen
 - iii. Aliquot $1 \mu L$ of sample and $19 \mu L$ of the Rediload loading buffer prepared into a 96 well Twintec plate using appropriate program on the Janus Perkin Elmer.
 - iv. Load 20 μL of the molecular ladder in the designated position on the 1% agarose gel
 - v. Load $20\,\mu$ L of the samplessample prepared onto the 1% agarose precast 96 well gel from Invitrogen.
 - vi. Run 10 minutes on the E-Gel system from Invitrogen on EG setting.
 - vii. Once run is finished, take picture on Gel Imaging system
 - viii. Upload Image into Information tracking System.
 - ix. Recap screw capped tubes, decap using tubes Hamilton LabElite ID Capper.
 - 3.2. Quantify samples using Pico green assay.
 - i. Prepare 1x TE from the provided 20x TE bottle
 - ii. Prepare standards for standard curve using the provided Lambda DNA standard at $100\,\mu g\,mL^{-1}$
 - For High range Standard curve do 1 in 2 serial dilutions in 1x TE
 - For Low range standard curve do a 1 in 10 dilution of the provided Lambda DNA and from there do 1 in 2 serial dilutions
 - Aliquot each in triplicate into a 96 well plate (columns 1,2,3 contain High range standards ; columns 4, 5,6 contain Low range standards. See Table E.1 for the set of final concentrations.
 - iii. Prepare 11 mL of 1x TE and 60.0 µL PicoGreen©reagent for every 96 well plate

needed to be assayed ; protect from light

- iv. Vortex well to mix and transfer into 1/4 size reagent reservoir from Perkin Elmer
- v. Aliquot 99 μ L PicoGreen©TE mix per well in a 96 well half area black, flat bottom assay plate from Corning and 1 μ L of the standards from standard plate created in step 9.2.12.2 using the appropriate Janus Perkin Elmer Pico program; Note: one plate is needed for standards only for each set of plates to be Qc'd at one time
- vi. Aliquot 99 μ L PicoGreen©TE mix per well in a 96 well half area black, flat bottom assay plate from Corning and 1 μ L of the samples using the Janus Perkin Elmer Pico program.
- vii. Scan plates on Tecan Spark 10M plate reader (excitation 480 nm, emission 520 nm) using Magellan program entitled "Pico_4plates"
- viii. Upload Pico green quantification values into Information tracking system.
- 4. Hazardous waste disposal:
 - 4.1. The Invitrogen 1% precast gels used in section 2.15 contain Ethidium Bromide [CAS# 1239-45-8]; wear gloves, lab coat and safety glasses when manipulating; dispose of gel in designated biohazardous waste.
 - 4.2. The Quant-iT[™]PicoGreen©dsDNA reagent [CAS# 177571-06-1] used in section 2.16 contains dimethylsulfoxide; wear gloves, lab coat and safety glasses when manipulating; dispose of in designated biohazardous waste bin.
 - 4.3. All biological material and and labware having come into contact with the biological material must be discarded in a biohazard bag and incinerated.

Table E.1: Standard curve data

High range Standard Curve	Low range Standard curve
$100 \mu g m L^{-1}$	$10 \mu g m L^{-1}$
$50 \mu g m L^{-1}$	$5 \mu \mathrm{g}\mathrm{mL}^{-1}$
$25 \mu\mathrm{g}\mathrm{mL}^{-1}$	$2.5 \mu g m L^{-1}$
$12.5 \mu g m L^{-1}$	$1.25 \mu g m L^{-1}$
$6.25 \mu g m L^{-1}$	$0.625 \mu g m L^{-1}$
$3.125 \mu g m L^{-1}$	$0.3125\mu gm L^{-1}$
$1.5625\mu gm L^{-1}$	$0.15625\mu gm L^{-1}$
$0 \mu g m L^{-1}$	$0 \mu g m L^{-1}$

Protocol 2 NEXTERA low coverage library adapted from Baym (2015)

Version.

