The terroir of the finch:

Spatio-temporal dynamics in the evolution and ecology of Darwin's finches

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Para el abue, por enseñarme
el verdadero amor por la naturaleza.

Contents

Abstract

Studying the factors that influence the spatio-temporal variation of species' adaptive traits, their diversity and abundance is crucial for understanding how organisms interact with their environment, how they respond to changing conditions and how they maintain the functionality of ecosystems.

In today's human-dominated landscapes, identifying factors that drive ecological and evolutionary processes is crucial for predicting future scenarios and protecting ecosystems. Islands offer a great opportunity to understand these dynamics because, as closed ecosystems, the impacts of human development occur more rapidly and often in an exacerbated manner. In this thesis, I use a famous example of adaptive radiation, Darwin's finches in the Galápagos Islands, to investigate how environmental factors influence spatial and temporal variation in phenotypic traits, species diversity and abundance.

Most evidence suggests that Darwin's finches evolve in response to drastic weather events, but little is known about the spatial biotic and abiotic factors that shape their phenotypic variation. In the first chapter, I assess the main contributions of temporal and spatial effects to phenotypic variation in Darwin's finches, using 10 years of data on beak and body traits of a medium-sized ground finch, *Geospiza fortis,* and environmental factors associated with food availability. This study shows that the spatial effect is strong in Darwin's finches, consistent with the hypothesis of diversification facilitated by ecological differences.

Nevertheless, longer-term changes in weather may influence the phenotypic trajectories of Darwin's finches, particularly in the context of anthropogenic climate change. In chapter two, I examine the impact of climate change on the phenotypic traits of Darwin's finches using a 24-year dataset of beak and body traits of the medium-sized ground finch (*G. fortis*) at two sites, and data on precipitation and temperature. My results show that phenotypic variation in Darwin's finches is more responsive to short-term changes in temperature and precipitation than to long-term changes such as climate change - even when the latter is present in the Galapagos Islands.

In addition, other human-related activities such as urbanization can also alter the habitat of species with potential effects on their phenotypic variation. In chapter three, I examine the parallel and non-parallel responses to urbanization impacts in two urban-dwelling species, the medium (*G. fortis*) and small (*G. fuliginosa*) finches. My results indicate that even when the impact of urbanization on adaptive traits is small, there are parallel responses within and between species in Darwin's finches.

Finally, human activities such as agriculture are another factor that can influence species ecology and evolution. In chapter four, I extended my analyses to examine the environmental determinants of species diversity and abundance in the landbird communities of the agricultural areas of Galapagos. My results indicate that factors such as vegetation cover and elevation, rather than vegetation type or agricultural practices, explain most of the variation in species richness, evenness and relative abundance.

Overall, my thesis demonstrates the influence of short-term environmental changes, human activities, and spatial variation on the ecology and evolution of Darwin’s finches. It highlights critical factors impacting island species and underscores potential future risks as human activity increases.

Résumé

L'étude des facteurs qui influencent la variation spatio-temporelle des traits adaptatifs des espèces, leur diversité et leur abondance est cruciale pour comprendre comment les organismes interagissent avec leur environnement, comment ils réagissent aux conditions changeantes et comment ils maintiennent la fonctionnalité des écosystèmes. Face aux importants développements humains, il est particulièrement urgent d’identifier les facteurs qui influencent les processus écologiques et évolutifs afin de pouvoir prédire les scénarios futurs et prendre les mesures nécessaires pour protéger les écosystèmes. Les îles offrent une excellente occasion de comprendre ces dynamiques car en tant qu'écosystèmes fermés, les impacts du développement humain se produisent plus rapidement et souvent de manière exacerbée. Dans cette thèse, j'utilise un exemple célèbre de radiation adaptative, les pinsons de Darwin des îles Galápagos, pour étudier comment les facteurs environnementaux influencent la variation spatiale et temporelle des traits phénotypiques, de la diversité et de l'abondance des espèces.

Les recherches actuelles suggèrent que les pinsons de Darwin évoluent en réponse à des événements météorologiques drastiques, mais on ignore comment les facteurs spatiaux peuvent façonner leur variation phénotypique. Dans le premier chapitre, j'évalue les principales contributions des effets temporels et spatiaux à la variation phénotypique chez les pinsons de Darwin, en utilisant 10 ans de données sur des traits associés au bec et au corps du Géospize à bec moyen, *Geospiza fortis*. J’évalue aussi les facteurs environnementaux associés à la disponibilité de la nourriture. Cette étude montre que l'effet spatial est important chez les pinsons de Darwin, ce qui est cohérent avec l'hypothèse d'une diversification facilitée par les différences écologiques.

Néanmoins, des changements météorologiques à plus long terme peuvent influencer les trajectoires phénotypiques des pinsons de Darwin, en particulier dans le contexte du changement climatique anthropique. Dans le deuxième chapitre, j'examine l'impact du changement climatique sur les traits phénotypiques des pinsons de Darwin en utilisant un ensemble de données sur 24 ans concernant les traits du bec et du corps du Géospize à bec moyen (*G. fortis*) à deux sites différents. Je combine ensuite ces données phénotypiques avec des données sur les précipitations et la température. Mes résultats montrent que la variation phénotypique des pinsons de Darwin est plus sensible aux changements à court terme de température et de précipitations comparés aux changements à long terme comme le changement climatique - même si ce dernier est présent dans les îles Galápagos.

D'autres activités anthropiques, telles que l'urbanisation, peuvent également modifier l'habitat des espèces et avoir des effets potentiels sur leur variation phénotypique. Dans le troisième chapitre, j'examine les réponses parallèles et non parallèles aux impacts de l'urbanisation chez deux espèces qui habitent des milieux urbains, le Géospize à bec moyen (*G. fortis*) et Géospize à bec petite (*G. fuliginosa*). Mes résultats indiquent que même lorsque l'impact de l'urbanisation sur les traits adaptatifs est faible, il existe des réponses parallèles au sein des espèces et entre les espèces chez les pinsons de Darwin.

Finalement, l'agriculture est une autre activité anthropique qui est susceptible d'influencer l'écologie et l'évolution des espèces. Dans le chapitre quatre, j'élargis mes analyses pour examiner les déterminants environnementaux de la diversité et de l'abondance des espèces dans les communautés d'oiseaux terrestres des zones agricoles des Galápagos. Mes résultats indiquent que des facteurs tels que la couverture végétale et l'altitude, plutôt que le type de végétation ou les

pratiques agricoles, expliquent la majeure partie de la variation de la richesse d’espèces, de la régularité d’espèces et de l'abondance relative des espèces.

Dans l'ensemble, ma thèse contribue à notre compréhension de la manière dont les populations en milieu naturel réagissent aux changements d’habitat. Elle fournit des informations pertinentes sur les facteurs qui ont un impact majeur sur les dynamiques écologiques et évolutives des espèces insulaires, et met en évidence ceux qui, même s'ils ont un faible impact, ont le potentiel de devenir des facteurs majeurs au fur et à mesure que les exigences humaines augmentent.

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Contribution to Original Knowledge

All the manuscript chapter of this thesis (Chapter 1-4) represent original contributions to scientific knowledge.

In chapter one, I assess the contributions of space, time and their interaction to the phenotypic variation of Darwin’s finches. My findings suggest that the spatial effect is the main driver of phenotypic variation in Darwin’s finches and environmental variables relates to food availability. These results reinforce the hypothesis that diversification in Darwin's finches is driven by ecological differences and brings perspective to further studies on Darwin’s finches’ ‘rapid’ evolution.

In chapter two, I explore climate change impact on the phenotypic variation of Darwin’s finches. My results suggest that even when there is evidence of climate change in certain sites of Galápagos, Darwin’s finches’ phenotypic trajectories seem to be unsensitive to it, and that rather short-term weather changes are the one that drive selection in this system.

In chapter three, I analyze parallel and non-parallel responses in Darwin’s finches phenotypic variation in face to urbanization impact. My results indicate that although urbanization has a small effect on the phenotypic variation of Darwin’s finches, it can drive parallel responses within and across urban-dwelling species.

In chapter four, I investigate the environmental determinants that drive species diversity and abundance in landbird communities in the agricultural areas of Galapagos. My results indicate that landbird diversity and abundance are mainly driven by vegetation cover and elevation, and not by vegetation types or agricultural practices.

Thesis Format

This thesis follows a manuscript-based format that includes a general introduction, four manuscript chapters (Chapter 1-4), and general discussion and conclusion. Linking statements help connecting the ideas between chapters. I am the leading author of the manuscripts in chapter one, two, and four, and leading co-author in chapter three. The first chapter has been published in a peer-reviewed journal, the second chapter will be submitted for publication, and chapters three and four are being corrected for journal submission. I have received permission from all co-authors to include the manuscripts in this thesis.

Chapter 1:

Carrion-Avilés, Paola, Joost A. M. Raeymaekers, Luis F. De León, Jaime A. Chaves, Diana M. T. Sharpe, Sarah K. Huber, Anthony Herrel, Bieke Vanhooydonck, Kiyoko M. Gotanda, Jennifer A. H. Koop, Sarah A. Knutie, Dale H. Clayton, Jeff Podos and Andrew P. Hendry. (2022). The terroir of the finch: How spatial and temporal variation shapes phenotypic traits in Darwin's finches. *Ecology and Evolution*, *12*(10), e9399. (DOI: 10.1002/ece3.9399)

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Chapter 3:

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Chapter 4:

Carrion-Avilés, Paola, Francisco Laso, Andrew P. Hendry, Jaime A. Chaves, and Birgit Fessl. Environmental determinants of landbird diversity and abundance in the agricultural areas of the Galápagos Islands. *In preparation.*

Contribution of Authors

Chapter 1: Paola Carrion-Avilés, curated and analyzed the data, wrote manuscript, prepared visualization of data. Joost A. M. Raeymaekers and Andrew P. Hendry, collected data, conceptualized and supervised the project, contributed with main corrections. Luis F. De León, Jaime A. Chaves, Diana M. T. Sharpe, Sarah K. Huber, Anthony Herrel, Bieke Vanhooydonck, Kiyoko M. Gotanda, Jennifer A. H. Koop, Sarah A. Knutie, Dale H. Clayton, Jeff Podos, collected data and provided secondary corrections and suggestions. Jaime A. Chaves obtained the research permits. Andrew P. Hendry provided funds to the project.

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General Introduction

Many evolutionary and ecological processes in nature result from environmental changes. These various changes occur at spatial and temporal scales to which species must respond to by either adapting or going extinct. In evolution, environmental variation creates different selection regimes to which populations respond by modifying their phenotypes in a plastic or evolutionary manner (Moran et al. 2016). In ecology, changes in the environment produce rather quick responses that affect populations, which present changes in their abundance (Chen et al. 2011, Johnson et al. 2013) and/or distribution (Ehrlén et al. 2015). Previous studies have found some major drivers of phenotypic (Joswig et al. 2022, Rubalcaba et al. 2023), species diversity (Gagné et al. 2020, Jaureguiberry et a. 2022, Hald-Mortensen 2023), and abundance variation (Gregory et al. 2023) that include temporal factors such as climate change and spatial factors such as habitat modification.

Here, I provide an overview of the main factors that influence the spatio-temporal variation in phenotypes, species diversity, and abundance with emphasis on the human-related activities that have the potential of causing long-lasting changes in the ecology and evolution of species, and the dynamics between them.

1.1 Determinants of spatial variation in phenotypic traits, species diversity and abundance

From an evolutionary point of view, phenotypic variation can be the product of plasticity or selection. Therefore, research often focuses on understanding how spatial environmental factors relate to variation in selection estimates or plasticity. Several studies have found that habitat heterogeneity can create different selection regimes that lead to different phenotypes (e.g Endler 1980, McKinnon & Rundle 2002, Urban et al. 2011, Siepielski, et al. 2013). Whereas other studies have found that this spatial variation is rather the result of a plastic phenotypic response (Schmid et al. 2019). Yet, in both scenarios, consideration must be given to the scale of spatial variation (micro versus macrogeographical) since it play an important role on our understanding of local adaptation and the impact of gene flow (Richardson et al. 2014).

From an ecological point of view, multiple processes that occur at different scales shape biodiversity and abundance (Laiolo et al. 2015). Although size is probably the most studied determinant of variation in species diversity (e.g Turner 2001, Hart et al. 2017), other studies have also emphasized the role of environmental heterogeneity in promoting diversity, endemism, and abundance (Schmeller et al. 2018, Murali et al. 2021). Examples of environmental heterogeneity shaping diversity and abundance have been seen across latitudes (Rohde 2002), and elevational ranges (Laiolo et al. 2018). However, since human presence is rapidly expanding across habitats, it is now crucial to understand biodiversity patterns in human-dominated landscapes and their specific drivers.

1.1.1 Human-related spatial factors that influence the variation in phenotypic traits, biodiversity, and abundance

Habitat loss is currently one of the major threats for phenotypic variation and biodiversity worldwide (Montrás-Janer et al. 2024). Specifically, habitat loss caused by urbanization and intensive agriculture have shown negative effects on several evolutionary and ecological processes.

In evolution, various studies have highlighted the detrimental effects of urbanization on genetic diversity, gene flow, and mutation rates (reviewed in Johnson and Munshi-South 2017), yet others suggest that urbanization could increase plastic phenotypic variation if relaxed selection and environmental variation allow for different phenotypes to persist (Thompson et al. 2022). Additionally, factors such as intensive agriculture can change phenotypic variation by modifying selection patterns through the persistent use of pesticides and in this way promote pest adaptation (Palumbi 2001). Agricultural ecosystems and/or domesticated species can also provide new niches for wild species to occupy (reviewed in Turcotte et al. 2017), whereas interactions between wild and domesticated species promote gene flow and introgression (Marshall et al. 2014).

In ecology, urbanization has been shown to affect species diversity and abundance in ways that vary according to the characteristics of the city of interest (Elmqvist et al. 2013). Yet, some general patterns have emerged in which older and larger cities seem to host more non-native and generalist species (Pyšek et al. 2004, Pyšek and Jarošík 2005), native species richness decreases with increased urbanization (Dunn 2011). Finally, research has shown that intensive agriculture has severe detrimental effects on biodiversity (Green et al. 2005, Newbold et al. 2014), yet within the variety of agricultural agroecosystems, practices that encourage forest growth and shade have the opposite effect and they rather promote higher levels of diversity and abundance (reviewed in Oakley and Bicknell 2022).

1.2 Determinants of temporal variation in phenotypic traits, species diversity, and abundance

Diversity of life forms on earth is doubtless the product of historical climate variation across decades and millions of years (e. g Ricklefs et al. 1999, Wiens and Donoghue 2004, Svenning et al. 2015). Yet the unprecedent and rapid change of climate caused by human activities deserves special consideration since it is drastically affecting our world in a way that is now considered a major threat for the world's current biodiversity. These threats are affecting diversity at all levels—from genes to entire biomes (Scheffers et el. 2016).

Over the past few decades, precipitation and temperature seem to be the main drivers of climate-change related phenotypic variation, (Siepielski et al. (2017), species diversity and abundance declines (Şekercioğlu et al. 2012). For instance, birds have advanced their breeding time in response to increasing temperatures (Nussey et al. 2005), whereas a decrease in precipitation has caused a severe reduction in desert's species diversity and abundance (Iknayan and Beissinger 2018).

From an evolutionary perspective, changes in phenotypic traits are often misinterpreted as the result of evolutionary change (heritable genetic changes) in response to climate change, yet evidence suggest that these responses can be also plastic (Merilä and Hendry 2014). In any case, there is an increasing number of examples in both scenarios. Genetically based phenotypic responses to human-caused climate change include changes in organisms' migration (Kovach et al. 2012), breeding timing (Charmantier and Gienapp 2014), and variation in thermal and spatial range shifts (Parmesan et al. 1999, Thomann et al. 2015). Other traits such as body size and other appendages size, on the other side, seem to have a plastic basis rather than genetic nature (Teplitsky et al. 2008).

From and ecological perspective, human-related climate change can rapidly impact species abundance and diversity depending on their thermo-tolerance. For instance, only in the past few decades, around 50% of warm-tolerant marine species and European bird populations have increased, whereas 50 % of their cold-tolerant counterparties have decreased (Gregory et al. 2009, Poloczanska et al. 2016). Furthermore, some thermo-tolerant disease vectors that affect both terrestrial and marine bird species have increased in abundance in response to increasing global temperatures (Munson et al. 2008) (Randall and van Woesik 2015).

Global analyses including plants and animals have shown that increasing temperatures and precipitation are responsible for biodiversity loss across all vertebrates (e. g Habibullah et al. 2022), and that endemic species are particularly vulnerable to these changes (Manes et al. 2021). Finally, although terrestrial plant growth has increased globally as a response to climate change, this response can also be related to natural climatic events such as El Niño and La Niña (Scheffers et al. 2016). Moreover, the potential consequences of this increase in plant growth remain unknow.

1.3 Factors that influence spatio-temporal variation in phenotypic traits, biodiversity, and abundance in Galápagos

The Galápagos Islands are located in the Pacific Ocean 1000 miles west from continental Ecuador to which they belong (90°01' - 89°16' W, 1°40' S - 1°36' N). This archipelago of volcanic origin has a land surface of 798 500 ha and is composed by 13 major islands, 5 minor islands, and 216 islets and rocks (DPNG, 2014). In 1978, the Galápagos Islands were declared a World Natural Heritage Site by UNESCO (UNESCO 2024) due to their unique biotic and abiotic characteristics. Since 1959, 97% of its area is considered protected and is regulated by the Galápagos National Park, whereas the remaining 3% is occupied by urban and agricultural areas (DPNG 2014). Spatial and temporal factors such as their remote location, climate, and topography have enabled the development of a high level of endemism and biodiversity across the Galápagos Islands (Tye et al. 20002). This incredible amount of endemism and biodiversity is currently under threat by increasing human-related activities such as urbanization, agriculture, and tourism.

1.3.1 Location

The Galápagos archipelago is formed by active volcanic islands that are approximately 4 million years old (Heads and Grehan 2021). The islands are located on the equator where three main oceanic currents converge: the Cromwell current coming from the east, the Panama current coming from the north, and the Humbolt current coming from the south (Liu et al. 2014). The interaction between the different currents creates a gradient of oceanic conditions that interact with different atmospheric settings to further create a unique variable climate in both the marine and land ecosystems.

1.3.2 Climate

Fluctuations in oceanic currents and winds in Galápagos are governed by a warm band called Inter-Tropical Convergence Zone (ITCZ) that moves inter-annually creating two seasons (Trueman and d'Ozouville, 2010). A warm season from December to May, characterized by increased rainfall (500 mm overall, approximately 185 mm in the lowlands, and 1670 mm in the highlands), and a cold season from June to November with reduced precipitation (130 mm overall, 65 mm in the lowlands and 1050 mm in the highlands) (Paltán et al. 2021). Temperature oscillates between 22 and 26 ° C, being higher during the warm season (Paltán et al. 2021). During the cold season, water from the sea surface rises and condenses in the highlands creating a constant slight rain locally called '*garúa'* (Trueman and d'Ozouville, 2010). There is high inter-annual variation in temperature and precipitation across the Galápagos which becomes even more variable with El Niño events. In Galápagos, El Niño years are characterized by severe rainfall, especially during the warm season (3000 mm of mean annual precipitation for an El Niño year vs 1100 mm for non-El Niño year) (Sell and Rea 1999, Paltán et al. 2021). Additionally, following El Niño, La Niña events commonly occur, and in Galápagos are characterized by severe and extensive periods of drought (Trueman and d'Ozouville, 2010).

The impacts on Galápagos biodiversity of drastic weather events such as El Niño and La Niña have been studied across both marine and land ecosystem. The result of this research suggests that the impacts on marine and land ecosystems are often different (Dueñas et al. 2021). Marine ecosystems are severely affected by El Niño events because they cause an increase in sea temperature which reduces plankton productivity and decreases essential nutrients needed for sustaining these ecosystems. Thus, El Niño events have negative on marine populations abundances (e.g Valle and Coulter 1987, Vinueza et al. 2006, Champagnon et al. 2018). In land ecosystems, increases in rainfall caused by El Niño increase primary productivity and with it the abundance of some invertebrates and land bird populations that depend on them (Grant et al. 2000). Yet, other species such as the Galápagos tortoises can be negatively affected given that abundant rains destroy their nests and bring up invasive ants that feed on their eggs (Wauters et al. 2018). Additionally, during El Niño years the prevalence of certain avian diseases appears to be higher (Jiménez-Uzcátegui et al. 2007), and nestling parasitism becomes exacerbated (Dudaniec et al. 2007).

1.3.3 Vegetation

Vegetation in the Galápagos is strongly influenced by climate, seasonality, isolation, geological conditions and, more recently, human impacts (Estrella et al. 2021). Islands, especially the large ones, present several vegetation zones across an elevation gradient that have the following classification (Wiggins and Porter 1971):

- Littoral zone: vegetation has direct contact with the sea, characterized by salt-tolerant small trees and shrubs such as mangroves.

- Arid zone: immediate zone after the littoral zone occurring between 80 and 120 m. Characterized by several species of native and endemic cacti, small and spiny shrubs and trees.
- Transition zone: as its name indicates this zone is characterized by evergreen transition plants that overlap the arid and the *Scalesia* zones, with larger trees and more humid vegetation between 80 and 200 m.
- *Scalesia* zone: between 180 and 400 m characterized by humid vegetation and several endemic species of the genus *Scalesia,* whose trees can reach 20 m or more.
- *Miconia* zone: between 400 and 500 m characterized by humid vegetation of dense shrubs of the genus *Miconia.*
- Fern zone: characterized by humid vegetation of small shrubs, grasses, and a variety of fern species occurring between 500 and 700 m.

Using pollen fossil records, Restrepo et al. (2012) have shown that vegetation in Galápagos has remained mostly stable for the past 2690 years. However, more recent studies indicate that Galápagos vegetation has been drastically changing since the intensification of human activities such as agriculture, urbanization, and the introduction of invasive species in the 70s (Bastille-Rousseau et al. 2017, Rivas-Torres et al. 2018).

1.3.4 Anthropogenic impact

The development of the first official settlements in the Galápagos started in 1832 after annexed the islands were annexed as part of Ecuador (Stahl et al. 2020). Yet, it was not until the

90s that the human population started to rapidly expand as a product of intensification in agricultural, fishing, and touristic-related activities (Stahl et al. 2020). Today, the Galápagos Islands have four small cities distributed across their main islands: Puerto Ayora (15,700 habitants), Puerto Villamil (2,350 habitants), Puerto Velasco Ibarra (149 habitants), and Puerto Baquerizo Moreno (7,100 inhabitants), this last one being the capital of the province (INEC, 2015).

Insular ecosystems, such as the Galápagos, are fragile to change given their isolation, environmental conditions, and high levels of endemism (both of flora and fauna). These unique features make the islands highly susceptible to negative human impacts and thus, a global conservation priority (Kier et al. 2009). Nowadays the main threats to Galápagos biodiversity are habitat loss, climate change, and the introduction of exotic species (Bensted-Smith et al. 2002).

Habitat loss in the Galápagos is mainly caused by conventional agricultural practices, urbanization, and invasion of exotic species (Watkins and Cruz 2007). The highlands of Galápagos, which are the most diverse and productive areas, are nowadays mostly covered by invasive plant species and pastures. As a result, only a small fraction remains as native forests (Laso et al. 2019). However, studies that assess the impacts of these threats to the native diversity of these ecosystems are scarce. Geladi et al. (2021) found that landbird species richness in the highlands is higher in forest patches and coffee plantations compared to pastures. Similarly, De la Torre (2012) found higher diversity of macroinvertebrates in organic agricultural areas compared to pastures.

Urbanization is also a main driver of habitat loss in the Galápagos. Although local laws prevent further expansion of the urban frontier in Galápagos, there has been an annual increase of 3.3 % in urban growth (impervious surface) over the last three decades (Benítez et al. 2018). The impacts of urbanization on Galápagos species have been mostly studied from an eco-evolutionary perspective and mainly focusing on Darwin's finches (e.g Hendry et al. 2006, De León et al. 2011).

Finch communities at urban sites seem to be less diverse (Rivkin et al. 2021) and have less diverse gut microbiota (Solomon et al. 2023). However, these urban populations tend to have higher reproductive success (Harvey et al. 2021). Additionally, De León et al. (2011, 2019) found that Darwin´s finches prefer human-food items (e.g. rice) over food items found in their natural habitats, and that Correlations between beak traits and bite force with diet are weaker at urban sites versus non-urban.

Finally, another factor causing habitat loss in Galápagos are invasive species. Many endemic plant species such as *Scalesia spp.* are continuously being displaced by invasive plant species such as blackberry and guava in agricultural areas (Rentería et al. 2012). Moreover, endemic animal species are also suffering the impacts caused by invasive parasites such as the parasitic fly *Philornis downsi* that feeds on nestling blood (Fessl and Tebbich 2002), or predation by feral cats and dogs that prey on several reptiles, marine and land birds, and small mammals (Carrión and Valle 2018).

1.4 Study system

Darwin's finches are an extensively studied system and a famous example of adaptive radiation and contemporary evolution. Today the Galápagos Islands are home to 17 endemic species, whereas Cocos Island (territory of Costa Rica) is home to a single endemic species. Darwin's finches belong to the tanager family Thraupidae and their adaptive radiation started around 1.5 million years ago. The radiation is thought to have started from a common ancestor that inhabited Central or South America (Petren et al. 2005, Lamichhaney et al. 2015). Their beaks have evolved into a variety of different sizes and shapes in response to variable climatic conditions that in turn dictate food availability (seed, flowers, nectar, insects, among others) (Lack 1947, Smith et al. 1978, Grant and Grant 1993). Previous studies have found that beak size, beak shape, and body size are the main traits behind the diversification of Darwin's finches (Lack 1947, Smith et al. 1978, Grant and Grant 1993). These adaptive traits are highly heritable (Boag 1983), and studies have found several large-effect genes associated to each of them (e.g., *HMGA2* and *DLK1*, Chaves et al. 2016, Lamichhaney et al. 2016). Additionally, Darwin's finches mate assortatively according to beak traits (Huber et al. 2007, Podos et al. 2010, Grant and Grant 2018) yet cases of hybridization and introgression although not common, have been registered (Grant and Grant 1994, 2016, 2019, 2021).

In the first three chapters of my thesis, I study a specific group within the Darwin's finches called ground finches (*Geospiza*, Gould) which emerged around 100 000 to 400 000 years ago (Lamichhaney et al. 2015). I specifically study two species within this group: the small ground finch (*Geospiza fuliginosa*) that feeds mostly on small sized seeds, and the medium ground finch (*Geospiza fortis*) that feeds mostly on medium-large seeds (De León et al. 2014). These two species are common residents across the entire archipelago with exception of Genovesa, Espanola, Darwin and Wolf Islands (Fessl and Kleindorfer 2022).

In my fourth chapter, I expanded the scope of the study system to include all resident landbirds of Galápagos. There are currently 28 endemic bird species which include 17 Darwin's finches, four mockingbirds, three flycatchers, one dove, one martin, one rail, and one hawk; and three endemic subspecies which include one yellow warbler and two owls. In addition to these endemic species, the islands are also home to four native bird species that include three rails and one cuckoo. Finally, the Smooth-billed Ani is the only introduced bird species (Fessl and

Kleindorfer 2022). Among all these landbirds, there are 18 species that are considered threatened by the IUCN (2022).

Summary of thesis content

In Chapter 1, I explore the contributions of both time (years) and space (finch populations at sites within and between islands) in explaining the phenotypic variation in beak and body traits in the medium ground finch *Geospiza fortis*. I use data on finch traits and the environmental variables across three study sites, EG and AB in Santa Cruz Island, and the small island of Daphne Major, across 10 years (2003-2012). First, I analyze how much variance in beak traits, body traits, and environmental data can be explained by site, year, and their interaction (site-by-year). Second, I explore in more detail the role of space on the variation of finch beak and body traits by assessing the direction, magnitude, and shape of the phenotypic trajectories corresponding to each site across time. Finally, I compare the contributions of time and space in Darwin's finches phenotypic variation with the contributions of time and space in other well-known systems in evolutionary biology. My findings suggest that phenotypic variation in Darwin's finches is mainly driven by the site effect, affecting beak size but not beak shape. I suggest that further studies can include other finch populations to isolate the special effect of within-islands from the one of between-islands.

In Chapter 2, I explore the potential impact of climate change on Darwin's finches phenotypes by assessing three main questions. 1) Are Darwin's finches time-series of phenotypes responding to short-term weather changes. 2) Is climate change present in Galápagos? 3) Are time-series of Darwin's finches traits showing consistent trends to the ones present in climate change variables? For answer these questions, I use over 20 years of data on beak and body traits of the medium ground finch *Geospiza fortis* at two sites (AB and EG) in Santa Cruz Island and compared them to data on precipitation and temperature. I first conducted cross-correlation analyses to look for short-term correlations (between one and five years) between precipitation and temperature time-series, and beak and body traits time-series that would confirm previous findings in Darwin's finches. Second, I use Bayesian time-series analyses to identify trends in precipitation and temperature time-series which might indicate the presence of climate change at my study sites. Finally, I use Bayesian time-series analyses to identify trends in beak and body trait time-series that would be consistent with the trends found in the environmental variables. My findings suggest that even when there is climate change presence in Galápagos, Darwin's finches do not show long-term consistent responses in their phenotypic traits.

In Chapter 3, I explore parallel and non-parallel patterns of phenotypic variation in Darwin's finches in response to urbanization impact. Here, I use beak and body trait data of two urban-dwelling species of Darwin's finches: the small (*Geospiza fuliginosa*) and medium (*Geospiza fortis*) ground finches occurring in urban and non-urban sites in three islands of the Galápagos. First, I explore how much variation in phenotypic traits is explained by urbanization across and within species. Second, I assess the direction and magnitude of the phenotypic trajectories between urban and non-urban places across and within species using phenotypic trajectory analysis (PTA). My results show that urbanization has an incipient impact of Darwin's finches' phenotypic variation. Even when the effect size of urbanization is overall small, finches do show parallel responses in beak shape variation within and between species.

In Chapter 4, I expand the scope of my thesis to explore the environmental determinants of landbird diversity and abundance in the agricultural areas of Galápagos. Information on main drivers of species diversity and abundance on this archipelago is scarce; thus I use diversity and abundance data from bird surveys between 2008 and 2020, and maps of vegetation types and agroecosystems to assess the main determinants of bird biodiversity and abundance. First, I use geographical information systems (GIS) to conduct spatial analyses to classify the agricultural areas into different vegetation and agroecosystem types, and to extract information relating to patch area, patch diversity, vegetation cover, distance to closest native vegetation patch, and number of native vegetation patches. Second, I use this information to create mixed-effect models to analyze the contributions of several environmental factors to the variation in species richness, evenness, and relative abundance of landbirds across all the agricultural zones in Galápagos. My results indicate that landbird diversity and abundance is mainly explained by vegetation cover and elevation rather than by specific types of vegetation or agricultural practices.

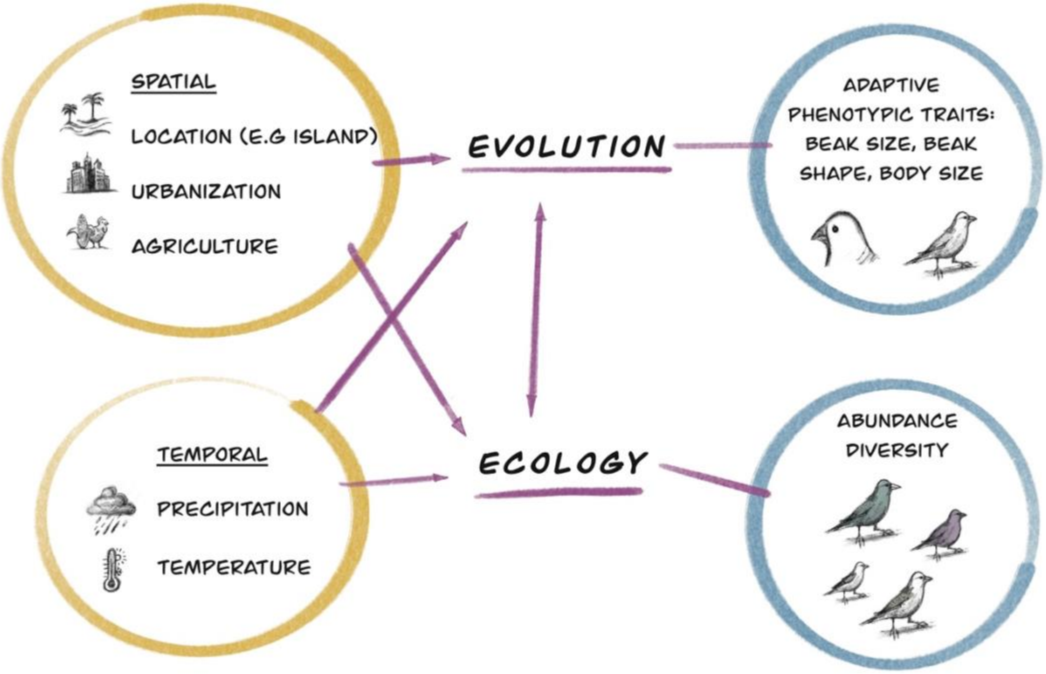

Figure 1. Spatial and temporal factors that influence species' ecological and evolutionary processes, and the interactions between them.

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Chapter 1

The terroir of the finch: how spatial and temporal variation shapes phenotypic traits in Darwin's finches

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1.1 **Abstract**

The term *terroir* is used in viticulture to emphasize how the biotic and abiotic characteristics of a local site influence grape physiology and thus the properties of wine. In ecology and evolution, such terroir (that is, the effect of space or “site”) is expected to play an important role in shaping phenotypic traits. Just how important is the pure spatial effect of terroir (e.g., differences between sites that persist across years) in comparison to temporal variation (e.g., differences between years that persist across sites), and the interaction between space and time (e.g., differences between sites change across years)? We answer this question by analyzing beak and body traits of 4388 medium ground finches (*Geospiza fortis*) collected across 10 years at three locations in Galápagos. Analyses of variance indicated that phenotypic variation was mostly explained by site for beak size ($\eta^2 = 0.42$) and body size ($\eta^2 = 0.43$), with a smaller contribution for beak shape ($\eta^2 = 0.05$) and body shape ($\eta^2 = 0.12$), but still higher compared to year and site-by-year effects. As such, the effect of terroir seems to be very strong in Darwin’s finches, notwithstanding the oft-emphasized inter-annual variation. However, these results changed dramatically when we excluded data from Daphne Major, indicating that the strong effect of terroir was mostly driven by that particular population. These phenotypic results were largely paralleled in analyses of environmental variables (rainfall and vegetation indices) expected to shape terroir in this system. These findings affirm the evolutionary importance of terroir, while also revealing its dependence on other factors, such as geographical isolation.

1.2 **Introduction**

'*Terroir*' is considered critical to the properties of wine (Tonietto and Carbonneau, 2004; Van Leeuwen et al., 2004; Gladstones, 2011). Particular combinations of regional and local conditions – both abiotic (elevation, sun exposure, aspect, soil granularity, etc.) and biotic (competitors, predators, parasites, etc.) – strongly shape the physiology of grape vines. Those physiological responses then alter the chemical properties of grapes which are then detectable in wine. As a result, terroir factors into decisions about which wine varietals (e.g., Pinot Noir or Cabernet Sauvignon) are grown in a given area, in a given vineyard, and in a given 'block' (Jones 2018, Schmidtke et al. 2020). Then, for a given set of these choices, terroir can further influence the color, aroma, and flavor of the resulting wine (Jones 2018).

This concept of terroir as a "sense of place" has been applied – albeit under different guises – to a wide range of ecological and evolutionary patterns and processes. In ecology, the number of species and their relative abundances at given sites are strongly influenced by local conditions, such as temperature regimes or precipitation schedules (Meier et al., 2010; Lembrechts et al., 2019). In evolutionary biology, the genotypes and phenotypes of populations at different places typically adapt to local conditions because of spatial variation in temperature, precipitation, predators, parasites, or competitors (Endler, 1986; Schulter, 2000; Hereford 2010; MacColl 2011). In eco-evolutionary dynamics, the effects of particular phenotypes and genotypes on ecological processes are highly context-dependent, varying from place to place in response to local temperatures, nutrients, and moisture levels (Johnson and Agrawal, 2005; Tack et al., 2010; Hendry et al., 2017; Urban et al., 2020). Just as in viticulture, these – and many other – effects of terroir can be seen on very small spatial scales (Kavanagh et al., 2010; Willi and Hoffmann, 2012; Richardson and Urban, 2013; Richardson et al., 2014; Urban et al., 2020).

However, the pure spatial effect of terroir is not always at the fore. As with spatial variation, temporal variation such as inter-annual temperature or precipitation changes can cause large fluctuations in the abundance of species at any given site (Van der Putten et al., 2010; Ehrlen and Morris, 2015; Ash et al., 2017). Inter-annual variation in environmental drivers can also act as a selective pressure (Hoffmann and Sgro, 2011; Siepielski et al., 2017) that can lead to local adaptations (Hendry et al., 2008; Nosil et al., 2018). In eco-evolutionary dynamics, inter-annual variation in weather can dramatically alter the importance of phenotypes in population dynamics (Ezard et al., 2009) and other ecological processes (Hendry, 2017).

Finally, these two broad categories of effects – space and time – can interact. That is, the spatial effect of terroir can influence how organisms respond to temporal variation in abiotic or biotic conditions. Stated more broadly, the responses of communities, populations, phenotypes, or genotypes to particular changes in precipitation or other environmental factors can depend on other properties of local environments. In ecology, communities in shaded environments are less sensitive to changing temperatures (Clough et al., 2009; Tscharntke et al. 2011). In evolutionary biology, adaptive responses to climate change vary dramatically among populations of a given species (Both and Visser, 2001). In eco-evolutionary dynamics, the contributions of trait variation to population growth vary among years in ways that differ between populations (Ezard et al., 2009; Hendry, 2017).

A series of questions arise when considering the effect of terroir in ecology, evolution, and eco-evolutionary dynamics such as (1) What is the relative importance of spatial variation (terroir) versus temporal variation (year) in various patterns and processes? (2) More precisely, to what extent does terroir maintain temporally-consistent differences among sites (i.e., "main effect" of space) as opposed to shaping site-specific responses over time (i.e., interaction between space and time)? (3) To what extent do these two broad contributions of terroir differ over various spatial or temporal scales? In a scenario of two populations A and B, (1) main differences in traits will remain among populations despite climate variation across years (higher terroir effect), or traits will change along climate variation despite site differences (higher temporal effect), or (2) traits will differ among populations A and B in a site-specific way that varies based on climate. Finally, (3) spatial and temporal differences in traits between population A and B can increase/decrease depending on their location and how long have they been monitored. Here we explore these questions by analyzing a 10-year dataset of environmental features and phenotypic traits in three populations of Darwin's finches. We then compare our results to those from other classic systems in evolutionary biology. We close with a discussion of how the concept of terroir might be useful in helping to re-frame and re-invigorate considerations of how temporal and spatial effects contribute to ecology, evolutionary biology, and eco-evolutionary dynamics.

Darwin's finches

Terroir is likely to be very important for Darwin's finches in the Galapágos because different islands, and even different sites within an island, can show dramatic differences in species composition and -for some species- striking variations in morphological traits (Lack, 1947; Grant and Grant, 1989). A major driver of community and trait variation among sites is food resources, especially seed types and sizes (Schluter and Grant, 1984; Grant, 1999; Grant and Grant, 2008; 2014). These differences in food resources result partly from variation in soil and precipitation, which are themselves the result of differences in physical features, such as elevation, direction of prevailing winds, localized clouds, and solar radiation (Trueman and d'Ozouville, 2010). These physical differences are reasonably consistent through time and thus should generate terroir, which we can quantify as the main effect of spatial variation.

At the same time, many studies have emphasized the impact of inter-annual variation in rainfall, especially due to El Niño or La Niña events, on food availability, which has been observed to cause rapid shifts in finch communities and traits (Grant and Grant, 2002; Grant and Grant ,2006; Grant and Grant, 2008). The extent to which these temporal effects are shared across sites can be quantified as the main effect of year and thus contrasted with the main effect of space (as above). Finally, distinct physical features could generate site-specific responses to inter-annual variation. For example, sites at higher elevations might be less susceptible to climate fluctuations because prevailing winds push warm, moist air upward, where – even in dry periods – it condenses and falls as rain (Trueman and d'Ozouville, 2010). We can quantify the importance of this second form of terroir as the interaction between space (site) and time (year).

These effects and their relative impacts have not been formally quantified and compared for Darwin's finches because no study to date has quantified and compared both spatial variation (multiple sites) and temporal variation (multiple years) in the same analysis. We do so here by compiling annual environmental and trait data for three populations of the medium-ground finch (*Geospiza fortis*) across a 10-year period. We first use Analysis of Variance (ANOVA) to partition the variation in environmental variables (rainfall and vegetation) into the main effect of site, the main effect of year, and the interaction between site and year. We then use univariate and multivariate ANOVAs for a similar partitioning of beak and body trait data. Finally, we use phenotypic trait trajectory analyses (PTA) to explore the contributions of space (site) to temporal changes in multivariate trait means. We conduct these analyses first using all three populations: the small island of Daphne Major and two sites (Academy Bay and El Garrapatero) on the large island of Santa Cruz. Then, because Daphne Major appears to be a special case, we repeat the analyses using only the two sites on Santa Cruz.

1.3 Methods

Study sites

We studied finches from Daphne Major (DM; 0° 25' 21.1" S 90° 22' 19.6" W) and from two lowland sites on the island of Santa Cruz: Academy Bay (AB; 0° 44' 21.3" S, 90° 18 '06.3" W) and El Garrapatero (EG; 0° 41' 15.7" S, 90° 13' 18.3" W) (Figure 1A). Academy Bay is located along the southeastern shore of the island, and it is contiguous with the town of Puerto Ayora. El Garrapatero is located along the eastern shore of the island approximately 10 km northeast of Puerto Ayora. El Garrapatero is not adjacent to any human settlement, although a road constructed mid-way through our sampling regime, in 2008, now passes through our study site, to a parking lot that is used to access a beach (Figure 1A). Daphne Major is located approximately 10 km from the north shore of Santa Cruz (Figure 1A).

Climate and vegetation

We obtained rainfall and spectroradiometric indices of vegetation for the 10 years of our study, 2003-2012 (Figure 1B). Daily rainfall data for Santa Cruz were based on a rain gauge maintained by the Charles Darwin Research Station (Charles Darwin Foundation, 2014). These data are considered representative of both AB (500 m from the gauge) and EG (10 km distant) because the two sites are both on the windward side of the island at similar elevations (20 m for AB, 27 m for EG). However, our personal experience suggests that less rainfall occurs at EG than AB, although no rain gauge was maintained at EG to confirm this suspicion. For DM, we used daily rainfall data from the rain gauge at Baltra Airport, which is 10 km from DM and has a similar climate (Grant and Boag, 1980) and elevation (maximum altitude: 100 m).

Remote sensing data were used to obtain four indices associated with vegetation cover over the 2003-2012 period. More specifically, from the Moderate Resolution Imaging Spectroradiometer (MODIS) database (ORNL DAAC, 2012) we extracted monthly readings for the Normalized Difference Vegetation Index (NDVI), the Enhanced Vegetation Index (EVI), the Leaf Area Index (LAI), and the Fraction of Photosynthetically Active Radiation Index (FPAR) (Figure 1B). These indices are commonly used in studies of spatiotemporal variation in vegetation at global (Alexandridis et al., 2020), regional (Pettorelli et al., 2005), and local (e.g the Galápagos Islands) (Charney et el., 2021) scales, and they provide robust indicators of primary productivity and vegetation cover state (Charney et al., 2021).

For AB and EG, NDVI and EVI were obtained for an area of 250 m × 250 m (i.e., one pixel), and LAI and FPAR were obtained for an area of 1 km^2, in each case the pixel was centered on the sampling area. DM is too small for calculating accurate spectroradiometric indices owing to light reflection from the surrounding ocean. For DM, we therefore used a 250 m × 250 m (for NDVI and EVI) and 1 km^2 (for LAI and FPAR) area directly north of the Baltra Airport, which is nearby to DM and has similar physical characteristics as explained above.

Capture and measurement of finches

Morphological data were collected for the medium ground finch (*Geospiza fortis*) each year from 2003 to 2012 in the three study sites (DM, AB, EG). In all cases, the birds were captured with mist nets and then banded with uniquely numbered metal leg bands to ensure that individuals were not sampled multiple times. Each bird was inspected and classified – based on plumage, beak color, and the presence of a brood patch – as a juvenile, male, or female (Grant, 1999). Distinguishing females from juveniles sometimes can be difficult, whereas adult males can be readily identified based on their black plumage (Grant, 1999).

Each bird was measured following Boag and Grant (1984 – see also Grant, 1999) for beak length (anterior edge of nares to anterior tip of upper mandible), beak depth (at the nares), beak width (at the base of the lower mandible), mass (weight), wing chord (length of longest relaxed right primary feather), and tarsus length (between the nuchal notch at the upper end of the right tarsometatarsus and the lowest undivided scute). Beak and tarsus measurements were made to the nearest 0.01 mm using calipers for EG and AB birds, and dividers (compasses) for DM birds. Wing chord measurements were made to the nearest 0.01 cm using a wing and tail ruler. Mass measurements were made to the nearest 0.01 g using a portable digital scale for AB and EG birds, and a spring scale for DM birds. On DM, each bird was measured by a single person (Peter Grant). At EG and AB, each trait was measured three times (the median value was used for analysis) and measurements were made by multiple people.

Data analyses

Variation in climate and vegetation – Linear fixed-effect models with Type III Analysis of Variance (ANOVA) were used to examine how spatial variation (main effect of site), temporal variation (main effect of year), and the interaction between these two factors explained variation in rainfall and vegetation indices. Type III Sums of Squares were used given the presence of the site-by-year interaction term in our models. The comparisons that could be made were (1) Baltra (for DM) versus AB for log-transformed daily rainfall, and (2) Baltra (for DM) versus EG versus AB for the monthly average of vegetation indices (EVI, NDVI, FPAR, LAI). Additionally, the same analyses were performed after excluding Baltra (DM) so that we could test the extent of variation between two sites (AB and EG) on the same island. Effect sizes for each of these factors were quantified using partial eta square (η^2) as suggested in Cohen (1965) when having models with two or more independent variables.

Variation in finch morphology – Combining all sites and years, we conducted principal component analyses (PCA) separately for beak traits (length, depth, and width) and then for body traits (mass, tarsus length, and wing chord). PCA based on the covariance matrix was performed for beak traits, following previous analyses (Grant and Grant 1999), given that all of these traits were measured on the same scale (mm). PCA based on the correlation matrix was used for body traits given the different scales (mm, cm, gr). (Note: the results reported later do not depend on the use of covariance versus correlation matrices.) As in previous work on this species (e.g., Grant, 1999; 2002; Hendry et al. 2006; 2009), higher values of PC1 (93.7% of the total variation) correspond to larger beak sizes (positive loadings for all traits) and higher values for PC2 (4.3% of the total variation) correspond to pointier (as opposed to blunter) beaks (positive loadings for beak length and negative loadings for beak depth and beak width) (Figure 2A). For body traits, larger values for PC1 (75.6% of the total variation) correspond to larger bodies overall (positive loadings for all traits), as seen in other work with *G. fortis* (e.g., Grant and Grant, 2006), and larger values for PC2 (15.4% of the total variation) correspond to relatively longer wings (positive loading for wing chord but negative loadings for mass and tarsus length) (Figure 2B).

The resulting values for beak size (PC1 of beak traits), beak shape (PC2 of beak traits), body size (PC1of body traits), and body shape (PC2 of body traits) were analyzed using separate linear fixed-effect models with Type III ANOVAs applied to quantify the relative contributions (i.e., effect sizes: partial η^2) of spatial variation (site), temporal variation (year), and their interaction. Sex (male or female) was included in the models as a fixed effect. Juveniles were excluded given that their beak and body traits are still developing (Grant, 1999). Similar to our approach for analyzing climate and vegetation (see above), these finch trait analyses were performed both with and without DM – so as to inform the particular contribution of that small island, and then within-island site variations, to our assessment of terroir. Finally, all analyses were repeated for adult males only, to test if and how variation in sex ratio might impact our conclusions. Because the above analyses relied on PCA-restructured trait (co)variances, as has been typical for research on finches, we also analyzed the original trait measurements in multivariate analyses of variance (MANOVA) using the 'Pillai' test, which accounts for our varying sample sizes. These analyses were run separately for beak and body traits, and effect sizes were again quantified as partial η^2 for the year, site and site-by-year interaction terms. As above, we first ran the analyses with the data corresponding to all the study sites (AB, EG, and DM), and then excluding DM.

Variation in phenotypic change trajectories – Phenotypic Trajectory Analysis (PTA: Adams and Collyer 2009) was used to further explore how terroir (site) might have influenced multivariate trait change across years. For each site, trajectories were generated connecting the multivariate phenotypic means of finch traits at one year to the multivariate phenotypic mean of finch traits at the next year. This procedure was done for beak and body traits separately. We then calculated differences between the trajectory lengths (ΔL) and directions (angles θ) in a pair-wise fashion (DM vs. EG, AB vs. EG, DM vs. AB). Trajectory length comparisons inform the difference among sites in the amount of among-year multivariate trait variation along primary axis of inter-annual change. Trajectory direction comparisons inform the difference among sites in the multivariate orientation of those primary axes of inter-annual change. See Adams and Collyer (2009) for further explanation of PTA.