01.09.2023 - Adapted from Baym et al. (2015), originally adapted by Sarah Bouchemousse, Claudia Michel & Julia Geue (ETH Zurich). Here, further adapted by Xenia Wietlisbach, Ilektra Schulz & Liam Singer

Objective.

Tagging DNA fragments, amplification using polymerase chain reaction (PCR), and size selection of DNA fragments.

Use.

Library preparation of Darwin's finches DNA extractions. For future use of the protocol, we would not recommend the pooling step before size selection the way it was done here.

We used *Illumina Tagment DNA TDE1 Enzyme and Buffer (Large Kit; 20034198)* and *Nextera XT Index Kit v2 (Set A [FC-131-2001] and D [FC-131-2004])* from Illumina.

Protocol

DNA: Normalize at 3.5 - 7 ng μ L⁻¹ in a volume of 20 μ L (in 96-plates, using the Brand LHS robot). **Indices:** A combination of sets A and D can be used to generate 384 different indices: (A-A, A-D, D-A, D-D). Adapters start with a concentration of 5 μ M and are diluted at 1:3 to 1.25 μ M in the plates before using.

Tagmentation

- Keep everything on ice
- Mix well and centrifuge down after every step
- Prepare aliquots of the Tag-enzyme
- Handle the Tag-enzyme carefully. **Don't vortex it** just mix gently and spin down.
- Prepare the heat block in advance (set to 55 °C)
- 1. Thaw DNA, vortex and spin down briefly
- 2. Prepare MasterMix (MM)
 - 2.1. 2.5 μL Tag-Buffer + 0.5 μL Tag-enzyme (for every sample). Allow for 10% pipetting error
 - 2.2. Mix by pipetting up and down 10x
 - 2.3. Centrifuge at 280 rcf for 30 seconds (rcf=g)
- 3. Pipette 3 µL Tag-MM into new PCR plate
- 4. Add $2 \mu L$ DNA into wells. Pipette up and down 10x
- 5. Centrifuge at 280 rcf for 30 seconds (rcf=g)
- 6. Incubate at 55 °C for 10 minutes. While waiting, prepare for PCR:
 - 6.1. Thaw indices and KAPA Hifi mix at room temperature
 - 6.2. Invert to mix gently and spin down briefly
 - 6.3. If there is time, prepare a MM of KAPA and H_2O (as seen below)
- 7. Cool the samples down on ice again

PCR

• Make sure indices and KAPA are thawn at room temperature

- Mix well and centrifuge down after every step
- Program the PCR machine beforehand
- 1. Create a MM from 12 μL KAPA Hifi Mix and 4 μL H₂O (for every sample). Allow for 10% pipettig error
- 2. Cap KAPA-H₂O-MM and spin down briefly
- 3. Make sure the tagmented DNA is cooled down
- 4. Add $16 \mu L$ KAPA-H₂O-MM and the corresponding $4 \mu L$ IDT Adapter-Mix at $1.25 \mu M$ into the tagmented DNA. Mix by pipetting up and down 10x after adding
- 5. Cover and spin at 300 rcf for 30 seconds
- 6. Add to cycler (120 N with a 96-well-plate and seal, or at 60 N when using strips)
- The total volume for PCR is $25 \,\mu$ L per sample

Table E.2: PCR steps for protocol NEXTERA low coverage library

72 °C 95 °C	3 min 3 min	
98 °C 62 °C 72 °C	20 s 15 s 1 min	13 cycles
72 °C 4 °C	1 min ∞ or as i	needed

Single size selection - pool 8 samples

The size selection is performed in pools of 8 samples each, to ensure enough volume for working with the Ampure beads. Only short fragments are removed in this step. Long fragments are removed by the sequencing facility for the entire sequencing line.