Comparison of Spatial and Temporal Effects with other systems- We advocate application of our terroir-motivated analysis to other patterns in ecology and evolution. We start by placing our findings for *G. fortis* into the context of some other systems that seek to understand the spatiotemporal forces shaping trait variation. To do so, we leveraged studies of multiple populations over multiple years in the ornate tree lizard (*Urosaurus ornatus*: Gilbert and Miles, 2019), the snail kite (*Rostrhamus sociabilis*: Cattau et al., 2018), the Trinidadian guppy (*Poecilia reticulata*: Gotanda and Hendry, 2014), and the pied flycatcher (*Ficedula hypoleuca*: Camacho et al., 2013). In each case, we calculated the variation (partial η^2) among sites and years from the reported F-values and the degrees of freedom associated to them following Cohen (1965). The resulting partial η^2 values for each term in each study can then be compared to our own estimates for *G. fortis*.

All the analyses were performed in the statistical program R version 4.1.1 (R Core Team, 2021).

1.4 Results

*Climate and vegetatio*n – Yearly averages of the four spectroradiometric indices were strongly correlated with each other at each site (Pearson correlations: all $r > 0.79$; all $p < 0.001$;

N=10 per site), and all of these indices were correlated with total annual rainfall at each site (AB 2003-2012: all $r > 0.79$; all $p < 0.0002$; N=10; DM 2003-2012: all $r > 0.73$; all $p < 0.001$; N=10). Not surprisingly, then, all indices yielded similar insights into terroir.

ANOVAs revealed that the strongest effect sizes for rainfall and vegetation cover were associated with site, rather than with year or the site-by-year interaction (Table 1). In short, climate and vegetation data suggest very strong and consistent site-specific environmental differences that should underpin effects of terroir. In particular, DM always had lower rainfall than AB and less vegetation than EG, which in turn always had less vegetation than AB (Fig. 1B). This strong and consistent site effect was evident even in the face of dramatic variation across years in overall rainfall across years. In particular, our time series included a dry period from 2003 to 2007 (AB average rainfall = 182.22 mm, Baltra average rainfall = 67.06), followed by a wet period from 2008 to 2012 (AB average rainfall = 536.86 mm, Baltra average rainfall = 284.90) – with the exception of 2009, which was also dry (Figure 1B). This regionally consistent (i.e., across all sites) temporal variation in rainfall was echoed in similarly consistent inter-annual variation in vegetation cover, such that the vegetation indices showed greater values at each site in years where rainfall was greater (Figure 1B). An additional finding from our analyses is that for both rainfall and vegetation, the main effect of year was always stronger than the site-by-year interaction. Thus, the primary contribution of terroir was seen in differences among sites that were consistent through time, rather than in a strong contribution of site in modifying the effects of temporal variation.

After removing DM from the analyses, vegetation index effect sizes decreased (relative to the same term in analyses with DM) by approximately 70% for the main effect of site, increased (relative to the same term in analyses with DM) by approximately 17% for the main effect of year, and decreased by approximately 20% for the site-by-year effect. These overall reductions in the relative importance of site suggests that spatial consistency across years across our entire sample is mainly driven by substantial differences between DM and the two Santa Cruz sites (AB and EG). However, it is important to note that site effects were still strong when comparing some vegetation indices within Santa Cruz Island, between EG and AB (Table S1).

Variation in finch morphology – A total of 4388 individuals were captured and measured (AB: 1786, EG: 1229, DM: 1373). PCA-based analyses showed strikingly smaller beaks, pointier beaks, smaller bodies and larger wings in *G. fortis* at DM as compared to AB and EG (Figure 2A, 2B). Further, *G. fortis* at EG and AB were much more variable in all traits than were *G. fortis* at DM (Table 2). These general differences between the finch populations have been reported in earlier analyses that did not simultaneously assess temporal variation (Boag and Grant, 1984; Grant et al., 1985). During our 10-year study period, mean values for beak and body size typically varied much more among years at AB and EG than at DM (Figure 2C), with exception of an abrupt change between 2004 and 2005 at DM reported as a result of character displacement event reported by Grant and Grant (2006). Beak shape, however, was similarly variable among the three sites (Figure 2C).

Echoing the above-noted differences between sites, ANOVA and MANOVA analyses indicated that the main effect of site explained most of the variation, followed by the main effect of year and then the site-by-year interaction (Table 3; Figure 3). The largest effect sizes for site were evident for beak size ($\eta^2 = 0.42$) and body size ($\eta^2 = 0.43$), both of which were much larger than the corresponding effect for beak shape ($\eta^2 = 0.05$) and body shape ($\eta^2 = 0.12$). The main effect of year and the site-by-year interaction were of similar magnitude in all cases (Table 3). That is, inter-annual variation in *G. fortis* traits had roughly comparable contributions from shared regional changes (main effect of year) and interactions of regional variation with site-specific factors (site-by-year interaction). These results follow those seen for rainfall and vegetation indices in that the main contribution of terroir lies in generating site-specific phenotypic differences that mainly persist across year.

After removing DM from ANOVA and MANOVA analyses of finch morphology, overall effect sizes for site decreased (relative to the models with DM) by 95%, year effects increased by 28%, and site-by-year effects decreased by 50% (Table 3). Thus, variation was now (considering only AB and EG) explained roughly equally across the year and site-by-year terms, which were both slightly greater than the site term. These changes in statistical outcomes reveal that terroir in our *G. fortis* dataset revolves mostly around the beak size and body size (but not shape) of DM birds relative the Santa Cruz (AB and EG) populations.

Phenotypic trajectory analyses (PTA) revealed differences among sites in the length and direction of the multivariate trajectories for mean beak and body traits (Table 4, Figure 4). That is, the *magnitude* (ΔL) and *direction* (θ) of temporal variation in beak and body traits further illustrated the importance of terroir (effect of site) in *G. fortis* traits. Specifically, for beak traits, average differences were greater in the direction of trajectories compared to their magnitude, which indicates the effect of terroir in creating divergent phenotypic trajectories (Table 4). For body traits, terroir equally influenced the differences in magnitude and direction of trajectories (Table 4). When pair-wise comparisons were made across sites, differences were much larger (and significant) only for DM versus for the other two sites (Table 4). These results again confirm that terroir is mostly driven by the distinctions between DM and the Santa Cruz populations.

Comparison of Spatial and Temporal Effects with other systems- The importance of terroir differed among traits and study systems (Figure 5). Overall, the main effect of site tended to be only slightly greater than the main effect of year across systems, but finch traits showed the highest site effect among all, which suggests that terroir is stronger in finche (when DM is included) than in those other classic systems. When DM was excluded, the main effect of site for finches decreased markedly and was – in fact –lower than the estimates of the other study systems. In short, terroir is exceptionally strong in *G. fortis* in comparison to other systems, but only for the presence of the DM population.

1.5 Discussion

Our use of the term *terroir* is intended to highlight the importance of local biotic and abiotic conditions in shaping organismal attributes. One way that terroir could play out for Darwin's finches would be differences among sites in finch traits and finch community composition. Indeed, spatial differences among finches were the focus of early studies on this group (Lack, 1947; Bowman, 1961; Grant et al., 1976). More recently, however, emphasis has shifted toward temporal changes within finch populations – especially on the island of Daphne Major (Boag and Grant, 1981; Grant and Grant, 2002; 2006; Laminchhaney, 2016). At present, the relative importance of these two main factors – that is, spatial and temporal effects – remains unknown for this group – simply because no study has formally assessed both components of variation for a common set of populations over a common time frame.

Our study fills this information gap by analyzing data collected annually over a 10-year period for three populations of the medium-ground finch (*Geospiza fortis*). Most prominently, our analysis revealed a very strong signature of 'terroir' – that is, temporal changes in beak and body traits were typically small relative to the magnitude of phenotypic differences among sites. Moreover, these patterns of trait variation closely mirrored the strong and temporally-consistent differences among sites in climate (rainfall) and vegetation indices (Table 1, Fig. 1B). Importantly, however, the effect of terroir was highly variable among traits and sites. In particular, spatial effects were greatest relative to temporal effects for body and beak *size*, as opposed to beak and body *shape*. Further, spatial effects were greatest when including the small island of Daphne Major, as opposed to just the two sites on Santa Cruz Island (AB and EG) (Table 3, Fig 3). These variable contributions of space and time provide a new context to discuss, evaluate, and interpret the terroir of the finch.

Why is terroir so strong for Darwin's finches?

Terroir could manifest as temporally-consistent differences among sites (i.e., the main effect of site) or as site-specific temporal changes (i.e., the interaction between site and year). Our results mainly fall into the first category; that is, consistent differences among sites tend to be more important than site-specific temporal changes. This outcome likely reflects physical features of the sites that generate consistent differences in rainfall which generates consistent differences in plants which generate consistent differences in finch traits.

The starting point for finch terroir is thought to be topographic differences among sites in relation to wind direction and ocean currents (Trueman and D'Ozouville, 2010). In particular, Daphne Major (DM) is only 0.33 km^2 with a peak elevation of 120 m, and it falls in the rain shadow (given the prevailing winds) of Santa Cruz (Boag and Grant, 1984b; Snell et al., 1996). Santa Cruz, by contrast, is 986 km^2 and has a maximal elevation of 855 m, which generates considerable rainfall when prevailing winds push moist air to higher and thus colder elevations (Snell et al., 1996; Pryet et al., 2012). Correspondingly, DM experiences less than half the precipitation and has less than half the vegetation cover of our two Santa Cruz sites (Table 1). Not surprisingly, plant communities and seed distributions differ markedly between DM and Santa Cruz (Abbott et al., 1977). Although it is not possible to confidently link specific seed differences to specific beak differences between these populations, it is at least tempting to note that some foods (e.g., *Cordia lutea* seeds) often eaten by large morphs of *G. fortis* on Santa Cruz (e.g., De León et al., 2014) are lacking on DM (Boag and Grant, 1984), where these large *G. fortis* are similarly absent.

The two sites on Santa Cruz – Academy Bay (AB) and El Garrapatero (EG) – are both located in the lowlands and are more similar to each other – in all respects – than either site is to DM. For instance, average values for *G. fortis* traits did not differ consistently between the two sites. Instead, the only noteworthy difference between these populations is in modality of the beak size distribution, with bimodality more evident at EG than at AB (Hendry et al., 2006). We should note that these differences in modality do likely reflect some aspect of terroir. For example, AB has greater vegetation cover than does EG (Table 1), at least in part due to their different positions along the coast of Santa Cruz (southeastern vs. eastern shore). Further, AB has approximately twice the overall seed abundance as does EG (De León et al., 2011). However, the most likely reason for differences in modality is the role of recent human influences. AB (but not EG) is located next to a human settlement. A meta-analysis performed by Liu and Niyogi (2019) found an average rainfall increase of 16% in sites close to urban settlements, and indeed our own personal experience suggests that rainfall was more frequent and heavier at AB than at EG (no rainfall gauge is present at EG to confirm this experience). Further, AB houses many exotic plants and human foods that are used by finches (De León et al., 2011; 2019). These various human influences at AB appear to break down the diet-morphology-performance relationships that are critical to maintain bimodality in *G. fortis* beak size (Hendry et al. 2006; De León et al., 2011; 2019).

A second-order result of our analysis was that terroir appears to be much more important for beak and body *size* than for beak and body shape, the later mainly being relative wing length (Fig. 3). Previous studies have highlighted important differences in beak shape *among* finch species (Bowman, 1961; Foster et al., 2008); however, differences in beak shape *within Geospiza* species are less striking (Foster et al. 2008). Perhaps the main reason is that *G. fortis* – whether large or small – tend to crack seeds in a similar way by exerting bite forces that relate to beak depth and width rather than beak length (Herrel et al., 2005a; 2005b). Beak length, by contrast, seems to be associated with food manipulation (Price et al., 1984; Grant 1999). Hence, selection on beak size might be strongly divergent (or disruptive), whereas selection on beak shape might be stabilizing for optimal manipulation, irrespective of seed size. Of course, this statement is a speculative generalization given that different food types do, in fact, require different beak movements (Grant, 1981). Further, other forces, such as gene flow, can influence beak shape. For instance, introgression into *G. fortis* from *G. scandens* has led to an increase in beak length of *G. fortis* (Grant and Grant, 2002). In summary, our main point here is not that the effects of terroir are absent for beak shape – merely that they are much weaker than for beak size.

Why is Daphne Major special?

Our results indicate that *terroir* makes a very strong contribution to beak and body size variation – but really only due to the inclusion of DM. On average, *G. fortis* at DM have 23% deeper beaks, 17% longer beaks, and 30% lighter bodies than do finches at AB and EG (Table 2, Fig.2). This observation is not a new one, as previous studies have emphasized the relatively small size of DM *G. fortis* and the relatively large size of Santa Cruz *G. fortis* (Boag and Grant, 1984; Grant et al., 1985; McKay and Zink, 2015; Bruniche-Olsen et al., 2019). Not surprisingly, then, our estimates of the importance of terroir drop dramatically when we remove DM from the analyses (Table 2, Fig. 3). To explain the particular importance of terroir for DM birds, we here summarize four possible contributors: overall "harshness," habitat complexity, competitive interactions, and gene flow/introgression.

First, as previously mentioned, DM is much drier and has less vegetation than AB or EG, a difference verified by our vegetation indices. Hence, smaller body sizes (and thus smaller beak sizes) might reflect their more extreme and challenging environment. This hypothesis could be tested by analyzing phenotypic variation among additional populations in relation to average climate and vegetation measures. *G. fortis* exist on many islands and existing finch data (Lack 1947; Schluter and Grant, 1984; Grant, 1999; Grant and Grant 2008) could be combined with newly available remote sensing datasets to achieve this goal. At the same time, overall local climate harshness cannot be the only reason for the distinctiveness of the DM site. For instance, the morphology of *G. fortis* at Borrero Bay on Santa Cruz is more similar to that at climatologically-different AB (~ 26 km away) and EG (~ 25 km away) (Foster et al., 2008) than to climatologically similar DM (~ 10 km away) (Grant et al., 1985).

Second, DM offers a much smaller and more homogeneous habitat than does EG or AB, or Santa Cruz as a whole, which supports extremely diverse habitats (Trueman and D'Ozouville, 2010). As a result, Santa Cruz should be able to support a wider diversity of phenotypes within species than would be possible on DM. Indeed, the primary cause of the average beak size difference between *G. fortis* on the two islands is not that Santa Cruz lacks small *G. fortis,* but rather that DM lacks large *G. fortis*: that is, the range of beak sizes is greater on Santa Cruz, especially at the large end of the distribution (Grant and Grant, 2014). It seems likely that the more diverse range of food types on Santa Cruz (Abbott et al., 1977) contributes to a greater range of intra-specific variation, which then shapes persistent differences in average beak size between Santa Cruz and DM.

Third, composition of the finch community on DM differs from that at AB and EG, which could precipitate divergent patterns of selection. For starters, only DM lacks the small ground finch (*Geospiza fuliginosa*), which could favor smaller *G. fortis* individuals who could take advantage of the smaller seeds that *G. fuliginosa* would otherwise eat. Further, the colonization and rapid increase of the large ground finch population (*Geospiza magnirostris*) on DM precipitated a character-displacement shift toward even smaller beak sizes (Grant and Grant 2006). Thus, it seems possible that different patterns of inter-specific competition contribute to why *G. fortis* on DM are so much smaller (on average) than those on Santa Cruz.

Fourth, divergence of finch traits between DM and Santa Cruz could be driven by distinct patterns of gene flow from other *G. fortis* populations or other *Geospiza* species. In particular, hybridization between *G. fortis* and *G. magnirostris* on Santa Cruz might have seeded the genetic variation necessary for the evolution of large *G. fortis* there (Chaves et al., 2016). By contrast, *G. magnirostris* has colonized DM only recently (Gibbs and Grant, 1987; Grant and Grant, 1995), which would limit the scope for gene flow effects. Further, gene flow appears to be substantial for *G. fortis* across Santa Cruz, with only minimal genetic differences over even large distances (De León et al., 2010). By contrast, *G. fortis* immigrants to DM are relatively rare (Grant and Grant, 2009; 2010). Hence, *G. fortis* on DM might – by virtue of their spatial isolation – have more ability to independently evolve to local optima.

In summary, the distinctive nature of the DM *G. fortis* terroir probably reflects a combination of environmental differences and isolation that together shape ecological and evolutionary responses to local conditions. That is, differences in terroir are much more likely to cause differences in communities and traits when places with different properties are not linked by the movement of materials or organisms. This view comports with the classic interpretation of beak traits in finches being shaped by the combination of local food resources (Schluter and Grant, 1984), inter-specific competition (Schulter and Grant, 1984; Schluter, 2000; Grant and Grant, 2006), and patterns of gene flow or introgression (Petren et al. 2005; Grant and Grant, 2009; 2010; Farrington et al., 2014, Chaves et al., 2016).

Are Darwin's finches special compared to other systems?

Despite the site effect in finches being the largest among systems due to the presence of the DM population. It is important to note, however, that our two Santa Cruz sites (EG and AB) were in similar lowland arid habitats, whereas *G. fortis* in other habitats on Santa Cruz and on other islands might also show a stronger signal of terroir. Indeed, work on another ground finch species *G. fuliginosa* has reported noteworthy beak and foot size differences between vegetation and climatic zones on Santa Cruz (Kleindorfer et al., 2006). Future work would benefit from adding more diverse habitats on Santa Cruz, thus helping to separate the classic driver of terroir (environmental conditions) from the importance of isolation (DM).

Finally, we note that the small inter-annual effects (relative to site effects) in our study system could be due to the fact that Darwin's finches are long lived, and that beak size is very strongly genetically determined (Chaves et al., 2016; Lamichhaney et al., 2016). Hence, a 10-year period might be insufficient to observe dramatic evolutionary changes similar to those found among sites. However, organisms that have short generation times (e.g., guppies) also often show stronger spatial than temporal variation (Figure 5; Gotanda and Hendry, 2014). Further, studies have shown how evolutionary changes in Darwin's finches can happen over only a few years (Grant and Grant, 2002; Lamichhaney et al., 2016). Longer monitoring during more consistent changes in climate (e.g., due to global warming) could perhaps resolve these uncertainties.

Conclusions

The large effect of site or "terroir" in explaining not only the phenotypic variation in finches but also the environmental characteristics associated with food availability reinforce the classic hypothesis that diversification in Darwin's finches is driven by ecological differences among locations (Lack, 1947; Bowman, 1961; Schluter and Grant, 1984; Grant, 1999). This realization brings some needed perspective to the current emphasis on contemporary evolution of beak size within finch populations (e.g Lamichhaney et al. 2016, Chaves at al. 2016). That is, recent studies have highlighted the influence of temporal changes in beak traits by prolonged droughts caused by La Niña or abundant rains caused by El Niño (Grant and Grant, 2002; Grant and Grant, 2006). Yet, our results make clear that such contemporary or "rapid" evolution within a population is very small relative to spatial factors that have generated consistent spatial variation – and thus driven the radiation of Darwin's finches. Perhaps evolution is extremely rapid when finches colonize a new environment; but, after that, it wobbles around much more subtly around a local optimal dictated by temporally consistent environmental variation. Our results lay the groundwork for further studies that include other islands and sites with different conditions for Darwin's finches. Further, we encourage exploration of the spatio-temporal evolutionary variation of species with different life histories.

1.5 Figures

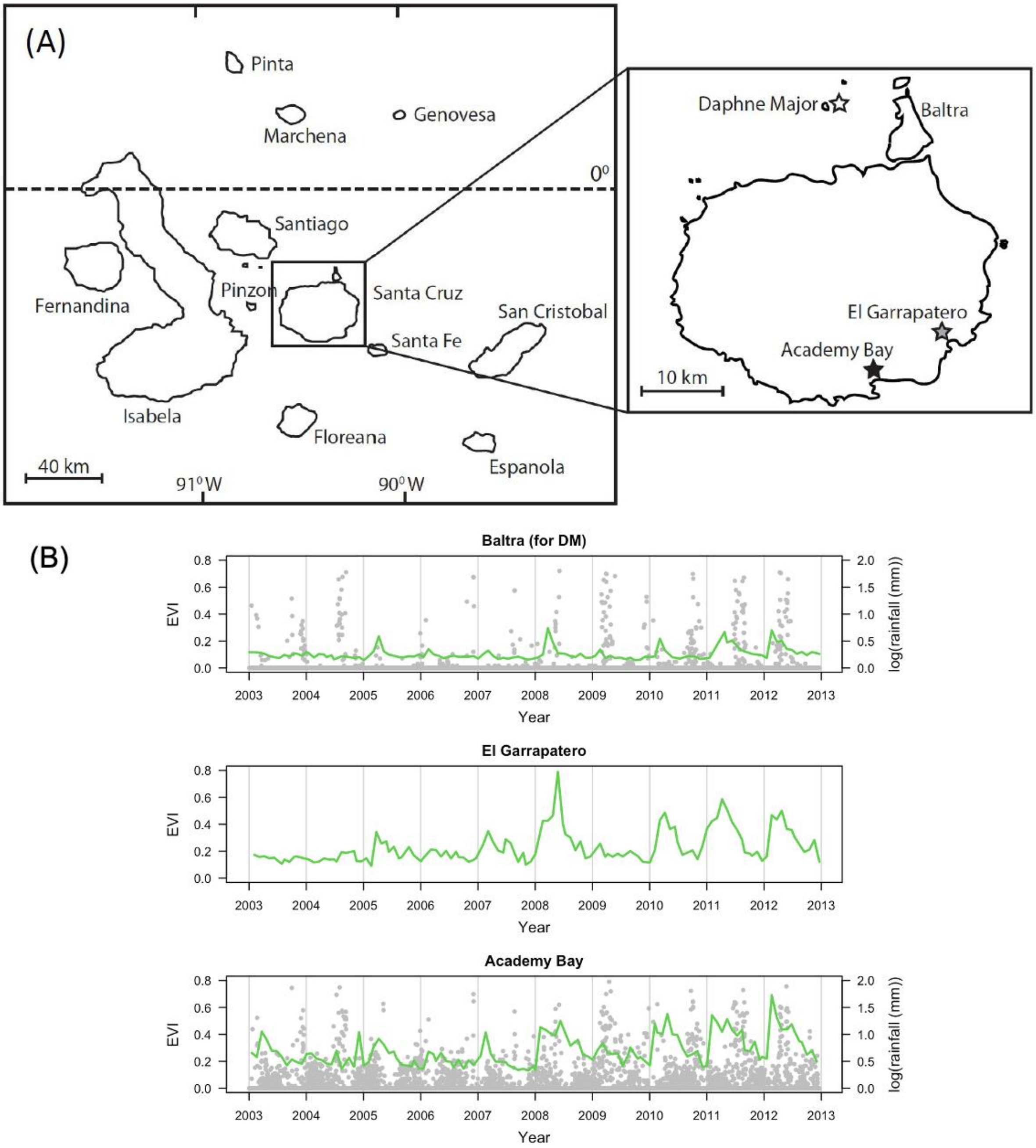

Figure 1. A) Map of the Galápagos archipelago showing the three study sites: DM for Daphne Major (white star), EG for El Garrapatero (grey star), and AB for Academy Bay (black star). B) Site-specific daily values for enhanced vegetation index (EVI; green lines) superimposed on daily rainfall (log-transformed; grey dots) from 2003 to 2012. Rainfall data were not available for El Garrapatero, and values for Daphne Major are from the adjacent Baltra Island.

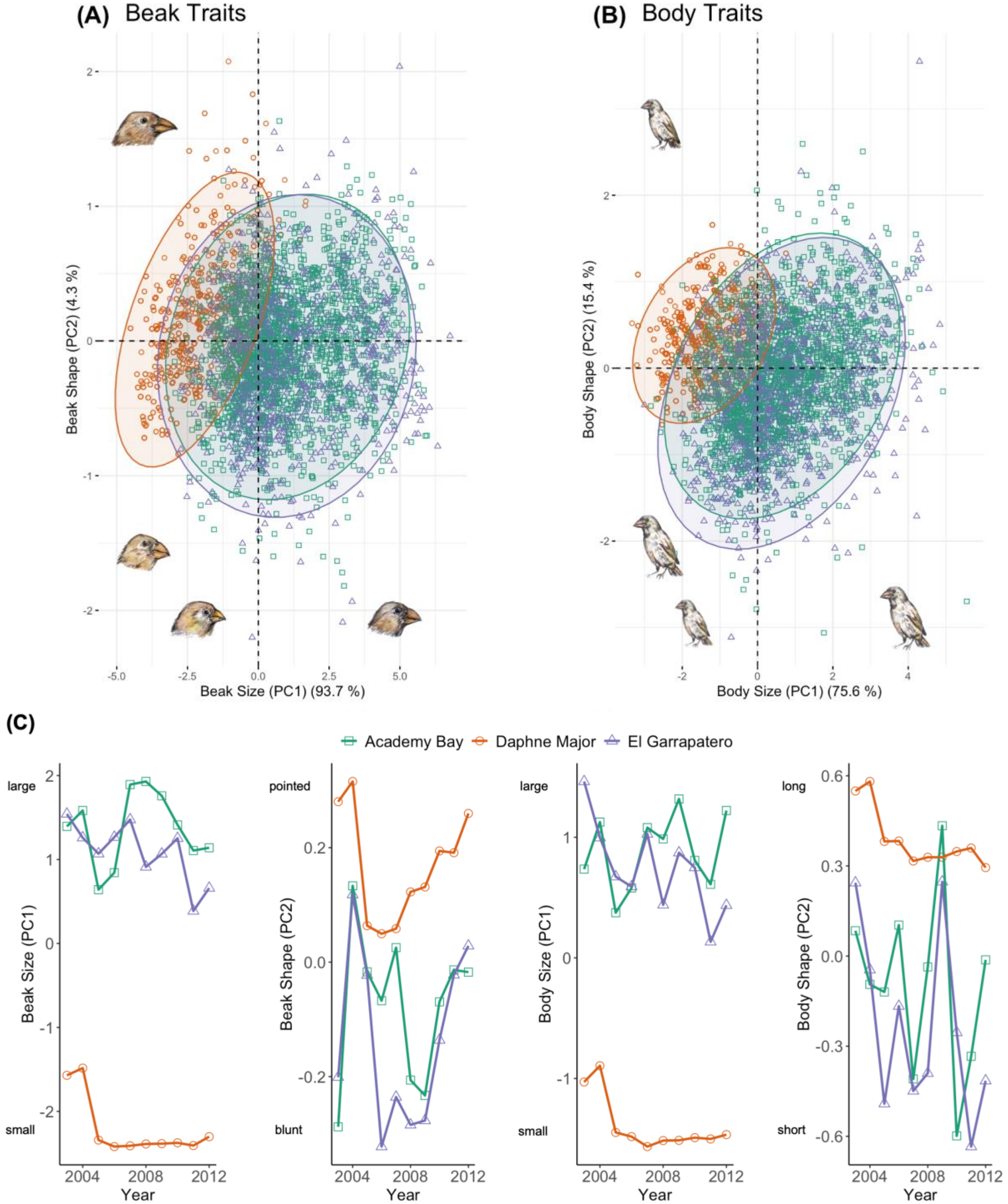

Figure 2. Principal components analysis for (A) beak traits and (B) body traits in *G. fortis* at the three study sites. (C) Trajectories for beak size (PC1), beak shape (PC2), body size (PC1), and body shape (PC2) across 10 years (2003-2012) for the three study sites.

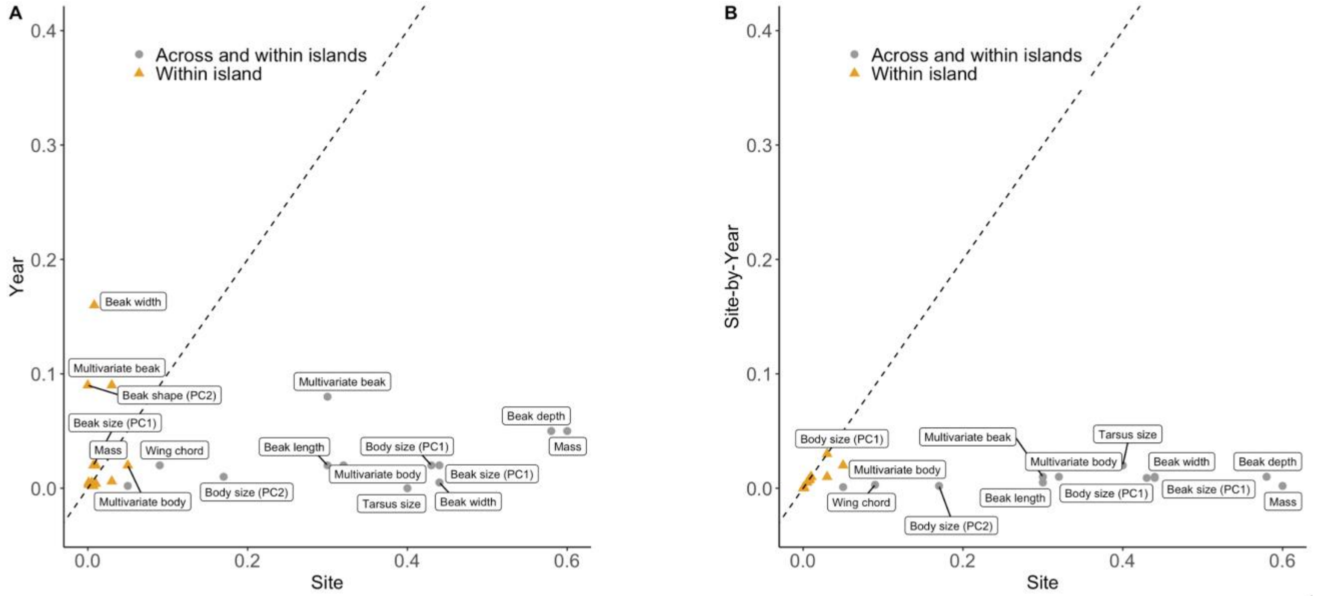

Figure 3**.** Effect sizes (partial η^2) for A) the main effect of site versus the main effect of year, and B) the main effect of site versus the site-by-year interaction for beak length, beak depth, beak width, beak size (PC1), beak shape (PC2), multivariate beak size/shape, mass, tarsus length, wing chord, body size (PC1), body shape (PC2), and multivariate body size/shape for comparisons across islands (gray: AB, DM, EG) and between the two sites on Santa Cruz island (yellow: AB and EG).

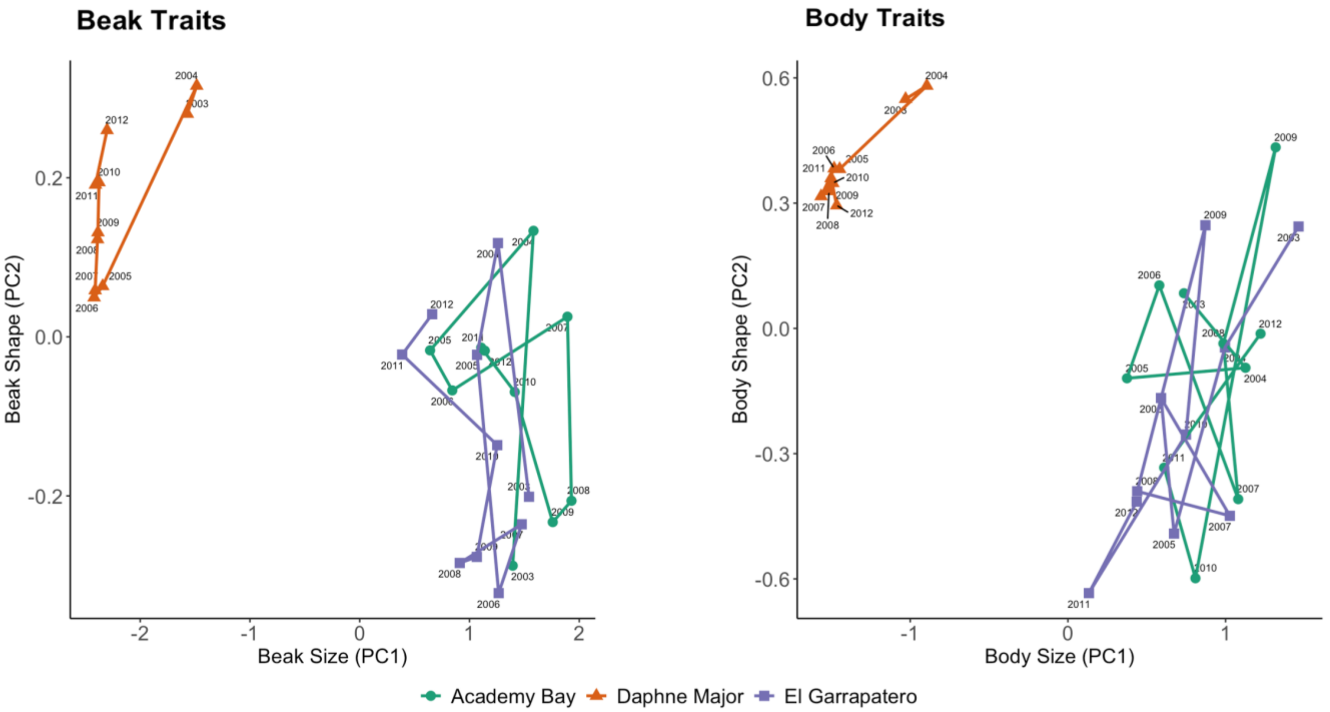

Figure 4. Phenotypic trajectories from Phenotypic Trajectory Analysis across years for beak and body traits at the three study sizes from 2003 to 2012.

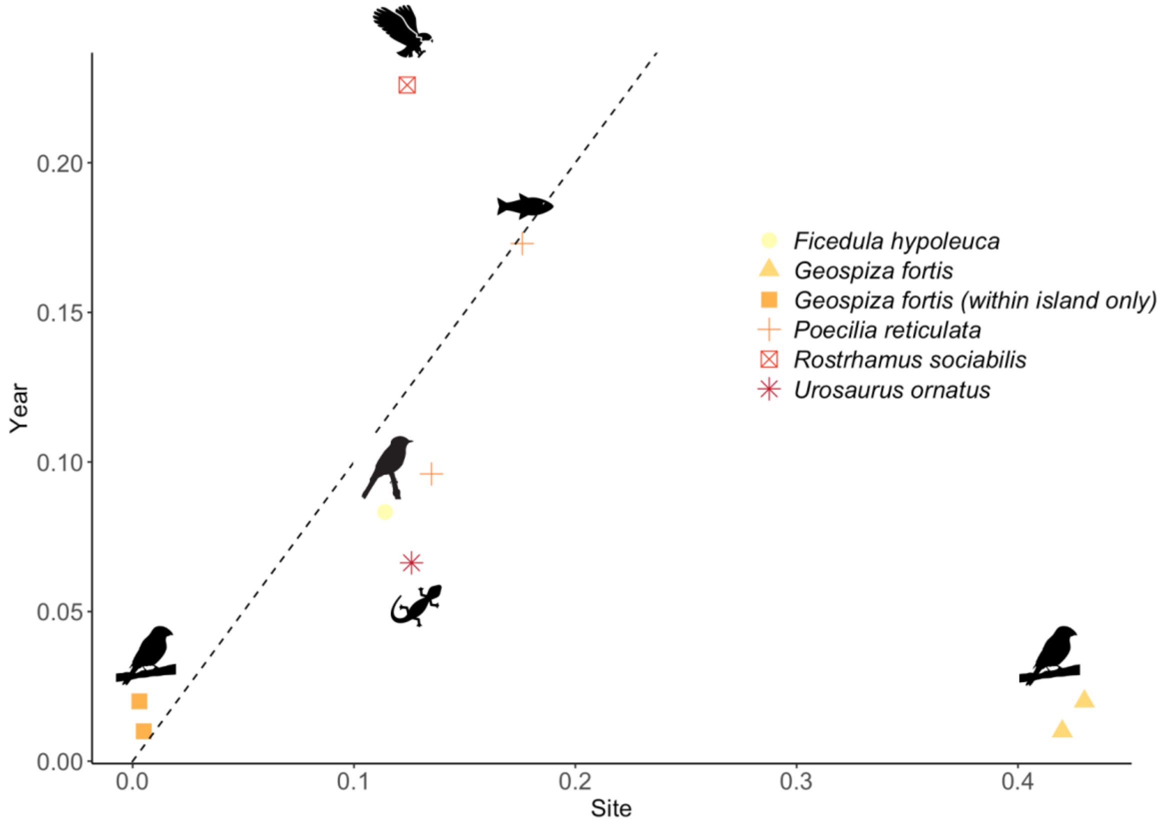

Figure 5. Effect sizes (partial eta-squared: η^2) for the main effects of year (temporal) and site (spatial) calculated for different study systems. Each point represents a particular phenotypic trait.

1.6 Tables

Table 1. A) Total rainfall and average spectroradiometric values for the three study sites from 2003 through 2012. B) Analysis of variance for log-transformed rainfall and spectroradiometric values testing for the effect of year, site, and interaction. P-values in bold mark significant effects. η2 quantifies effect size. The spectroradiometric data from Baltra Island served as proxy for Daphne Major. EVI: enhanced vegetation index; NDVI: normalized difference vegetation index; LAI: Leaf Area Index; FPAR: Fraction of Photosynthetically Active Radiation.

A) Parameter	Daphne Major (DM)	El Garrapatero (EG)	Academy Bay (AB)
Rainfall (mm)	148 (± 124)	—	360 (± 224)
EVI	0.107 (± 0.022)	0.227 (± 0.071)	0.28 (± 0.066)
NDVI	0.245 (± 0.043)	0.481 (± 0.084)	0.58 (± 0.073)
LAI	0.188 (± 0.050)	0.579 (± 0.189)	1.20 (± 0.423)
FPAR	0.098 (± 0.024)	0.257 (± 0.062)	0.42 (± 0.074)

B) Parameter	Effect	F	*p*	η2
Rainfall (log)	Year	F (9, 7306) = 20.95	**< 0.0001**	0.02
	Site	F (1, 7306) = 258.20	**< 0.0001**	0.03
	Year * Site	F (9, 7306) = 1.36	0.1977	0.002
EVI	Year	F (9, 549) =23.18	**< 0.0001**	0.29
	Site	F (2, 549) = 223.04	**< 0.0001**	0.46
	Year * Site	F (18, 549) = 3.34	**< 0.0001**	0.10
NDVI	Year	F (9,549) = 16.77	**< 0.0001**	0.23
	Site	F (2,549) = 394.53	**< 0.0001**	0.60
	Year * Site	F (18,549) = 1.95	**0.01069**	0.06
LAI	Year	F (9,1289) = 23.62	**< 0.0001**	0.14
	Site	F (2,1289) = 377.97	**< 0.0001**	0.38
	Year * Site	F (18,1289) =6.82	**< 0.0001**	0.09
FPAR	Year	F (9,1289) = 23.03	**< 0.0001**	0.14
	Site	F (2,1289) = 674.33	**< 0.0001**	0.52
	Year * Site	F (18,1289) = 3.43	**< 0.0001**	0.05

Table 2. Mean and standard error for beak and body traits at the three study sites.

	BEAK TRAITS			BODY TRAITS		
	Beak length (mm)	Beak depth (mm)	Beak width (mm)	Tarsus length (mm)	Wing chord (mm)	Mass (gr)
Academy Bay	11.79 ± 0.022	11.25 ± 0.029	9.93 ± 0.023	20.81 ± 0.031	69.22 ± 0.089	21.35 ± 0.089
Daphne Major	10.46 ± 0.021	8.68 ± 0.020	8.37 ± 0.015	18.99 ± 0.021	66.72 ± 0.062	15.39 ± 0.048
El Garrapatero	11.72 ± 0.028	11.27 ± 0.038	9.91 ± 0.029	21.23 ± 0.038	68.77 ± 0.115	21.35 ± 0.089

Table 3. Analysis of variance (univariate ANOVAs and multivariate MANOVAs) for beak and body traits for *G. fortis* at the three study sites (AB: Academy Bay, EG: El Garrapatero, DM: Daphne Major) by year, site, and site-by-year interaction including males and females. P-values in bold mark significant differences. Partial eta-squared (η^2) quantifies effect size.

		ALL POPULATIONS (AB, EG, DM)			ONLY AB vs. EG		
BEAK TRAITS	Term	F	*p*	η2	F	*p*	η2
PC1 (beak size)	Year	F (9, 4357) = 6.64	**< 0.0001**	0.01	F (9, 2994) = 4.60	**< 0.0001**	0.01
	Site	F (2, 4357) = 1589.41	**< 0.0001**	0.42	F (1, 2994) = 13.51	**< 0.0001**	0.005
	Site * Year	F (18, 4357) = 4.38	**< 0.0001**	0.02	F (9, 2994) = 4.12	**< 0.01**	0.01
	Sex	F (1, 4357) = 143.75	**< 0.0001**	0.03	F (1, 2994) = 76.29	**< 0.0001**	0.02
PC2 (beak shape)	Year	F (9, 4357) = 13.66	**< 0.0001**	0.03	F (9, 2994) = 16.32	**< 0.0001**	0.05
	Site	F (2, 4357) = 126.42	**< 0.0001**	0.05	F (1, 2994) = 2.81	0.093	0.001
	Site * Year	F (18, 4357) = 4.44	**< 0.0001**	0.02	F (9, 2994) = 3.05	**< 0.001**	0.01
	Sex	F (1, 4357) = 26.29	**< 0.0001**	0.006	F (1, 2994) = 77.28	**< 0.0001**	0.03
MANOVA (Beak length, beak depth, beak width)	Year	F (9, 4357) = 34.96	**< 0.0001**	0.07	F (9, 2994) = 35.69	**< 0.0001**	0.09
	Site	F (2, 4357) = 642.67	**< 0.0001**	0.31	F (1, 2994) = 19.41	**< 0.0001**	0.02
	Site * Year	F (18, 4357) = 10.28	**< 0.0001**	0.04	F (9, 2994) = 6.20	**< 0.0001**	0.02
	Sex	F (1, 4357) = 68.84	**< 0.0001**	0.05	F (1 2994) = 52.84	**< 0.0001**	0.05
BODY TRAITS	Term	F	*p*	η2	F	p	η2
PC1 (body size)	Year	F (9, 4357) = 10.41	**< 0.0001**	0.02	F (9, 2994) = 7.38	**< 0.0001**	0.02
	Site	F (2, 4357) = 1651.12	**< 0.0001**	0.43	F (1, 2994) = 7.88	**< 0.0001**	0.003
	Site * Year	F (18, 4357) = 4.86	**< 0.0001**	0.02	F (9, 2994) = 4.15	**< 0.0001**	0.01
	Sex	F (1, 4357) = 489.01	**< 0.0001**	0.10	F (1, 2994) = 273.48	**< 0.0001**	0.08
PC2 (body shape)	Year	F (9, 4357) = 29.08	**< 0.0001**	0.06	F (9, 2994) = 22.42	**< 0.0001**	0.06
	Site	F (2, 4357) = 298.19	**< 0.0001**	0.12	F (1, 2994) = 33.58	**< 0.0001**	0.01
	Site* Year	F (18, 4357) = 15.43	**< 0.0001**	0.06	F (9, 2994) = 19.85	**< 0.0001**	0.06
	Sex	F (1, 4357) = 544.88	**< 0.0001**	0.11	F (1, 2994) = 3.33	0.0679	0.001
MANOVA (Mass, wing chord, tarsus length)	Year	F (9, 4357) = 18.92	**< 0.0001**	0.04	F (9, 2994) = 21.52	**< 0.0001**	0.06
	Site	F (2, 4357) = 694.48	**< 0.0001**	0.31	F (1, 2994) = 42.43	**< 0.0001**	0.04
	Site * Year	F (18, 4357) = 10.61	**< 0.0001**	0.04	F (9,2994) = 8.99	**< 0.0001**	0.03
	Sex	F (1, 4357) = 391.00	**< 0.0001**	0.21	F (1, 29994) = 291.04	**< 0.0001**	0.22

Table 4. A) Results for Phenotypic Trajectory Analysis (PTA) of *Geospiza fortis* at the three study sites from 2003 to 2012. ΔL: Average difference between in the length of trajectories in mm. θ: Average differences in the direction of trajectories given in angle degrees. B) Pairwise comparisons of phenotypic trajectories between the three study sites (AB: Academy Bay, DM: Daphne Major, EG: El Garrapatero). P-values in bold indicate significant differences.

A)	ΔL (mm)	p- value	θ (angle degrees)	p-value
Beak traits	1.228	**0.005**	119.869	**0.001**
Body traits	59.26	**0.001**	72.773	**0.001**

B)

Population	ΔL (mm)	p-value	θ (angle degrees)	p-value
Beak traits				
AB vs. DM	2.797	**0.002**	21.902	**0.006**
AB vs. EG	0.639	0.360	6.621	0.504
EG vs. DM	2.158	**0.005**	27.84	**0.001**
Body Traits				
AB vs. DM	13.559	**0.001**	28.214	**0.001**
AB vs. EG	0.463	0.808	18.102	**0.028**
EG vs. DM	14.022	**0.001**	11.257	0.152

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Linking statement 1

Environmental variation is a key factor in the ecological and evolutionary dynamics of organisms and the feedbacks between these dynamics. The first chapter helped to understand the role of *terroir,* or spatial effect, in the phenotypic variation of Darwin's finches. I show that the variation in beak and body size - but not beak shape - of Darwin's finches is mainly explained by the spatial effect compared to the temporal effect. I further discuss that even when these results are consistent with the hypothesis of diversification of Darwin's finches facilitated by ecological differences, temporal effects may not be evident in this study because Darwin's finches are long-lived organisms, and I only used data of a 10-year period.

Previous studies on the small island of Daphne Major in the Galápagos Islands have shown how Darwin's finches evolve in response to drastic weather changes such as El Niño or La Niña over short periods of time. Therefore, in the second chapter, I 1) assess whether populations of the medium-sized ground finch, *G. fortis*, at two sites on Santa Cruz Island show the same responses to short-term changes in temperature and precipitation. I then follow this study by analysing the impact of long-term weather changes (over 20 years), that is climate change, on the phenotypic variation of Darwin's finches by 2) identifying trends of climate change in time series of precipitation and temperature that would indicate the presence of climate change, and 2) identifying trends in time series of finch phenotypic traits consistent with trends in environmental variables.

Chapter 2

Darwin's finches and climate change: insights from a resilient system.

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2.1 Abstract

Climate change is known to influence biodiversity worldwide, with changes in some organismal traits observed in many populations of many species. Such effects are not universal, however, with other traits showing remarkable stability through time. Time-series analyses that link environmental variables to trait values can generate useful insights into trait evolution and its ecological bases. We use 24 years of data for beak and body traits of two species of Darwin's finch in the Galápagos Islands, alongside data on temperature and precipitation, to answer three questions: Q1) to what extent does weather (year-to-year changes) influence annual variation in beak and body traits in Darwin's finches? Q2) how is weather changing through time; that is, to what extent is climate change present in our study sites? and Q3) do time-series of annual values of beak and body traits show detectable trends that suggest climate change effects? For both species, cross-correlation analyses show that precipitation has a lagged, negative correlation with beak and body traits (effect size: – 0.632): that is, increased precipitation leads to smaller traits in subsequent years. Associations of finch traits with temperature were more variable. We next found that temperature and precipitation have been increasing over the past two decades – although this trend is minor in comparison to year-to-year variation. Finally, we found that phenotypic time-series of beak and body traits showed no detectable sign of climate change trends, instead behaving either as random walks or as stable (stasis) trajectories. We close by discussing the reasons why Darwin's finches react to short-term weather changes but not to long-term climatic trends, leading to suggestions for further studies to better understand climate change impact on highly variable insular ecosystems such as Galápagos.

Keywords: rapid-evolution, resilience, evolutionary patterns, thermoregulation, climate-warming.

2. 2 Introduction

Climate change can influence biodiversity in many ways, often with far-reaching ecological and evolutionary consequences (Karell et al. 2011, van Asch et al. 2013; Scheffers et al. 2016; Cotto et al. 2017). Most obviously, climate change can influence the evolution of traits related to physiology, behavior, and morphology that have further effects on the phenology (Franks et al. 2007; van Asch et al. 2013), abundance (Bowler et al. 2017), distribution (Johnston et al. 2013), and life-history of species (Gardner et al. 2011; Pearson et al. 2014). Some specific examples include the advancement of breeding and migration timing in response to temporal changes in resource availability (e.g Gienapp et al. 2008; Goodman et al. 2012; Charmantier and Gienapp 2014), changes in the strength of sexual selection between divergent species due to increases in temperature and consequent changes of these species ranges (Qvarnström et al. 2016), altered frequencies of color morphs responding to habitat changes produced by milder winters (Karell et al. 2011), and changes in body size due to shifting food resources or temperature susceptibility (Millien et al. 2006; Blois et al. 2008; Oke et al. 2020; Jirinec et al. 2021).

Despite these and many other examples of climate-related trait changes, effects are not evident in all instances. Indeed, the meta-analysis by Sanderson et al. (2021) found that the average effect of climate change on organismal traits was not particularly striking – mainly because effects ranged from very large to non-existent. How then might we explain the many instances of minimal change? First, climate change is highly heterogenous at many scales across the globe, and some populations might thus experience little climate change (Foden et al. 2019), or any climate change trend might be trivial in relation to shorter-scale weather variations such as those seen on daily, seasonal, or annual scales. Second, some populations might lack the genetic or plastic potential to respond to climate change (Merilä and Hendry 2014). In these instances, climate change could be strong and thus favor trait change; yet resulting trait changes might be minimal. Third, some organisms might be adapted to specific resources or environments that are relatively insensitive to climate change. In such cases, climate change might be strong, but traits might not change because they are more attuned to environmental features not showing a climate change signal.