- Let the Ampure beads warm up to room temperature for at least 30 minutes
- Keep Ampure beads mixed up well by vortexing and spinning down briefly repeatedly
- Ampure-MM and 80% ethanol can be prepared in advance. 80% ethanol mix has to be prepared freshly every time!
- Keep some 2 mL Eppendorf tubes filled with H_2O on a heat block set to 65 °C for elution

Removing short fragments

- 1. To create a pool, add half of the PCR product $(11.5 \,\mu\text{L})$ of 8 samples into a shared 1.5 mL Eppendorf tube
- 2. Mix by pipetting up and down 10x
- 3. Prepare MasterMix
 - 3.1. 122.4 μL beads + 48 μL H₂O (for every pool of 8 samples. Results in 0.72x for size selection). Allow for 10% pipetting error
 - 3.2. Keep vortexing MM before every use
- 4. Add 170.4 µL MM into PCR product pool tube. Vortex and centrifuge.
- 5. Wait 10 min (vortex and centrifuge rapidly every 2-3 minutes)
- 6. Bring the tube in contact with the magnet
- 7. Wait for 3 minutes
- 8. **DISCARD** the supernatant

Wash beads

- 9. Add $800 \,\mu\text{L} 80\%$ ethanol to pellet
- 10. Wait for 30 seconds, then remove it again
- 11. Wait for 5 minutes (if not dry wait another 5 minutes) to make sure that the ethanol is evaporated. The sample pellet should appear dull and not smell of ethanol anymore.

Prepare eluate

- 12. Make sure that the H_2O prepared for elution is heated to 65 °C
- 13. Remove tube from the magnet and elute in $100 \,\mu\text{L}\,\text{H}_2\text{O}$
- 14. Vortex and centrifuge
- 15. Wait 10 min (vortex and centrifuge rapidly every 2-3 minutes)
- 16. Bring the tube in contact with the magnet
- 17. Wait for 3 minutes
- 18. Transfer the eluate into a new $0.5 \,\mu\text{L}$ tube or a 96-well plate

Protocol 3 Reconditioning PCR for DNA library pools

Version.

01.09.2023 Xenia Wietlisbach, Ilektra Schulz & Liam Singer

Objective.

For library pools showing a PCR bubble (unexpected secondary artifact peak in the distribution of fragment length) on the Tapestation plot, we employ the use of a reconditioning PCR to dissolve this bubble. Libraries with PCR bubbles do not cause problems while sequencing, but their Tapestation fragment length distribution and Qubit concentration measurements are inaccurate and therefore normalization between library pools is hindered. Be advised that the use of a reconditioning PCR can increase the proportion of duplicates during sequencing)

Use.

Used after protocol 'NEXTERA low coverage library' when a PCR bubble was found.

Protocol

• Make sure primers and KAPA are thawn at room temperature

- Program the PCR machine beforehand
- 1. Prepare PCR-strip or 96-well plate
- 2. Prepare MasterMix (amounts given per library pool)
 - 2.1. 10 µL KAPA
 - 2.2. 1 µL standard Illumina P5 primer
 - 2.3. 1 µL standard Illumina P7 primer
 - $2.4.~6\,\mu L~H_2O$
 - 2.5. Mix by pipetting up and down 10x
- 3. Pipette $2\,\mu$ L library pool into the PCR-strip or 96-well plate
- 4. Add 18 µL PCR-MM into the PCR-strip or 96-well plate. Mix by pipetting up and down 10x
- 5. Cover and spin at 300 rcf for 30 seconds
- 6. Add to cycler (120 N with a 96-well-plate and seal, or at 60 N when using strips)
- The total volume for PCR is $20 \,\mu$ L per sample

Table E.3: PCR steps for protocol Reconditioning PCR for DNA library pools

95 °C	3 min	
98 °C 62 °C 72 °C	20 s 15 s 30 s	3 cycles
72 °C	1 min	
4 °C	∞ or as	needed

• The size selection has to be repeated after the reconditioning PCR



Picture of the common cactus finch (G. scandens) on Isabela island.