One might distinguish among the three above scenarios using time-series analysis of rates and patterns of environment change in relation to rates and patterns of trait change, especially where the genetic and functional bases of the studied traits are well known. First, time-series analyses of climate variables can be used to ask whether a signal of climate change is detectable beyond shorter-scale (e.g annual) changes in weather (Mudelsee 2010). Second, time-series analysis can be used to assess trait changes and their potential causes – as has long been the case in paleontology (e.g., Hunt 2007; 2015; Hopkins and Lidgard 2012; Geerts et al. 2015). For instance, trait changes in time-series can be used to infer: 1) directional change, whereby trait values show a generally decreasing or increasing trend over time (Figure 1A), 2) stasis, whereby trait values fluctuate around a population mean with no net change across time (Figure 1B), or 3) random walks, whereby trait values show unpredictable increases or decreases from one year to the next (Figure 1C) (Hunt 2007; Tëmkin and Elredge 2015*)*. Time-series analysis can also reveal combinations of these categories, such as a directional trend with reversion to the population mean (Hunt et al. 2015; Lambert et al. 2020). Finally, lagged time-series of phenotypic traits can be compared to time-series of environmental data to identify short-term and long-term associations between environmental and trait variables (Hunt et al. 2015; Hannisdal et al. 2017). In the present paper, we employ time-series analysis to test trends and potential environment-by-trait correlations in two species of Darwin's finches.

Darwin's finches and climate change in Galápagos

The climate of the Galápagos Islands is tied to its location in the Eastern Tropical Pacific about 1000 km west of the coast of South America. Three primary oceanic currents converge on Galápagos and interact with prevailing winds coming from the southeast (Trueman and d'Ozouville 2010) to generate two seasons. The warm/wet season prevails from December through May and is characterized in most years by occasional to high precipitation and high temperatures. The dry/cold season prevails from June through November and is characterized by low precipitation and cooler temperatures (Trueman and d'Ozouville 2010). Importantly, wide variation in temperature and precipitation occurs within and between years and seasons owing to changing ocean conditions that include El Niño and La Niña events. El Niño events occur every two to seven years and, in Galápagos, are characterized by a rainy season with abnormally high levels of precipitation. La Niña events tend to occur right after El Niño events and, in Galápagos, are characterized by extended periods of drought (Trueman and d'Ozouville 2010; Liu et al. 2013). Amidst these patterns of seasonal and inter-annual variation, some signs of climate change have been detected. For instance, average annual temperatures on the islands were reported to increase by 0.6 C° from 1980 to 2017 (Paltán et al. 2021), whereas the first two decades of the present century have been in average 40 % drier compared to the precipitation on the 1981-1990 decade (Escobar-Camacho et al. 2021). Further, El Niño events over the past two decades appear to have increased in frequency and intensity (Rustic et al. 2015).

Effects of precipitation and temperature changes on Galápagos birds have been explored in relation to stress-responses, food scarcity, invasive species, and thermoregulation. For example, some land bird species, including the ground finches (*Geospiza* spp.), show higher stress-related hormone levels during El Niño events (Wingfield et al. 2018). Similarly, increased temperature and precipitation appear to increase parasitism by the introduced Avian Vampire *Philornis downsi* on Darwin's finch nestlings (Dudaniec et al. 2007). Further, food availability, shaped by high or low levels of precipitation, influences finch mortality and acts as a strong selective agent on beak size and shape (Grant and Grant 1993, 1996, 2002, 2006, Beausoleil et al. 2019). Finally, it has been suggested that increasing temperature due to climate change – independent of changes in precipitation – could influence beak size evolution for thermoregulatory reasons (Tattersall et al. 2018). These diverse studies suggest the value of using time-series analysis of finch traits to infer potential responses to climate change.

Interpretation of our results will be aided by an uncommonly strong understanding of the genetic and functional basis of several finch traits. First, inter-annual trait changes in beak traits are expected to reflect evolutionary responses (as opposed to plasticity) given the extremely high heritability of beak size (0.87-1.03 h^2) and shape (0.75-0.92 h^2) (Boag 1983, Grant and Grant 1993, 1997). Further, several large-effect genes influencing beak traits are known (Abzhanov et al. 2004; Chaves et al. 2016; Lamichhaney et al. 2016) – and have been documented to experience allele frequency changes that correspond to trait selection (Lamichhaney et al. 2016). Second, beak sizes and shapes are known to be closely tied to local food resources. For instance, the distribution of beak sizes and shapes in finch communities is linked to the types of food resources – especially seed sizes and hardnesses – that are present locally (Lack 1947; Abbott et al. 1977; Schluter 1984, De León et al. 2014). Furthermore, temporal changes in plant communities during El Niño and La Niña events lead to rapid evolutionary changes in beak traits (Grant and Grant 2002; 2006).

With the above motivation and context, we compile 24 years of data on beak and body traits in the small ground finch (*Geospiza fuliginosa*) and the medium ground finch (*Geospiza fortis)* at two sites on Santa Cruz Island, Galápagos, and similarly compile comparable time series for temperature and precipitation. We then use time-series analysis to answer three questions: Q1) how does weather (year-to-year changes) influence beak and body traits in our study system, as has been previously reported for other populations or time periods in Galápagos (e.g., Grant and Grant 2006; Beausoleil et al. 2019), Q2) to what extent is weather changing through time (i.e., "climate change") in our study sites, as has been found in other places in Galápagos (Paltán et al. 2021; Escobar-Camacho et al. 2021), and Q3) to what extent do time-series of beak and body traits show detectable trends consistent with responses to climate change?

2.3 Methods

Study sites and data collection

Our study focused on two lowland sites on Santa Cruz Island: Academy Bay (AB; 0° 44' 21.3" S, 90° 18 '06.3" W) and El Garrapatero (EG; 0° 41' 15.7" S, 90° 13' 18.3" W). Academy Bay lies along the southeastern shore of Santa Cruz, next to the town of Puerto Ayora. El Garrapatero lies along the eastern shore of the island, approximately 10 km northeast of Puerto Ayora. El Garrapatero is relatively far from any human settlement, although a road passes through the site giving tourists access to a beach. The road was paved in 2008. Both sites lie in the lowlands of Santa Cruz and thus are characterized by arid weather and arid-zone vegetation.

Precipitation and temperature data were obtained for the 24 years (1999 – 2022) of our study. Daily rainfall and temperature data for Santa Cruz were recorded by a gauge maintained at the Charles Darwin Research Station (Charles Darwin Foundation 2024). These data should be broadly representative of both sites given their similar biotic and abiotic conditions: AB (500 m from the gauge) and EG (10 km from the gauge). However, our personal experience suggests that EG experiences less rainfall than AB, which is supported by a previous study (Carrion et al. 2022) showing lower vegetation cover (Enhanced Vegetation Index) at EG compared to AB.

Morphological data were collected for the medium ground finch (*Geospiza fortis*) and the small ground finch (*Geospiza fuliginosa*) from 1999 to 2022 at the two study sites during the breading season of Darwin’s finches (January to May) (Table S1): AB between 1999 and 2022, and EG between 2003 and 2022. Data were not available from 2021 due to the COVID-19 pandemic. Briefly, birds were captured with mist nets and banded with color and metal leg bands that had unique numbers and combinations to ensure that each bird was included in our dataset only once for a given year. At the time of capture, each bird was classified – when possible – as juvenile, male, or female based on their plumage, beak color, and the presence of a brood patch (Grant 1999). Mature males can be easily identified based on their black plumage; however, it can be difficult to distinguish juveniles from mature females that do not have a brood patch (Grant 1999).

Each bird was measured following the methods of Boag and Grant (1984 – see also Grant, 1999). Specifically, we measured beak length (anterior edge of nares to anterior tip of upper mandible), beak depth (at the nares), beak width (at the base of the lower mandible), body mass (weight), wing chord (length of longest relaxed right primary feather), and tarsus length (between the nuchal notch at the upper end of the right tarsometatarsus and the lowest undivided scute). Beak and tarsus measurements were made to the nearest 0.01 mm using digital calipers. Wing chord was measured to the nearest 0.01 cm using a wing-and-tail ruler. Mass was measured to the nearest 0.01 g using a portable digital scale. In most cases, beak length, depth, and width were each measured three times for each bird, and the median value was then used for subsequent analysis. More information on these sites and their finch communities, as well as our field procedures, can be found in Carrión et al. (2022) and Beausoleil et al. (2023).

Is weather (year-to-year changes) affecting beak and body traits in Darwin's finches? (Q1)

To remove potential hybrid individuals from the raw data, we identified outliers using the interquartile range rule using the *boxplot.stats()* command in R (R Core Team, 2021). After removing outliers, annual mean values were calculated for each environmental variable (temperature and precipitation) and each morphological variable (beak length, beak depth, beak width, body mass, tarsus length, and wing chord). Each time-series was then checked for autocorrelation and partial-autocorrelation; that is, whether a variable was correlated with lagged values (between 1 and 5 years) of itself. We performed this analysis using the *acf()* and *pacf()* functions in R (Venables and Ripley 2002). If autocorrelation was present in a time-series, it was corrected by subtracting (from each of its values) the previous value (for autocorrelation at lag -1), the two previous values (for autocorrelation at lag -2), and so on. This correction was done using the *diff()* function of the timeSeries package in R (Hyndman and Killick 2023).

After these corrections, we tested for correlations (cross-correlations) between each morphological trait time-series and each environmental time-series at different lags using the *ccf()* function in R (Venables and Ripley 2002). As Darwin's finches have shown evolutionary responses between 1 and up to3 years after an environmental event (e.g., drought or heavy rain; Boag and Grant 1981; Gibbs and Grant 1987; Grant and Grant 1993), we tested correlations between traits and values of temperature and precipitation lagged between one and five years. Note also that the rule of thumb for cross-correlation analysis is that the number of lags tested should be no more than $T/4$, where T is the length of the time-series (Hamilton 1994; Box et al. 2015). The cross-correlation function (CCF) at lag k for two time series $\{Xt\}$ and $\{Yt\}$ is defined as:

$$\mathrm{CCF}\ (k)\ =\frac{\mathrm{Cov}\ ((X_t-\mathrm{mean}\ (X_t)),(Y_{t-k}-\mathrm{mean}\ (Y_{t-k}))}{\sqrt{\mathrm{Var}(X)\cdot\ \mathrm{Var}(Y)}}$$

where $\mathrm{Cov}(X_t, Y_{t-k})$ is the covariance between X_t and Y_{t-k} (observations of X at time t and Y at time $t-k$), and $\mathrm{Var}(X)$ and $\mathrm{Var}(Y)$ are the variances of X and Y, respectively.

Positive correlation (CCF) values indicate a positive relationship between the two series at a specific lag, whereas negative values indicate a negative relationship. Similarly, larger positive or negative values indicate a stronger relationship between the two series. Values that cross the dotted line in the resulting correlograms (Fig. 2) indicate a significant (z-test) correlation between a time-series and another time-series at lag *k*. As we were interested in the influence of values of precipitation and temperature on the lagged values of beak and body traits of finches, and not the opposite, only correlations from zero to the left on a correlogram were considered. Finally, the largest CCF coefficient per correlation was noted and reported in the results section. As an illustrative example (Fig. 2), beak length correlates negatively with precipitation four years prior: in other words, when it rains a lot in one year, beak length tends to be shorter four years later.

Is climate change present in the study sites in Galápagos (Q2)? and, do time-series of beak and body traits show detectable trends consistent with climate change (Q3)?

To identify whether each time-series was most consistent with a random walk, stasis, or a directional trend, we classified each environmental (*Q2)* and finch trait (*Q3)* time-series following a two-step procedure as in Lambert et al. (2020). First, we classified the series as random walks or stasis (mean-reverting) by estimating their persistence *r* (relation of current value to past values within a time-series that indicate whether a trait tends to stay stable or drift over time). For this we fit a Bayesian hierarchical model of first-order auto-regressive process (AR1), where the model predicts current values based on its immediately preceding value (one year before).

$$z(t) = \rho . z(t-1) + \epsilon(t)$$

Where:

$z(t)$ the trait/environmental value at time t

ρ persistence parameter

$\epsilon(t) \sim N(0, \sigma^2)$ normally distributed error with variance σ^2

To account for relationships among traits and to give equal weight to the random walk and stasis hypothesis, we allowed *r* to vary for all the traits simultaneously using a weak informative prior, yet the individual parameters were drawn from a common normal distribution of the form:

$$\rho(z) \sim \mathcal{N}(\bar{\rho}, \tau)$$

Where *z* is the trait or environmental value, $\bar{\rho}$ is the population mean of *r;* and τ is the s.d. of the population-level distribution.

If the 95th percentile of the posterior distribution of ρ was < 1 we classified it as stasis, and if not, as random walk.

After the above process, we estimated the level of bias (trend) in each time-series, δ. If a time-series was previously identified as random walk, we used a model of the form:

$$\Delta\bar{z}(t) = \delta + \epsilon(t)$$

where $\Delta\bar{z}(t)=\bar{z}(t)-\bar{z}(t-1)$, and e(t) is a normally distributed error term that represents random fluctuations or noise in the data.

If a time-series showed stasis (mean reversion), we used a model of the form:

$$\bar{z}(t)=\delta t+\epsilon(t)$$

For each trait, if the 5th and 95th percentiles of the posterior distribution of δ did not overlap zero, we classified it as directional trend. For each model, we ran four MCMC (Markov chain Monte Carlo) chains with 5000 iterations to reduce divergent transitions that might be caused by the small sample size and discarded the first half of samples as warm up. We used the R-hat diagnostic metric to assess whether the chains converged to stable posterior distributions. All models presented R-hat < 1.1, which indicates convergence and reliable estimates. The models were run using Stan package in R (Stan Development Team 2023).

2.4 Results

Is weather (year-to-year changes) affecting beak and body traits in Darwin's finches (Q1)?

For *G. fortis,* cross-correlation coefficients between precipitation and beak and body traits consistently showed negative relationships at both sites (Fig. 3A, Table S2) That is, as precipitation increased, trait sizes decreased. The strongest correlation coefficient for precipitation was with beak width at EG (CCF = -0.632, n = 20), whereas the weakest was with tarsus length at AB (CCF = -0.131, n = 24). Cross-correlation coefficients between temperature and beak and body traits showed a variety of positive and negative relationships (Fig. 3B, Table S2). As temperatures increased, some traits decreased in magnitude (beak depth, beak width, wing chord, mass), whereas other traits increased in magnitude (beak length, tarsus length). The strongest correlation coefficient for temperature was with wing chord at AB (CCF = -0.513, n = 24), whereas the weakest was with beak width at EG (CCF = 0.121, n = 20).

For *G. fuliginosa*, cross-correlation coefficients between precipitation and beak and body traits also showed negative relationships at both sites (Fig. 3C, Table S3): again, increasing precipitation led to decreasing trait sizes. The strongest correlation coefficient for precipitation was with wing chord at EG (CCF = -0.543, n = 20), whereas the weakest was with beak length at EG (CCF = -0.119, n = 20). Cross-correlation coefficients between temperature and beak and body traits for *G. fuliginosa* showed a mix of positive and negative relationships (Fig. 3D, Table S3) – as was also the case for *G. fortis* (see below). As temperatures increased, beak depth, wing chord, and mass decreased at both sites, whereas other traits increased in magnitude (beak length, tarsus length, beak width). The strongest correlation coefficient was for mass at EG (CCF = -0.495, n = 20), whereas the weakest was for tarsus length at EG (CCF = 0.185, n = 20).

Is climate change present in our study sites in Galápagos (Q2)?

Analysis of trends and classification of time-series revealed similar patterns for temperature and precipitation. Precipitation showed positive directional change (trend d = 0.015 cm^3, with 95 percent credible interval ranging between 0.005 cm^3 and 0.21 cm^3) with increasing fluctuation around the mean (r = 0.12 cm^3, with 95 percent credible interval ranging between -0.21 cm^3 and 0.45 cm^3) (Fig. 4A). Temperature also showed positive directional change (trend d = 0.006 °C, with 95 % credible interval ranging between 0.005 °C and 0.19 °C) with increasing fluctuations around the mean (r = 0.11 °C, with 95 % credible interval ranging between - 0.24 °C and 0.50 °C) (Fig. 4B). In summary, over the last 24 years, the lowlands of Santa Cruz Island have seen an annual increase of about 0.011 cm^3 in rainfall and 0.006 °C in temperature. Also, note that these are linear trends, whereas non-linear relationships could well be present – especially for temperature (Fig. 4).

Do time-series of beak and body traits show detectable trends consistent with climate change (Q3)?

Classification analyses for *G. fortis* showed that time-series for beak length, beak depth and beak width were mostly consistent with random walks, whereas time-series for tarsus length, wing chord, and mass were more consistent with stasis (Fig. 5A, Table S4). Analyses for *G. fuliginosa* showed similar patterns: time-series for beak traits were more consistent with random walks, whereas time-series for body traits were more consistent with stasis (Fig. 5B, Table S4). None of the time-series for beak and body traits in either species suggested a directional change or trend (Fig. 5, Table S4).

2.5 Discussion

The goal of our study was to test for potential associations of climate change with phenotypic evolution in two species of Darwin's finches. Studies on many other species have shown diverse impacts of climate change; yet such impacts might be minimal or hard to detect under certain conditions. We might expect minimal impact of climate change in areas where it is not very pronounced, where populations lack the ability to respond to climate change, or where the resources and conditions the species rely on are not strongly affected by climate change. Time-series analyses of traits with known genetic and functional properties allow some insight into these possibilities. We performed such analyses based on 24 years of data for beak and body traits in the two species, alongside data on precipitation and temperature for the study sites. Our first results revealed negative correlations between precipitation and beak and body traits for both species, alongside more variable correlations between temperature and those traits. Second, Bayesian time-series analyses detected precipitation, and temperature increases over the 24 years, although the trend was mild and weak relative to year-to-year fluctuations. Third, beak and body traits did not show detectable directional trends, with beak traits mainly showing random walk patterns, and body traits mainly showing stasis. We now discuss each of these three main results in more detail.

Is weather (year-to-year changes) affecting the beak and body traits in Darwin´s finches (Q1)?

Previous work has shown that beak traits of finches evolve partly in response to changes in seed availability that are mediated by inter-annual variation in weather (e.g., Grant and Grant 2002; 2006). We therefore expected to detect lagged correlations between time-series of environmental variables and time-series of beak traits. Indeed, our cross-correlation analysis revealed several interesting results.

Precipitation showed a lagged negative correlation with beak and body traits – that is, increased precipitation in one year led to smaller finch beaks and bodies in subsequent years (Fig. 3, Tables S2 and S3). This lagged effect is expected and consistent with previous findings. For instance, a severe drought on Daphne Major between 1976 and 1978 reduced small seed availability and favored finches with larger beaks that could crack larger and harder seeds (Boag and Grant 1981; Boag and Grant 1984; Price et al. 1984). The outcome was an increase in beak size the year following the drought. On the flip side, substantial rainfall on Daphne Major in 1983 during an El Niño promoted a larger diversity of small seeds such that large-beaked finches foraged less optimally, favoring finches with small beaks (Grant and Grant 1993). The outcome was a decrease in beak size in subsequent years. Similarly, in our study site at El Garrapatero, Beausoleil et al. (2019) documented a lagged effect of precipitation on the strength of selection acting on beak traits in *G. fortis*. In this last case, high rain in a given year led to high production and survival of young finches, which then seemingly increased competition in subsequent years, which thus increased selection. However, the specific nature (positive or negative) of such lags depends on the community context. For instance, after the large ground finch (*G. magnirostris*) invaded Daphne Major in 1982, another severe drought occurred in 2004, which caused *G. fortis* beaks to actually evolve to be smaller due to inter-specific competition (Grant and Grant 2006). In short, our cross-correlation analyses for beak traits and precipitation yielded outcomes consistent with previous findings that used other methods for other populations, time periods, or variables.

With respect to temperature, a common expectation is that warmer conditions favor smaller body sizes (Bergmann's Rule) but longer appendages (Allen's Rule), because both changes should allow more efficient heat loss in hotter environments (Bergmann 1848; Allen 1877; Symonds et al. 2010; *reviewed in* Teplitsky and Millien 2014). Our results, however, suggest much more nuanced outcomes. In *G. fortis*, we found a lagged positive correlation between temperature and beak and tarsus length, but a lagged negative relationship between temperature and beak depth, beak width, wing chord, and body mass (Fig. 3, Table S2). In *G. fuliginosa*, we found a lagged positive correlation between temperature and beak width, beak length, and tarsus length, but a lagged negative correlation with beak depth, wing chord, and body mass (Fig. 3, Table S3). It does not seem profitable to try to parse each of these individual correlations into specific putative causes, as doing so would be speculative. We emphasize that – unlike precipitation (see above) – temperature does not have a straightforward and consistent effect on finch traits. The likely reason is that finch beaks are multi-purpose tools where any thermoregulatory function (Tattersall et al. 2018; Friedman et al. 2019) is probably secondary (perhaps distantly so) to acquiring, manipulating, and consuming seeds (Lack 1947; Bowman 1961). Perhaps the strongest argument against an emphasis on thermoregulation as a driver of species divergence in morphology is that arid-zone finch communities are composed of a great diversity of species with diverse beaks and body sizes – all of which persist and succeed at the same very high temperatures. A meta-analysis by Siepielski et al. (2016) found that precipitation (and not temperature) is a global driver for natural selection.

Is climate change present in our study sites in Galápagos (Q2)?

Our analyses suggest that average temperature and precipitation have increased at our study sites over the past two decades (Fig. 3), which agrees with global trends and trends in the equatorial Pacific region (IPCC 2018). Specifically for Galápagos, Paltán et al. (2021) estimated that the lowlands have seen an increase of 0.6 C° over the past 35 years – higher than our estimate of 0.24°C over the past 24 years. Outcomes for precipitation are less consistent. Paltán et al. (2021) concluded that average precipitation decreased over the last 35 years. Escobar-Camacho et al. (2021), on the other hand, did not find any trends for precipitation in the Galápagos lowlands during the 2002-2017 period. These variable outcomes might be related to El Niño events, where unusually large amounts of rain can affect time-series analyses or can be related to the different number of locations (rain gauges) used to analyze climatic trends. Paltán et al. (2021) showed that precipitation follows an increasing trend when El Niño years (1982–83 and 1997–98) are excluded from the calculation. In our analysis, the period used did not include extreme El Niño years, and the most obvious effect was a small increase in rainfall over the last few years from 2019 to 2022 (Fig. 4).

Regardless of any slight long-term trend in temperature or precipitation, it is critical to emphasize the comparatively large inter-annual variation. For instance, we estimate that average temperature increased by 0.15 C° over 24 years, yet average temperature differed between adjacent years by up to 1.7 C° (e.g., 22.8 °C in 2008 versus 24.5 °C in 2009, Fig. 4B). Similarly, average precipitation was estimated to have increased by 0.36 cm^3 over 24 years, yet average precipitation differed between adjacent years by up to 1.53 cm^3 (e.g., 0.57 cm^3 in 2008 versus 2.10 cm^3 in 2009, Fig. 4A). Furthermore, temperature and precipitation can vary dramatically within a year – most obviously corresponding to the previously-mentioned “wet/warm” versus “dry/cold” seasons. In the lowlands, for instance, temperature varies from 26 C° during the wet season to 22 C° in the dry season, whereas precipitation varies from 6.5 cm^3 to 0.5 cm^3 (Paltán et al. 2021). Thus, short-term changes in temperature and precipitation faced by finches greatly exceed any long-term trends – and this distinction is likely critical to understanding any evolutionary trends, or the lack thereof.

Do time-series of beak and body traits show detectable trends consistent with climate change (Q3)?

Time-series of beak and body traits of finches did not show any detectable evolutionary trends over the 24-year period of our study (Fig. 5). For beak traits, time-series in both species could not be distinguished from a random walk pattern, meaning that they appear to have changed rather erratically and unpredictably. Two aspects of this pattern call for explanation: the high year-to-year variation and the minimal directional trend. The annual variation makes sense given the above-noted short-term association between weather – especially precipitation – and beak traits. That is, precipitation varies dramatically year-to-year and thus so do beak sizes as they show rapid – but lagged – evolutionary responses (see also Grant and Grant 2007; Beausoleil et al. 2019). Consistent with this interpretation, the inter-annual beak size changes are much smaller than the inter-annual precipitation changes – because finch beaks of various sizes can be successful under diverse conditions (i.e., selection does not vary as dramatically as does the environment) and because evolutionary responses are not instantaneous, in part because finches have long generation times (~ 4-5 years; Grant and Grant 1992).

For beak traits, the lack of directional trends also makes sense because – as noted above – the seasonal and inter-annual weather fluctuations are much greater than the "average" directional climate trend. Furthermore, beaks are directly tied to resources through their role in seed manipulation and cracking (e.g., Grant 1981; De León et al. 2011) – as opposed to being directly influenced by temperature or precipitation. In short, finch beaks are well adapted to particular sets of food resources and, as long as those resources are abundant, selection should maintain similar trait values. That is, each species experiences stabilizing selection around the beak size best suited for the food types it consumes (Lack 1947; Schluter and Grant 1984; Grant and Grant 2007; Beausoleil et al. 2023). As long as climate change does not severely deplete those resources (e, g., Daphne major case study; citation), the beak sizes of each species should remain relatively constant over long time periods. Indeed, plant regimes have remained reasonably stable in Galápagos over the past ~2500 years, despite major climatic events (Restrepo et al. 2012). Two further observations also highlight how this general stability through time is manifest for finches. First, the primary determinant of variation in beak size is spatial location (e.g., island) rather than temporal changes associated with climate – because food resources differ much more across space than they do through time (Schluter and Grant 1984; Grant and Grant 2007; Carrión et al. 2022). Second, every location contains a mixture of finch species with very different beak sizes and shapes, each maintained in sympatry due to specialization on particular food types, further strengthened by competition between species (Grant and Grant 2007; Beausoleil et al. 2023). As such, the system should be relatively insensitive to the small changes in climate.

For body traits, time-series analysis suggests mean-reverting or stasis patterns in both species. The absence of a directional trend might seem surprising given that many studies and meta-analyses suggest that body size declines in response to climate warming are general across regions and taxonomic groups (Sheridan and Bickford 2011; Scheffers et al. 2016; Ryding et al. 2021 and references therein). Moreover, birds specifically show some reasonably consistent responses to climate change, although most typically for migration or breeding times (Romano et al. 2022; Halupka et al. 2023). Body size shows more variable patterns, although some analyses suggest that sizes are declining more than expected by chance (Yom-Tov et al. 2001; 2006; 2010; Teplitsky et al. 2008; Gardner et al. 2009). Darwin's finches, however, fall into the category of the many bird species that are not showing any obvious body size trends with temperature – again probably for the above reasons that each species is specialized on a given food type, which then maintains selection for a particular body size (Grant 1999). As for why the non-directional patterns for body traits fluctuate less than those for beak traits, we do not have a clear explanation other than the possibly closer functional ties between precipitation, plants, and beak traits than between those factors and body size.

Conclusion

Climate change is ubiquitous and is altering the traits and fates of many species – yet such effects are not expected to be universal. Some places and species should experience less climate change, and some key traits of those (or other) species might not be strongly influenced by climate change. Darwin's finches might provide a case in point. Although precipitation and temperature appear to be increasing in Galápagos, any such increase is dwarfed by seasonal and inter-annual variation. That short-term variation in weather is known to cause rapid evolutionary responses in the finches, which presumably swamps any longer-term trend. Furthermore, the finches are specifically adapted to specific food resources (e.g., seed types) that vary in abundance from year to year without any consistent trend over long time periods. As such, the finch system appears relatively resilient to impacts of current climate change.

The above conclusion does not, however, mean that finches are "safe" moving forward. First, finch communities are negatively impacted by other forms of environmental change such as invasive predators (Kleindorfer et al. 2009; Gotanda 2020), invasive parasites (Fessl et al. 2010; O'Connor et al. 2010; Koop et al. 2016; Knutie et al. 2024), and habitat modification (Cimadom et al. 2014; Harvey et al. 2021), which can be exacerbated by climate change. Second, climate change might ultimately exceed the buffering capacity of the system that we have detected here. When this happens, a tipping point might be passed that can lead to dramatic changes (Dakos et al. 2019). Third, it is possible that some species in areas we did not study might currently be experiencing strong climate change impacts. Our focus was on abundant and widely-distributed species that exist across very large habitat gradients, whereas specialists on rare habitats might be more sensitive. For all these reasons, research should continue to monitor climate change in Galápagos – and the responses of their unique biota.

2.6 Figures

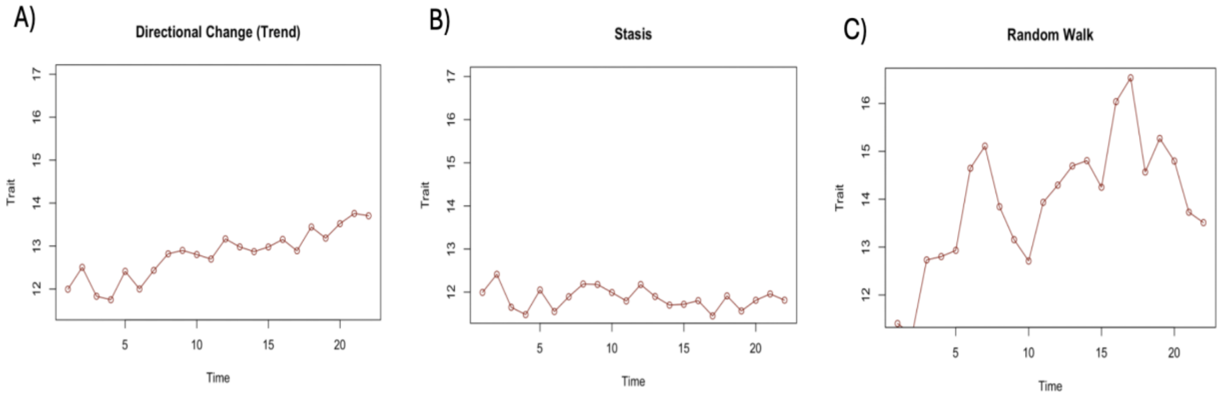

Fig. 1 Illustrative example simulations (red lines) of time-series types for finch beak length. Simulations were generated from original annual mean values of finch beak length between 1999 and 2022 at AB (Academy Bay) in Santa Cruz Island, using an Autoregressive (AR) model of order 1. We used 0.2 standard deviations for modelling the stasis process, and 0.09 slope for modelling the directional change.

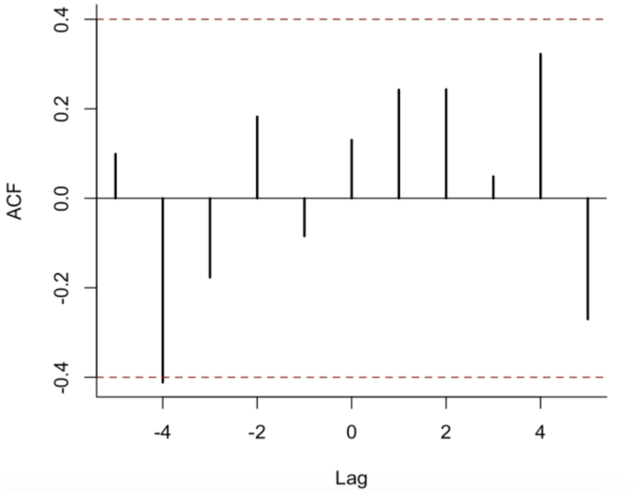

Fig 2. Example of a correlogram between beak length and precipitation time-series. Dotted lines indicate the significance threshold. We are here interested in negative lags because they refer to situations where weather influences finch traits in future years – as opposed to the illogical situation where finch traits would influence weather in future years.

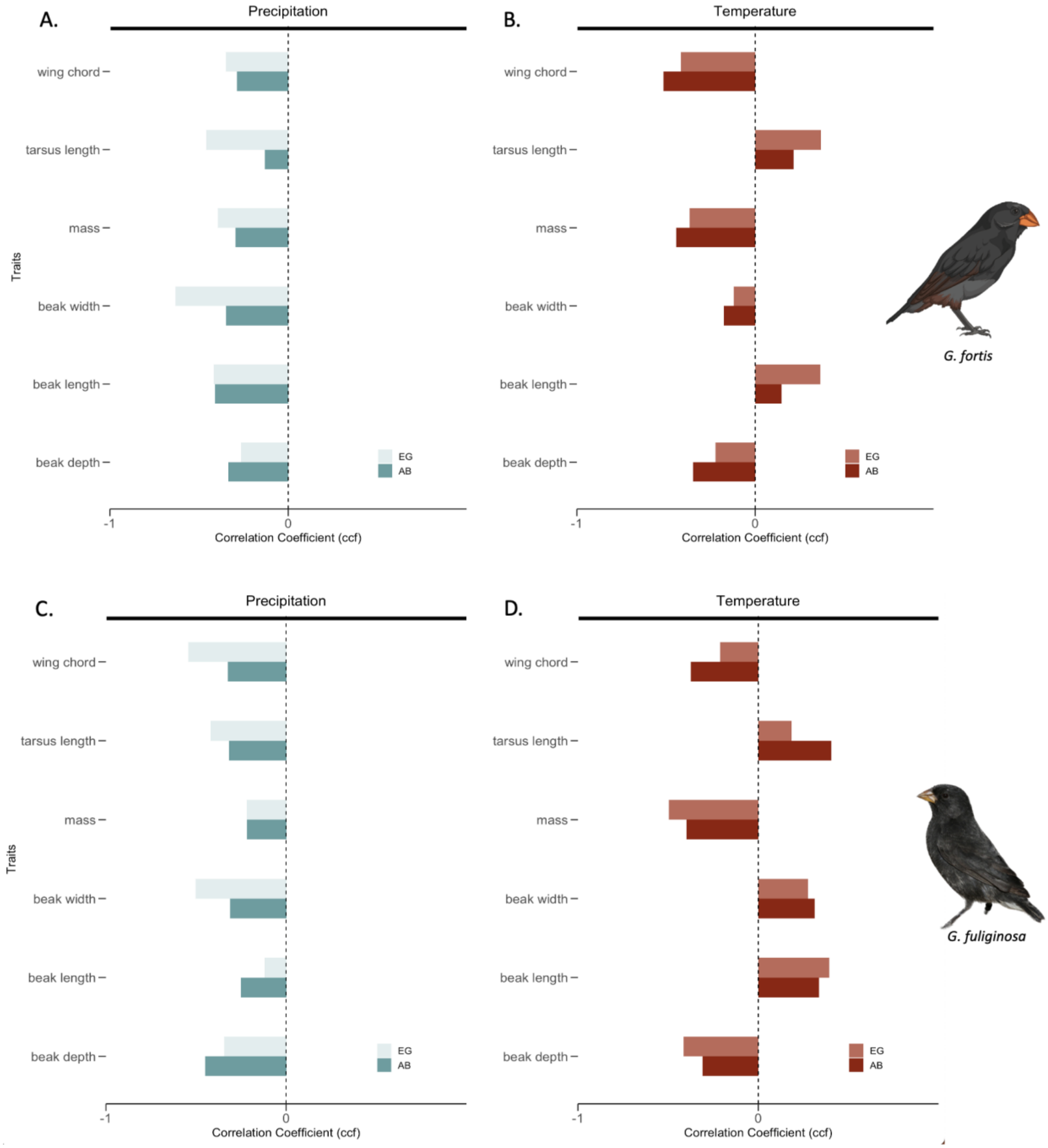

Fig. 3 Cross-correlation coefficients (CCFs) between lagged (from 1 to 5 years) time-series of precipitation (left-hand plots) and temperature (right-hand plots) for beak and body traits of *G. fortis* (A and B) and *G. fuliginosa* (C and D) at two sites AB and EG (different shading) on Santa Cruz Island, Galápagos. Bars correspond to the most extreme CCF coefficient per correlation.

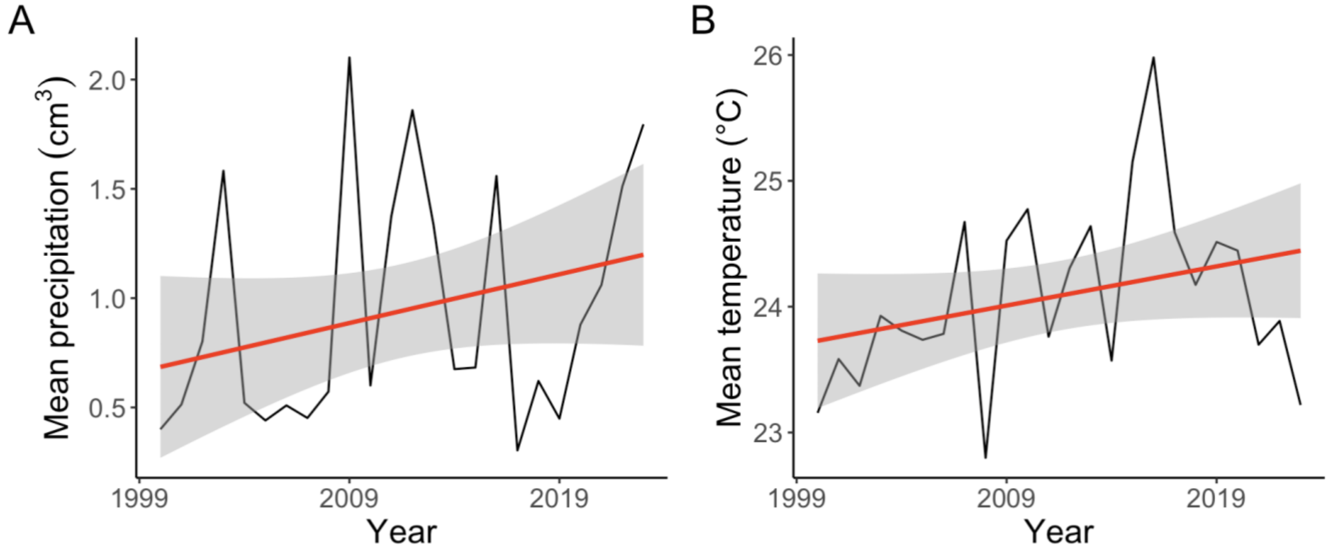

Fig. 4 Time-series of mean annual precipitation and temperature in Santa Cruz Island between 1999 and 2022. Lines in red indicate the estimated linear trend and the gray bar indicates the confidence interval on that estimate.

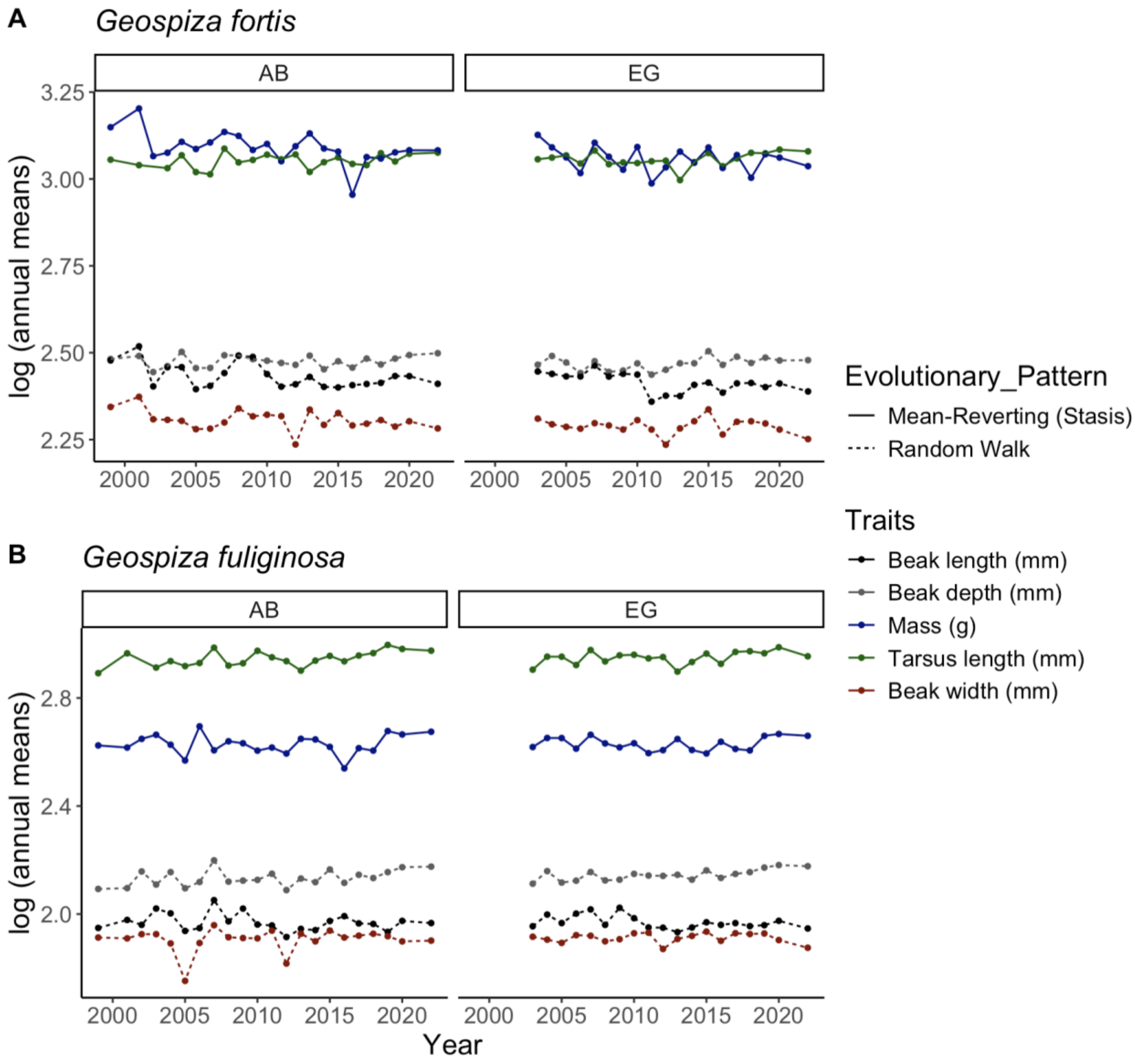

Fig. 5 Time-series of beak and body traits for *G. fortis* (A), and *G. fuliginosa* (B) between 1999 and 2022 at two sites (AB and EG) in Santa Cruz Island, Galápagos. Wing chord not displayed as its scale is drastically different.

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Linking statement 2

There is growing evidence on how human-induced climate change is affecting species around the world. Some common examples include changes in morphology, shifts in distribution, and changes in migration and breeding timing. In chapter two, I showed that Darwin's finches appear to be insensitive to climate change, as their phenotypic trajectories show no obvious trends over a 24-year period. Nevertheless, I discuss the importance of continuing long-term monitoring of finch populations, as trends in temperature and precipitation seem to keep increasing in the near future, and Darwin’s finches may reach a tipping point and no longer be resilient to such environmental variation.

In chapter three, we continue to examine human-related factors that influence the phenotypic variation of species populations. Urbanisation has recently received increased attention from scientists because cities create entirely new selection regimes to which species either adapt or die out. However, there is still little information on how species respond to urban environments and whether their responses are consistent. In this chapter, I examine parallel and non-parallel responses to urbanisation impacts in two species of urban-dwelling Darwin's finches to explore their phenotypic variation within and across species.

Chapter 3

Parallel and non-parallel responses to urbanization in Darwin's finches

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3. 1 Abstract

Urbanization has several impacts on the ecological and evolutionary processes of species. However, responses to urbanization impact in natural populations are often species-specific limiting our understanding of their predictability and impact on broader scale. Cities are unintentional replicates to study parallelism since they share similar feature that affect species or populations of the same species. Here, using data on two urban-dweller species of Darwin's finches, the medium and the small ground finch, across urban and non-urban sites at three islands in Galapagos I explore parallel responses to urbanization impact. I asked 1) what is the relative contribution of urbanization to the phenotypic variation of finch traits? 2) is this effect greater or equal than other site effects such as island, and 3) are responses in the phenotypic variation consistent across and within species, and if they do, 4) to what extent? We found that urbanization's contribution to beak and body variation in Darwin's finches is overall small (partial $\eta^2 = 0.004$) compared to the island effect (partial $\eta^2 = 0.05$), whereas parallel and non-parallel responses varied across species, populations, and traits. Finch populations in San Cristobal Island, the oldest island of the archipelago, showed parallel responses across and within species, compared to the other two islands that showed mixed responses. Finches in San Cristobal had larger pointer beaks at urban sites. Finally, urbanization overall explained more variation in beak shape (partial $\eta^2 = 0.004$) as opposed to beak size (partial $\eta^2 = 0.001$). Different responses to urbanization across and within species suggest an incipient effect of this factor that might be mediated by extrinsic features such as island and human settlement age, and intrinsic features such as species evolutionary history and genetics.

3.2 Introduction

As the human population grows, so do urban areas around the world. Nowadays, more people live in urban areas, whereas 68% of the world's population is projected to be urban by 2050 (*World Urbanization Prospects - United Nations*, 2018). Infrastructure and services needed in urban areas modify and fragment natural habitats which produces changes in local weather (Chapman et al. 2017), and often alters negatively the air (Qing 2018, Liu et al. 2022), water (Ren et al. 2014, Agrawal et al. 2021), light (McMahon et al. 2017), and sound quality (Rashed 2023). These impacts further influence the ecological and evolutionary processes of species and the feedbacks between them (Johnson and Munshi-South 2017, Alberti et al. 2015, 2017, 2020, Rivkin et al. 2019).

Urbanization creates artificial environments that can alter several evolutionary processes. Mutation rates can be exacerbated by high levels of pollution (Yauk et al. 2000). Gene flow is restricted as new fragments created by buildings and roads limit the movement and dispersal of organisms (Beninde et al. 2016), and in that way chances for an increase in isolation and genetic drift can be also seen, with negative consequences especially for small populations (Munshi-South et al. 2010). Furthermore, urbanization can generate new selective regimes to which species can respond. There is increasing evidence of species adaptations to urban environments that include changes in coloration as response to pollution such as the famous example of peppered moths in industrial settings (Kettlewell 1955), development of higher thermal tolerance as response to cities 'heat island' effect (Brans et al. 2017), less wary behavior to tolerate human presence (van Dongen et al. 2015), and several changes in morphology (Littleford-Colquhoun,et al. 2017, reviewed in Isaksson 2018), among others.

Although there is a growing number of studies on phenotypic differences between urban and non-urban populations, these often use a single city and/or a single species, leaving room for questions on how parallel the organism's responses to urbanization impact are. In this sense, cities represent good spatial replicates to perform studies of parallelism given that they often share similar features (Santangelo et al. 2020) and would thus exercise similar selection pressures on populations and related species. Examples of parallelism across cities include the tropical lizard *Anolis cristatellus* who presents longer limbs and lamellae in various urban sites of Puerto Rico (Winchell et al. 2016, 2023), the acorn ant *Temnothorax curvispinosus,* who lost cold tolerance in two cities in Ohio (Diamond et al. 2018), and the gray squirrel *Sciurus carolinensis,* who presented higher levels of melanism at urban sites compared to their rural counterparts across several North American cities (Cosentino and Gibbs 2022).

Even though urban evolution has gained popularity over the last decades, Santangelo et al. (2020) identified only 30 studies on 18 species that studied parallel responses to urbanization impact, and 93% of them occurred in the northern hemisphere. This invites further research, especially in rapidly growing urban settings such as the one in the global south.

Birds have received increasing attention as study systems on adaptation to urban sites. Evidence has shown that urbanization can alter birds behavioral, physiological, morphological and life-history traits (reviewed in Isaksson 2018). For instance, birds have responded to noise pollution by increasing the frequency of their calls and songs (Nemeth et al. 2013, LaZerte et al. 2017). They have also become more social (Kark et al. 2007) and have advanced reproductive timing in response to urban light pollution (Dominoni et al. 2013). Furthermore, broader analyses have shown that urban-tolerant birds tend to be smaller, less territorial, have larger clutch sizes, dispersal ability, and are more generalists in terms of diet and habitat use (Callaghan et al. 2020, Neate-

Clegg et al. 2023). Although these responses would indicate parallel responses, there are only few studies that have formally addressed parallel evolutionary responses to urbanization (Yauk et al. 2000, Miranda et al. 2013, Mueller et al. 2018),

In Galapagos, although Darwin's finches are famously known by their studies on beak evolution in response to drastic weather changes that alter food availability (e.g. Grant and Grant 2007), there is scarce information on how they adapt to urban settings and whether those changes are consistent within and across species. Finches in urban areas prefer feeding on human food items (De Leon et al. 2019), and correlations between their diet and beak morphology are weaker in urban sites (De Leon et al. 2011). This evidence can have further evolutionary responses. For instance, divergent selection has weakened in a historically bi-modal finch population at an urban site (Hendry et al. 2006). Additionally, higher environmental heterogeneity caused by urbanization have the potential to increase phenotypic variation (Thompson et al. 2022). De Leon et al. (2011) found that soft seeds are more abundant at an urban site compared to a non-urban. Thus finch populations living in urban areas would be expected to show less specialized and more variable beak traits. Furthermore, although finches' phenotypic variation is highly explained by a site component (e.g island) (Schluter and Grant 1984, Carrion et al. 2020), there is no evidence whether urbanization impact exceeds, equals or interacts with this effect. Finally, even when there is certain overlap in Darwin's finches' diet across species (De Leon et al. 2014), the ones with beaks that are more efficient at exploiting human food would likely show greater variance explained by urbanization (e.g larger effect size), since they could be maladapted to urban sites (De Leon et al. 2019).

Here, using data on phenotypic traits of two urban-dwelling species of Darwin's finches (*Geospiza fortis and Geospiza fuliginosa*) across several urban and non-urban sites in three islands of the Galapagos archipelago, we explore parallel and non-parallel responses to urbanization. Using variance partitioning analysis and phenotypic trajectory analysis we ask the following questions: 1) what is the relative contribution of urbanization to the phenotypic variation in Darwin's finches' traits? 2) is this effect greater or equal than other site effects such as island, and 3) are responses in the phenotypic variation consistent across and within species, and if they do, 4) to what extent? Our study thus provides relevant information on the dynamics of evolutionary parallelism among populations and across similar species in face of urbanization impact and further contributes to understand how natural populations are responding to anthropogenic pressure.

3. 3 Methods

Study Sites

The study was conducted on three islands in the Galápagos Archipelago: San Cristóbal, Santa Cruz and Floreana. Samples were collected at *urban* and *non-urban* sites on each island. In San Cristóbal Island, urban sampling was conducted at Tijeretas (0°53'33"S 89°36'39.5"W) and Playa Mann (0°53'43"S 89°36'31"W), whereas non-urban sampling was conducted at La Lobería (0°55'31"S 89°36'41"W). In Santa Cruz Island, urban sampling was conducted in Academy Bay (0°44'24"S 90°18'08"W), and non-urban sampling was conducted in El Garrapatero (0°41'24"S 90°13'17"W). In Floreana Island, urban sampling was conducted in Asilo de la Paz (1°18 '33"S 90°27'17"W) and Puerto Velasco Ibarra (1°16'33"S 90°29'06"W), and non-urban sampling was conducted in Cerro Pajas (1°17'49"S 90°25'54"W) and La Loberia (1°16'56"S 90°29'34"W). All sites were in the lowlands, except for Cerro Pajas and Asilo de la Paz that were in the highlands of Floreana Island. Although the Galapagos Islands received their first settlers in the mid 1800s, it was not until 1980, when human population started to grow rapidly, product of an increase in immigration and touristic activity (Benitez et al. 2018). Nowadays, Galapagos has a total human population of 28 583 habitants distributed among four islands: San Cristobal (8117), Santa Cruz (17233), Isabela (3050), and Floreana (183) (INEC 2023). All the cities have similar extensions (~ 2 km2), except for Floreana, which is smaller (0.3 km2). Almost 80% of Galapagos population is in urban areas, while 20 % live in rural areas (INEC 2023). Additionally, the islands receive approximately 300,000 tourists per year according to the last report of the Galapagos National Park Service (Parque Nacional Galapagos 2023).

Data collection of phenotypic traits

Morphological data was collected for two species of Darwin's finches: the medium ground finch (*Geospiza fortis*) and the small ground finch (*Geospiza fuliginosa*) each year from 2013 to 2022 (with exception for 2021 due to COVID-19 pandemic) at urban and non-urban sites in all the islands. Sampling was performed during the breeding season of Darwin's finches coinciding with the wet rainy season in the Galapagos Islands, between January and May (Trueman and d'Ozouville 2010). Birds were captured using mist nets and then banded with uniquely numbered metal leg bands. Each bird was inspected and classified – based on plumage, beak color, and the presence of a brood patch – as a juvenile, male, or female following Grant (1999). Each bird was measured following Boag and Grant (1984 – see also Grant, 1999) for beak length (anterior edge of nares to anterior tip of upper mandible), beak depth (at the nares), beak width (at the base of the lower mandible), mass (weight), wing chord (length of longest relaxed right primary feather), and tarsus length (between the nuchal notch at the upper end of the right tarsometatarsus and the lowest undivided scute). Beak measurements and tarsus size were measured to the nearest 0.01 mm using a digital caliper, whereas wing chord was measured to the nearest 0.01 cm using a wing ruler. Mass was measured to the nearest 0.01 g using a portable digital scale. At each island, beak and body measurements were made by multiple people.

Data analysis

In Darwin's finches it is often difficult to accurately distinguish females from juveniles, thus all the analyses were performed using only males to reduce biases related to sex misclassification. Given that beak and body traits in Darwin's finches are correlated, we performed PCA analysis to reduce the measurements to PC values that capture most part of the variation in traits. We combined urban and non-urban sites and all years for each island to extract PC values for beak traits (length, depth, and width), and for body traits (mass, tarsus length, and wing chord), respectively. We used a covariance matrix for beak traits, following previous analyses (Grant and Grant 1999), and a correlation matrix for body traits. For beak traits, higher PC1 values (97.2 % of the total variation) correspond to smaller beak sizes (as opposed to larger beaks) (negative loadings for all traits), and higher values for PC2 (1.7 % of the total variation) correspond to pointier (as opposed to blunt) beaks (positive loadings for beak length and negative loadings for beak depth and beak width) (Figure 2A). For body traits, higher values for PC1 (82.7 % of the total variation) correspond to smaller bodies (negative loadings for all traits), and higher values for PC2 (13.1% of the total variation) correspond to shorter tarsus (negative loadings for tarsus and positive loadings for mass and wing chord) (Figure 2B).

PC1 and PC2 values for beak traits, and PC1 values for body traits were used as response variables to create linear mixed-effect models. Type III ANOVAs were used to quantify the relative contributions of urbanization, island, species, and their interactions (urbanization-by-island, urbanization-by-species, species-by-island). Year was included as a random factor to control for temporal variation. Effect sizes for each explanatory variable were quantified using partial eta square (η^2) as suggested in Cohen (1965) for models with interaction terms between two or more independent variables. Partial eta squared (η^2) indicates the percentage of variation explained by term in a model, for instance $\eta^2 = 0.50$ indicates that 50 % of variance is explained by that particular term. As a rule of thumb, Cohen (1988, reviewed in Richardson 2011) indicated partial eta squared values of 0.01, 0.06, and 0.14 to describe small, medium and large effect sizes, respectively.

Finally, Phenotypic Trajectory Analyses (PTA: Adams & Collyer 2009) were used to further explore how urbanization influences multivariate trait change. For each species at each island, phenotypic vectors were created to connect the means of finch traits between urban and non-urban sites. This procedure was done for beak and body traits, separately. We then calculated the lengths (ΔL) and direction (angles θ) of all vectors and compared them across species and islands. Comparisons of vector lengths and directions indicate differences among sites and species on how populations change in reaction to urbanization along primary axes of multivariate space. See Adams and Collyer (2009) or further details on PTA.

All the analyses were performed in the statistical program R version 4.1.1 (R Core Team, 2024). For linear mixed-effect models and variance analysis we used the packages *lme4 (Bates 2015),* for calculating effect sizes we used the package *effectsize (*Ben-Shachar 2021), and for PTA we used the package *geomorph* (Adams et al. 2014).

3.4 Results

We analyzed a total of 1561 *G. fuliginosa* and 2133 *G. fortis* individuals at urban and non-urban sites in San Cristobal, Santa Cruz, and Floreana Islands (Table 1 and 2). PCA analysis showed marked differences between species as it was expected (Fig. 1). *G. fuliginosa* showed overall smaller beaks compared to *G. fortis,* yet no obvious differences in beak shape (Fig. 1A, Table 1). Similarly, *G. fuliginosa* showed smaller bodies and slightly larger tarsus compared to *G. fortis* (Fig. 1B, Table 2).

ANOVA analysis showed that most of the variation in beak size (PC1) was explained by species differences, followed by the interaction term island-by-species, and then by island (Fig. 2, Table 3). In beak shape (PC2), variation was mainly explained by differences between islands, followed by species and then the interaction term urbanization-by-species (Figure 2, Table 3). Finally, for body size (PC1) variation was mainly explained by island differences followed by species and then by the interaction term urbanization-by-species (Fig. 2, Table 3).

Specifically, for beak size (PC1) urbanization-by-species explained 0.01 % of the variation. In San Cristobal Island, both *G. fortis* and *G. fuliginosa* showed slightly larger beaks in urban sites compared to non-urban, whereas in the other island there are no differences (Fig. 2A). For beak shape (PC2), urbanization-by-species explained 0.04 % of the variation. In *G. fortis*, beaks were larger in urban versus non-urban sites in San Cristobal, were smaller in urban sites in Floreana, and showed no differences between urban and non-urban sites in Santa Cruz (Fig. 2B) In *G. fuliginosa*, beaks at urban sites were larger in comparison to non-urban places, and this pattern was seen at all islands (Fig. 2B). Finally, for body size (PC1) urbanization-by-species also explained 0.04 % of the variation. In *G. fortis*, body size was larger in urban sites in San Cristobal and Santa

Cruz and remained unchanged in Floreana (Fig. 2C). In *G. fuliginosa*, body size was larger in urban versus non-urban places in San Cristobal and Santa Cruz, and smaller in Floreana (Fig. 2C).

Phenotypic trajectory Analyses (PTA) for beak traits did not show significant differences in the distances nor in the direction within and across species (Fig. 3A, Table S1), except for the angle between *G. fortis* in Floreana and *G. fortis* in Santa Cruz. It is noticeable though, that all trajectories in *G. fuliginosa* are longer than in *G. fortis*, with exception of the trajectory in San Cristobal Island. Similarly, for body traits there were no significant differences in the magnitude or direction within and across species (Fig 3B, Table S2), with exceptions in the magnitude between *G. fuliginosa* in San Cristobal, and *G. fuliginosa* in Santa Cruz, and the direction between *G. fuliginosa* in Floreana and *G. fuliginosa* in San Cristobal, *G. fuliginosa* in Floreana and *G. fortis* in Santa Cruz, and *G. fuliginosa* in Floreana and *G. fuliginosa* in Santa Cruz.

3.5 Discussion

Urbanization can impact natural populations in several ways; however, the responses are not always predictable and can be site or species-specific. In birds, human food introduction in urban sites can alter the selection forces to which adaptive traits such as beak and body size respond, yet these responses are not always parallel whereas information is still scarce on how similar populations or species respond to same levels of urbanization. In this study, using data on adaptive traits of two urban-dwelling Darwin's finches across several cities and islands I explore the contribution of urbanization to the variation in phenotypic traits and the extent to which this variation is consistent within and across species. We found that, although urbanization explains a small part of the variation in phenotypic traits (Table 1), both species and populations of the small ground finch, present parallel responses in some traits as they have larger and pointer beak in urban compared to non-urban sites (Fig. 2). Overall, island and species differences are the main drivers of beak and body variation in these finch populations, whereas contributions from urbanization are rather small (Table 1). Urbanization effect sizes are larger for beak shape and body size compared to beak size. These findings indicate that although some responses to urbanization in Darwin's finches can be parallel, urbanization impact on other traits can vary depending on the species and location. We further discuss possible reasons for this parallel and non-parallel responses.

Although urbanization just accounted a small fraction of the variation in beak and body traits (0.01% to 0.04%), we observed some island-specific parallel responses (Fig. 2). In San Cristobal Island, finches at urban sites presented pointier and larger beaks and larger bodies sizes within and across species. Consistent responses to urbanization impact have been seen in organisms related to heat tolerance (Campbell-Staton et al. 2020), and pollutants resistance (Reid et al. 2016), yet parallel responses to human food acquisition are unknown. House finches (*Carpodacus mexicanus*) have shown local adaptation to urban sites by diverging in bite force and beak morphology from their dessert counterparts (Badyaev et al. 2008), and while Darwin's finches prefer human food in urban sites (De León et al. 2019) and have weaker relationships between beak morphology and diet at urban sites (De León et al. 2011), the evolutionary impacts have not been tested. Pointer beaks have also been found in the house finch at urban sites (Hutton and McGraw 2016), which could suggest that birds with pointer beaks are better at feeding on human food. Yet, in our study, the relative contribution of urbanization to phenotypic variation is very small, thus other factors such as species (Grant and Grant 2007) or islands (Carrion et al. 2022) are more dominant in explaining main differences in Darwin´s finches.

Interestingly, parallel responses were only seen in San Cristobal Island (Fig.2). This island is not only the oldest of the archipelago, but contrary to Floreana that received the first settlers, San Cristobal has the oldest formal urban sites in Galapagos. These factors might influence the evolutionary history of the Darwin´s finches that live in it, yet more specific information on urbanization impact with potential to alter beak and body morphology is needed such as impervious surface or human food abundance.

Less parallel responses to urbanization in *G. fortis* compared to *G. fuliginosa* (Fig. 3) also invite further discussion. De Leon et al. (2011) found that seed abundance and diversity differ between urban and non-urban sites in Santa Cruz, with soft seeds more abundant in urban sites. This could explain why *G. fuliginosa* -who predominantly feeds on small seeds- presents higher parallelism compared to the medium ground finch *G. fortis*. Possible signs of *G. fuliginosa* adaptation to urban sites can be their higher reproductive effort and success (Harvey et al. 2021) and reduced anti-predator behavior (Gotanda 2020) in urban areas compared to non-urban.

Our phenotypic trajectory analyses (PTA) showed that changes in magnitude and direction in beak and body traits are consistent within and across species, with few exceptions (Fig. 3). Notably, for beak traits trajectories in *G. fuliginosa* were longer than in *G. fortis*, which could suggest greater plasticity in *G. fuliginosa* to adapt to urban places or larger impact of urbanization, yet the lack of significant differences between trajectories can be also a sign of the small effect that urbanization has on finches' phenotypic variation. In any case, our results identified an incipient effect of urbanization that could potentially become a larger if current population growth in Galápagos continues.

Conclusion and future directions

Our study shows that, although having a small effect, urbanization can induce parallel responses within and across species, highlighting the need for further studies on ecological and evolutionary responses to anthropogenic impact. Further studies incorporating data on allele frequencies of genes associated to beak morphology, feeding behavioral data, as well as a broader information of urban environments, will be essential to fully understand the mechanisms driving these phenotypic changes and to assess the long-term evolutionary consequences of urbanization on Galápagos wildlife.

3. 6 Figures

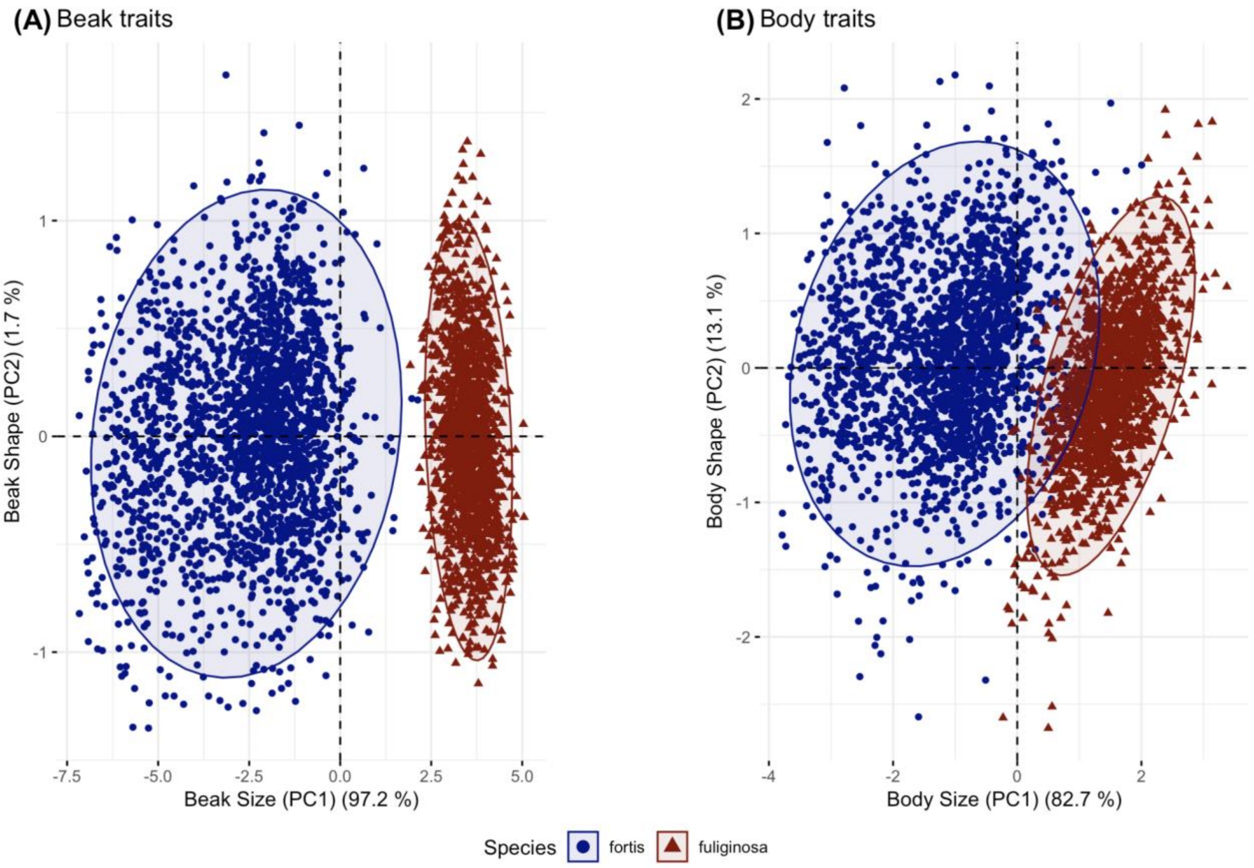


Figure 1. Principal components analysis for (a) beak traits and (b) body traits in *G. fortis* and *G. fuliginosa.*

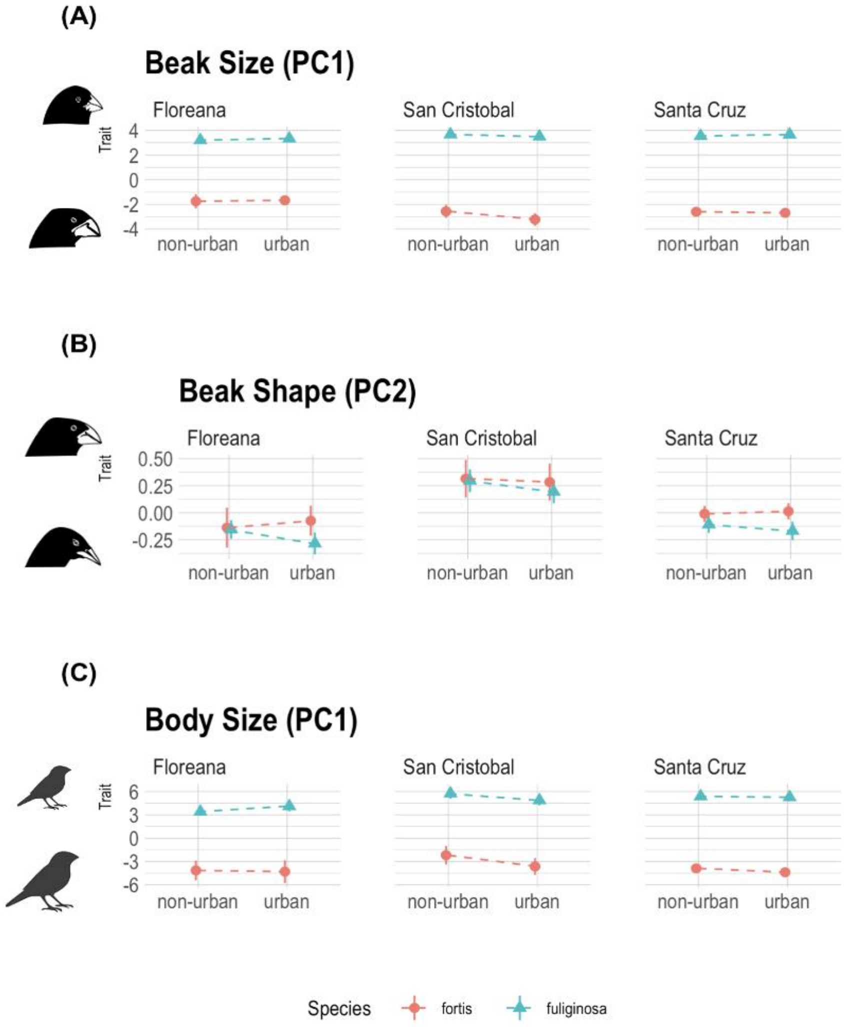


Figure 2. Phenotypic trajectories between non-urban and urban sites for A) beak size (PC1), B) beak shape (PC2), and c) body size (PC1) in *G. fortis* and *G. fuliginosa* at three islands in Galápagos.

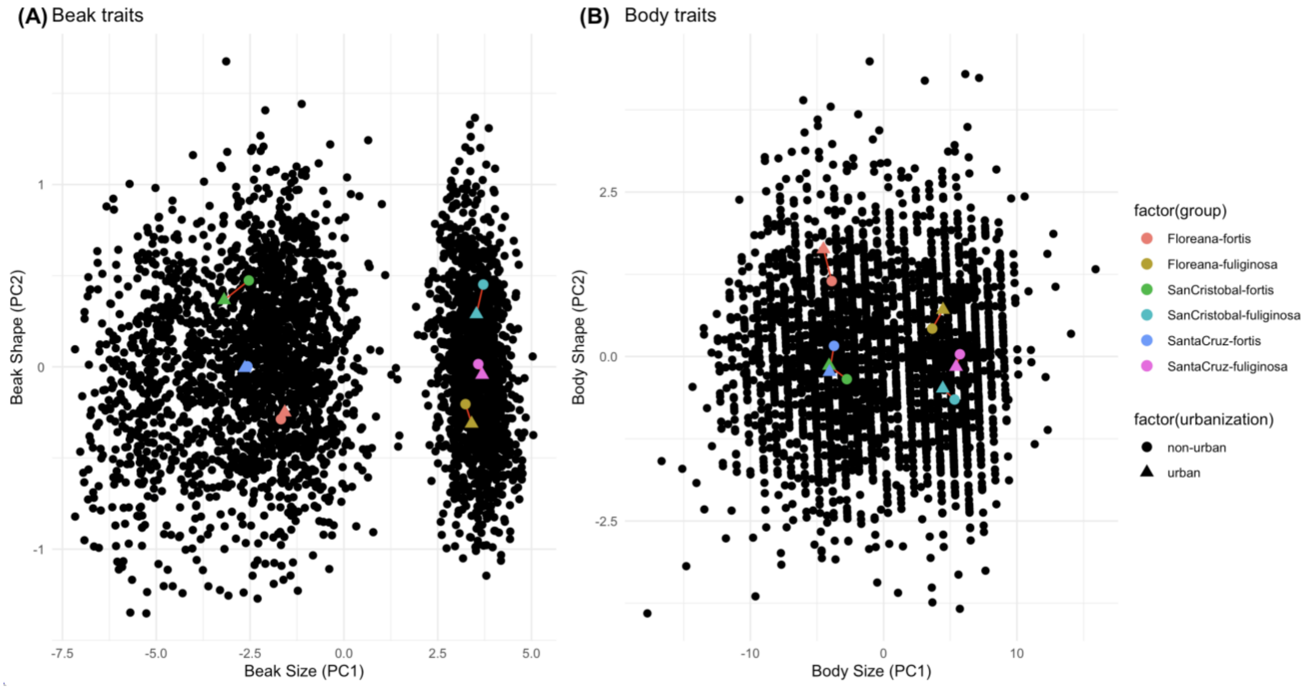
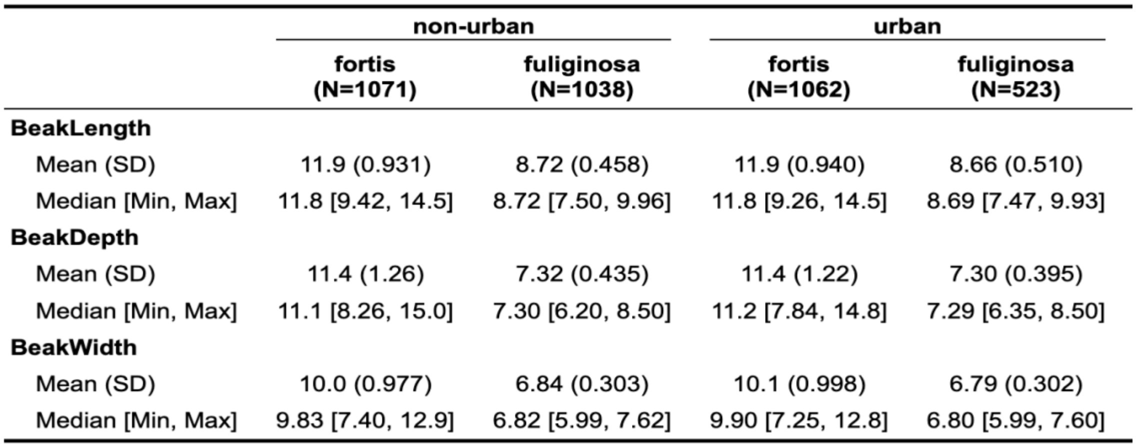


Figure 3. Phenotypic vectors between urban and non-urban sites from phenotypic trajectory analysis (PTA) for A) beak and B) body traits in *G. fortis* and *G. fuliginosa* at three islands in Galápagos.

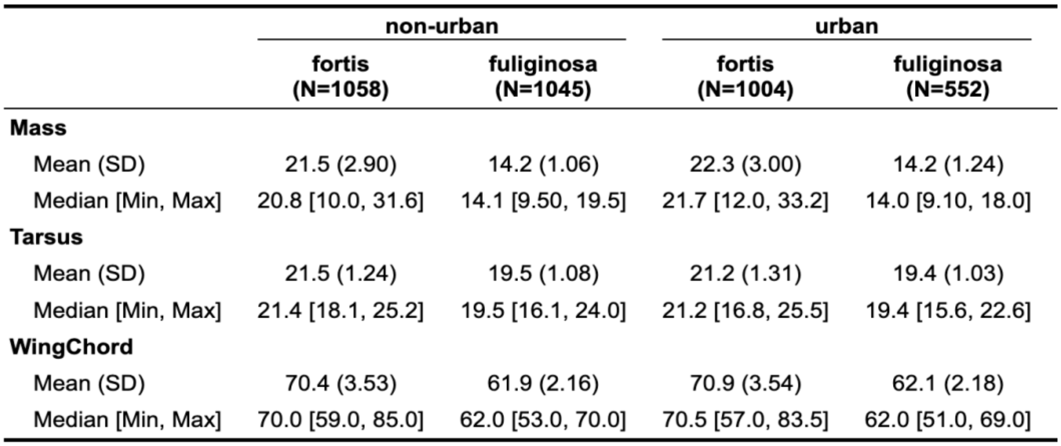
3.7 Tables

Table 1. Mean, median and standard deviation (SD) for beak traits in urban and non-urban sites.



	non-urban		**urban**	
	fortis (N=1071)	**fuliginosa (N=1038)**	**fortis (N=1062)**	**fuliginosa (N=523)**
BeakLength				
Mean (SD)	11.9 (0.931)	8.72 (0.458)	11.9 (0.940)	8.66 (0.510)
Median [Min, Max]	11.8 [9.42, 14.5]	8.72 [7.50, 9.96]	11.8 [9.26, 14.5]	8.69 [7.47, 9.93]
BeakDepth				
Mean (SD)	11.4 (1.26)	7.32 (0.435)	11.4 (1.22)	7.30 (0.395)
Median [Min, Max]	11.1 [8.26, 15.0]	7.30 [6.20, 8.50]	11.2 [7.84, 14.8]	7.29 [6.35, 8.50]
BeakWidth				
Mean (SD)	10.0 (0.977)	6.84 (0.303)	10.1 (0.998)	6.79 (0.302)
Median [Min, Max]	9.83 [7.40, 12.9]	6.82 [5.99, 7.62]	9.90 [7.25, 12.8]	6.80 [5.99, 7.60]

Table 2. Mean, median and standard deviation (SD) for body traits in urban and non-urban sites.



	non-urban		urban	
	fortis (N=1058)	**fuliginosa (N=1045)**	**fortis (N=1004)**	**fuliginosa (N=552)**
Mass				
Mean (SD)	21.5 (2.90)	14.2 (1.06)	22.3 (3.00)	14.2 (1.24)
Median [Min, Max]	20.8 [10.0, 31.6]	14.1 [9.50, 19.5]	21.7 [12.0, 33.2]	14.0 [9.10, 18.0]
Tarsus				
Mean (SD)	21.5 (1.24)	19.5 (1.08)	21.2 (1.31)	19.4 (1.03)
Median [Min, Max]	21.4 [18.1, 25.2]	19.5 [16.1, 24.0]	21.2 [16.8, 25.5]	19.4 [15.6, 22.6]
WingChord				
Mean (SD)	70.4 (3.53)	61.9 (2.16)	70.9 (3.54)	62.1 (2.18)
Median [Min, Max]	70.0 [59.0, 85.0]	62.0 [53.0, 70.0]	70.5 [57.0, 83.5]	62.0 [51.0, 69.0]

Table 3**.** Analysis of variance for beak and body traits for *G. fortis* and *G. fuliginosa* at urban and non-urban sites in three islands of Galápagos. Note: *p*-values in bold mark significant differences. Partial eta-squared (η^2) quantifies effect size.

Trait	**Explanatory Variable**	***F***	**df**	**p-value**	**Partial η2**
beak size (PC1)	Urbanization	0.22	1	0.6336	0.0001
	Island	5.314	2	**< 0.001**	0.006
	Species	4512.93	1	**< 0.00001**	0.55
	Urbanization x Island	2.441	2	0.0871	0.0001
	Urbanization x Species	4.751	1	**< 0.05**	0.001
	Island x Species	26.76	2	**< 0.0001**	0.01
	Urbanization x Island x Species	0.363	2	0.6954	0.0001
beak shape (PC2)	Urbanization	5.89	1	**< 0.05**	0.002
	Island	89.61	2	**< 0.00001**	0.05
	Species	65.69	1	**< 0.00001**	0.02
	Urbanization x Island	7.56	2	0.48	0.0001
	Urbanization x Species	13.72	1	**< 0.001**	0.004
	Island x Species	1.745	2	0.174	0.0001
	Urbanization x Island x Species	0.445	2	0.64	0.0001
body size (PC1)	Urbanization	2.496	1	0.1142	0.001
	Island	44.23	2	**< 0.00001**	0.05
	Species	6979.94	1	**< 0.00001**	0.02
	Urbanization x Island	3.3	2	**< 0.05**	0.001
	Urbanization x Species	3.756	1	0.0526	0.004
	Island x Species	2.863	2	0.0572	0.001
	Urbanization x Island x Species	0.13	2	0.869	0.0001

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Linking statement 3

Cities provide good scenarios for studying evolutionary parallelism due to their spatial replication and similar characteristics. Although there are some consistent responses among urban birds, such as smaller body size, increased breeding and feeding generalism, and larger clutch sizes, most of the evidence comes from the northern hemisphere, and few studies have specifically addressed parallel responses to urbanization in birds. In this chapter, we show that urbanisation explains only a small fraction of the phenotypic variation in Darwin's finches, but traits such as beak shape show parallel responses within and across species. Beaks in urban areas are more pointed than those in non-urban areas, which may provide an advantage in the acquisition of human food (e.g rice, crackers) compared to blunt beaks. I suggest further analysis on this topic, including other species in urban settings, and analysis of allele frequencies of genes associated with beak shape.

In chapter four, I broaden the focus of my thesis to examine another anthropogenic factor affecting species ecology and evolution, namely agriculture. In this chapter, I examine the main environmental factors that contribute to the variation in species diversity and abundance of landbird communities in the agricultural zones of Galápagos. Habitat loss due to intensive agricultural practices is undoubtedly one of the greatest threats to biodiversity worldwide, yet there is little information on this in the Galápagos. My results indicate that vegetation cover, elevation, distance to the nearest native vegetation patch, and heterogeneity are the main drivers of landbird diversity, evenness and abundance, rather than factors such as vegetation type or agricultural practices.

Chapter 4

Environmental determinants of landbird diversity and abundance in the agricultural areas of the Galápagos Islands

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4.1 Abstract

Intensive agricultural practices are nowadays responsible for most of bird population declines. Yet, most of the information about the factors that determine bird diversity and abundance come from protected areas. In Galapagos, most landbird species are threatened, and there is a serious decline of their populations especially in agricultural areas. Here, using information on vegetation and agroecosystem types, environmental data and landbird surveys between 2008 to 2020, we assess 1) what are the main drivers of landbird diversity and abundance variation in all the agricultural areas of Galapagos? 2) what are the agricultural practices that hinder/promote landbird diversity and abundance? 3) are these effects consistent across islands? Our results showed that most of the variation in landbird diversity and abundance is explained by vegetation cover and elevation, followed by distance to native vegetation patch, patch size, and patch heterogeneity. Effect sizes were greater for abundance compared to diversity. We did not find significant differences between agroecosystems or vegetation types, yet specific islands did show significant differences. We discuss possible global and island-specific factors that contribute to the variation of landbird communities in the agricultural areas of Galapagos. Finally, we highlight the importance of promoting vegetation cover, smaller patch sizes, and patch heterogeneity instead of specific agricultural practices for protecting these emblematic species.

4.2 Introduction

Identifying the factors that promote or hinder the diversity and abundance of species is crucial to understand the dynamics of ecosystems, how they respond to current changes, and ultimately to design better conservation strategies to protect them. On islands, studying these factors is pressing because, as closed ecosystems, their high levels of endemism and biodiversity are more susceptible to environmental change (Biber 2002). McArthur and Willson's theory provided ground information on the role of biogeographic factors such as island size and isolation as main factors that determine species diversity on islands (McArthur and Willson 1963). Additionally, other studies have focused on the role of environmental factors such as precipitation, temperature and altitude on island biodiversity (e.g Weigelt et al. 2016). Precipitation has a positive correlation with biodiversity and abundance (e.g Whittaker and Fernandez-Palacios 2007, Cabral et al. 2014, Barajas-Barbosa et al. 2025), whereas the relationship with altitude is often a curve that peaks at a certain level and then decreases, with thresholds that vary based on taxa (reviewed in Brown et al. 2013). Finally, the relation between temperature and insular biodiversity although variable has been mostly explored from a species distribution perspective. With increasing temperatures causing modification in the habitat range of species (reviewed in Taylor et al. 2016), which would have further repercussions on species diversity and abundance. However, information on how human-related factors influence the dynamics of insular ecosystems is still scarce and often centered on specific islands.

Nowadays, island biodiversity and abundance are mainly threatened by habitat loss, overexploitation, and introduction of species (Leclerc et al. 2018, Russell and Kueffer 2019).

Habitat loss by intensive agriculture and urbanization have caused large declines in biodiversity and abundance at local and global scales (Pereira et al. 2012, Newbold et al. 2015). Islands present one of the highest rates of biodiversity loss (Simberloff 2000, reviewed in Wood et al. 2017) with currently over 40% of insular species threatened by human activities (Russell and Kueffer 2019), and 87% of wetland ecosystems lost due to draining for agricultural purposes (Davidson 2014). Alternative agricultural practices have been implemented to reduce environmental impact. For example, agroforestry, an agricultural practice that includes trees conservation, have shown positive impacts on ecosystems by increasing vegetation cover (Steffan-Dewenter et al. 2007), and promoting landscape heterogeneity (Dallimer et al. 2012, Estrada-Carmona et al. 2022) which further benefits for species richness and abundance (Scales et al. 2008).

In Galápagos, agricultural areas represent a small percentage of their total area. Yet, in human inhabited islands, they occupy a large proportion, if not all, of the rich wet highlands, which are the most productive and diverse zones of the archipelago (Itow 1992, Rivas-Torres et al. 2018). Here, human activities have replaced the native forests with food crops and pastures through periods of land occupation and abandonments that have often caused the dominance of invasive plant species (Mena et al. 2020). For this reason, key habitats such as the *Scalesia* forest, which is home of several endemic plants and animals, has been drastically reduced to a 3 % of its original extension (Jäger et al. 2024). Today highlands in the Galapagos are mainly occupied by invasive species (28.5%), followed by pastures (22.3%), native vegetation (18.6%), permanent and transitory crops (18.3%), and mixed forests (11.6%) (Laso et al. 2019). All these forming heterogenous assemblages of vegetation to which we will refer as agroecosystems given the complex interplay of agricultural, ecological and conservation relations that occur within them (Velez Leon and Muriel 2023).

Although local governmental policies promote the concept of agroecosystems to engage with smallholders and motivate environmentally friendly agricultural practices that guaranty food security and invasive species control in the islands (Ministerio de Agricultura, Ganadería, Acuacultura, y Pesca; Ministerio del Medio Ambiente del Ecuador, 2014), there is still very few information on how different agroecosystem types influence the biodiversity and abundance in these areas, and the main environmental factors that influence these relations. Some studies have highlighted the diversity of certain species such as Galapagos tortoises (Pike at al. 2022), and macroinvertebrates (De la Torre 2012) in the agroecosystems of Galapagos, yet landbird communities are so far the most studied group. Native forests and agricultural zones in the highlands of Galapagos are home of various landbirds that include several species of Darwin's finches, mockingbirds, doves, flycatchers, warblers, among others (Dvorak 2012, 2017, Fessl et al. 2017). Yet long-term census has found declining populations in several of these species, -particularly in the agricultural areas- product of habitat degradation, predation and parasitism from introduced species, and diseases (Dvorak et al. 2012, Fessl et al. 2017). Insectivorous species such as three finches and flycatchers, that highly rely in insect communities from native vegetation, are the most affected, whereas populations of granivorous species such as ground finches have remained stable and can potentially be favored by human transformations of agricultural landscapes (Dvorak et al. 2012, 2020). Work from Geladi et al. (2021) in Santa Cruz Island found higher levels of landbird diversity in forests and coffee sites compared to pastures, and that forest patch presence is the main factor influencing landbird diversity and abundance. Nevertheless, further research is needed to have a broader perspective of the biodiversity and abundance patterns across islands, and to identify the factors that mediate these dynamics.

Here, using landbird surveys from 2008 to 2020 across all the agricultural areas of Galapagos islands, along information on agroecosystem and vegetation types, and environmental factors, we aim to answer the following questions 1) what are the main factors contributing to the variation in landbird diversity/abundance in insular agroecosystems, 2) what types of vegetation and agroecosystems promote higher biodiversity and abundance? And 3) are responses consistent across islands? Our results provide a broader perspective of the biodiversity dynamics in the agroecosystems of Galápagos, which allows the implementation of better conservation practices that not only benefit the environment but also promote a sustainable human development.

4.3 Methods

Study Sites

Agricultural areas in Galápagos are located on the highlands of the four inhabited islands of the archipelago (Santa Cruz, San Cristóbal, Isabela and Floreana), facing all south with elevations that range between 200 m and 700 m (Fig.1). Weather in the highlands present two seasons: the wet season from January to May, with sporadic but heavy rains, and the cool season from June to December with constant but light rains commonly known as 'garúa' (Trueman and D'Ozouville 2010*)*. Highlands in the Galapagos have on average more precipitation (813 mm mean annual precipitation), lower temperatures (16–20 °C mean minimum temperature), and higher humidity levels (85–93% mean relative humidity) compared to the lowlands (Trueman and

D’Ozouville 2010). High seasonal variation, along with unique topographic characteristics on this zone produce nutrient-rich soils that can grow a large variety of crops (Chiriboga et al. 2006), and harbor high plant biodiversity (Itow 1992).

Currently, the highlands of Galapagos are occupied mainly by pastures and invasive species, followed by native forests, permanent crop and transitory crops (Laso et al. 2019). Pastures occur naturally or they are cultivated to feed livestock. Pastures are often combined with forestry practices in what is called silvopastures, that include tree species such as lemon (*Citrus spp*.) and invasive species such as guava (*Psidium guajava*) (Cruz et al. 2007). Areas occupied by invasive species commonly include blackberry (*Rubus niveus*), guava (*Psidium guajava*), cedar (*Cedrela odorata*), rose apple (*Syzygium jambos),* and quinine *(Cinchona pubescens).* Native forests host several native and endemic plant species such as the *Scalesia* forest, whose extension has been severely reduced over the past decades due to increase of agricultural land (Villa and Segarra 2010, Jäger et al. 2024). Permanent crops include monocultures of coffee, banana, plantain, sugar and pineapple, and transitory crops include corn, manioc, watermelon and tomatoes (Laso et al. 2019).

Diversity and Abundance Data

Landbird biodiversity and abundance were calculated based on data provided by the Charles Darwin Foundation (Dvorak et al. 2012, 2017, 2020, Fessl et al. 2017, Charles Darwin Foundation: Galapagos landbird Conservation Project). Point count surveys were performed between 2008 to 2020 during the breading season (January-May) in all inhabited islands (Table 1).

Point counts were performed following Dvorak et al. (2012) from 7:00 am to 11:00 am and consisted of an observer registering all singing males for a 5-minute period in a snapshot approach that consisted on registering all singing birds as fast as possible, and then, the remaining minutes are used to record additional birds not detected in the first part (see detailed methods in Dvorak et al. 2012, 2015). Point counts were spaced 500 m apart. Since some areas were difficult to access, point counts were performed along existing paths or roads, while trying to include all the elevational ranges, agroecosystems and vegetation types.

Environmental data

At each count point, data on vegetation types and agroecosystems were extracted from Laso et al. (2019). For *vegetation types* we used the categories 1) native, in reference to all patches of native vegetation, and 2) introduced, in reference to patches of introduced vegetation including invasive species. For *agroecosystem* classification we used the information on Laso et al.(2019) and created a new classification based on landbird habitat preferences (Kasprzykowski and Goławski 2012, Marcacci et al. 2020, Geladi et al. 2020) with the following categories 1) forest, including all native and introduce vegetation that creates canopy cover for most landbirds (as opposed to only shrubs), 2) open vegetation, that includes pastures of different height and do not form canopy coverage, 3) permanent crops, that in Galapagos include banana, sugar cane and coffee, and 4) silvopastures, a practice that include pastures for cattle grazing but also forest to create shade for different plants and animals (Cruz et al. 2007). This latter was a stablished category in Laso et al. (2019).

Data for vegetation cover was extracted as the NDVI index (Normalized Difference Vegetation Index) from the NASA satellite MODIS Terra (MOD13Q1), with a spatial resolution of 250 m (Didan 2015) and data collection every 16 days. The NDVI index has a range value between 0 and 1, being 1 equivalent to high vegetation cover. Annual means of NDVI were calculated for the exact years when point counts were performed using the package *terra* (Hijmans et al. 2022) in R and later used in statistical analyses. Patch heterogeneity and number of native vegetation patches in buffer zones around the point counts were calculated using QGIS version 3.32.3-Lima (QGIS.org). Patch heterogeneity represents the total number of agroecosystem types found in a 40000 m2 buffer zone around a point count. Buffer size was determined based on information about core areas and home ranges in Darwin's finches from Beausoleil et al. (2022). Similarly, distance to the closest patch of native vegetation (m) and patch size (m^2) were calculated for each point count.

Statistical Analysis

All the analysis were performed in the statistical software RStudio version 2024.04.2. (RStudio Team 2024). Species richness was calculated as the total number of species present in a point count. *Evenness* was calculated from raw data using the Pielou's *J* evenness index that estimates how similar are the numbers of each species in a particular point count (Pielou 1966). Its value ranges from 0 to 1, being 1 the highest value, when the number of all the species within a point is the same and decreases as differences in species number increase. Abundance was calculated as the total number of individuals of all species within a point count. Both calculated using the R package *vegan* (Dixon 2003).

Linear mixed models (LMMs) were built using the *lme4* package in R (Bates et al. 2015) using species richness, evenness and abundance as response variables; and vegetation type, agroecosystem type, elevation, vegetation cover, patch heterogeneity, patch size, distance to closest native vegetation patch, number of native vegetation patches, and total number of landbird species as explanatory variables. This latter was used to control for island differences in species diversity. Survey year was used as random factor to control for temporal differences. Variance analyses (ANOVA) and effect size (partial eta-squared η_p^2) were calculated to assess the contributions of each explanatory variable to the variation in the response variables using the R packages *car* (Fox et al. 2012) and *effectsize* (Ben-Shachar et al. 2020).

4.4 Results

Environmental variables were significantly different between the agricultural areas of the different islands (Table 1). Vegetation cover (F = 117.59, df = 3, $p < 0.0001$), was highest in Floreana (mean = 0.55), and lowest in San Cristobal (mean = 0.43). Elevation of the agricultural area (F = 38.10, $p < 0.0001$, df = 3) was highest in Isabela (mean = 427.91 m) and lowest in Santa Cruz (mean = 308.70). Distance to the closest patch of native vegetation (F = 20.38, df = 3, $p < 0.0001$) was highest in Isabela (mean = 0.0059), and lowest in Floreana (mean = 0.0024). Patch size (F = 2.32, df = 3, $p = 0.07$) was highest in Santa Cruz (mean = 74.8 ha) and lowest in Floreana (mean = 32.1 ha). Finally, heterogeneity (number of agroecosystem types within a 40 000 m2 buffer area) (F = 48.07, df = 3, $p < 0.00001$) was highest in Santa Cruz (mean = 8.80), and lowest in San Cristóbal (mean = 6.65).

Landbird diversity

Species richness was significantly different between islands (F= 18.41, $p < 0.0001$, df = 3, n = 876), being Santa Cruz the island with the largest number of species (mean = 5.24), and Floreana the island with the lowest number of species (mean = 4.78) (Table 1). Furthermore, evenness between islands was also significantly different (F= 16.39, $p < 0.0001$, n = 876, df = 3), being San Cristobal the island with the most even landbird community (mean = 0.93), and Santa Cruz the least even (mean = 0.90).

Overall, there were no significant differences in species richness between vegetation types (native vs. introduced) or agroecosystems (Table S1). The largest contributors to species richness variation were vegetation cover ($\eta_p^2 = 0.008$) and elevation ($\eta_p^2 = 0.007$) (Fig. 2). Species richness was positively correlated with vegetation cover (R = 0.25, $p < 0.01$), and negatively correlated with elevation (R = -0.21, $p < 0.01$).

Similarly, there were no significant differences in evenness between vegetation types nor agroecosystems (Table S1). However, only in San Cristobal Island were there significant differences between agroecosystems (F = 3.03, df = 3, $p = 0.04$), with evenness being higher in silvopastures. Additionally, overall vegetation cover was the largest contributor to the variation in evenness ($\eta_p^2 = 0.02$) (Fig. 2) Evenness was slightly negatively correlated with vegetation cover (R = -0.025, $p < 0.05$).

Landbird abundance

Relative abundance was significantly different among islands (F = 23.50, df = 3, $p < 0.0001$), with the highest relative abundance in Isabela (mean = 13.74) and the lowest in Santa Cruz (mean = 10.45) (Table 1).

Overall, there were no significant differences in relative abundance between vegetation types or agroecosystems (Table S1). Yet, there were significant differences in relative abundance between vegetation types in Floreana ($p < 0.05$) and San Cristobal ($p < 0.001$) and between agroecosystems in San Cristobal ($p < 0.001$). In Floreana island, the relative abundance was higher in native patches of vegetation, yet in San Cristobal the abundance was higher in patches of introduced vegetation. Furthermore, the relative abundance of landbirds in San Cristobal was highest in the permanent crops, whereas the lowest abundance was in the silvopastures (Fig. 3)

Similarly to landbird diversity, vegetation cover ($\eta_p^2 = 0.03$) and elevation ($\eta_p^2 = 0.03$) explained the largest part of the variation in relative abundance (Fig. 2). Additionally, distance to the closest native vegetation patch ($\eta_p^2 = 0.01$), patch size ($\eta_p^2 = 0.006$), and heterogeneity ($\eta_p^2 = 0.003$) also explained an important part of the variation in relative abundance (Fig.1, Table S1). Landbird abundance showed a positive correlation with vegetation cover (R = 0.17, $p < 0.0001$), heterogeneity (R = 0.15, $p < 0.0001$), and distance to the closest native vegetation patch (R = 0.10, $p < 0.05$), and a negative correlation with elevation (R = - 0.17, $p < 0.001$), and patch size (R = - 0.10, $p < 0.05$) (Fig. 4).

4.5 Discussion

The emblematic Galapagos islands have been largely studied for their unique fauna and flora. Yet most of the information comes from the protected areas whereas little is known about the sites with high human impact such as the agricultural areas. Today, insular ecosystems are mainly threatened by habitat loss and invasive species therefore information on the environmental factors that promote, or hinder species diversity and abundance is urgently needed. Here, using information of agroecosystems and vegetation maps, environmental variables, and landbird surveys performed between 2008 and 2020 at all the agricultural areas of Galapagos we analyzed 1) the main factors contributing to the variation in landbird diversity and abundance, 2) the vegetation and agroecosystem types that promote them and 3) whether these results are consistent between islands. We found that the main factors contributing to the variation in landbird diversity and abundance in the agricultural areas are vegetation cover and elevation followed by distance to the closest native vegetation patch, patch size and heterogeneity (Fig. 2, Table S1). Analysis that included all the islands did not show significant differences in the diversity and abundance between vegetation types or agroecosystems, yet individual-island analysis did show significant differences. Highest landbird abundance was found in native vegetation patches in Floreana, and in introduced vegetation patches in San Cristobal. Finally, in San Cristobal the highest landbird abundances were found in permanent crops over forest, open vegetation, and silvopastures.

Different responses of bird communities to vegetation patterns or agroecosystems can often be related to the type of diversity index that is measured, the taxonomic group, and the spatial scale used for the study (e.g local versus regional) (Jeliazkov et al. 2016). For instance, landscape homogenization created by the decrease of crop diversity negatively impacted bird diversity at patch and farm level, but not at regional level (Jeliazkov et al. 2016). Higher use of pesticides and fertilizers affect more farmland bird specialists compared to generalists at patch, farm, and regional scales (Filippi-Codaccioni et al. 2010). Therefore, it may be that in Galapagos, even when agricultural practices or vegetation types seem to not affect landbird diversity and abundance at a local scale, the impact can be observed at a larger island level, and this would be the reason why we found significant differences in diversity and abundance across islands (Table 1). Alternatively, differences in landbird diversity and abundance across islands might be related to extrinsic forces such as island age, size, isolation that have a larger influence on colonization, speciation and extinction processes (Valente et al. 2020).

We found that environmental factors such as vegetation cover and elevation mostly explained the variation in landbird diversity, evenness, and diversity in all the agricultural areas of Galapagos (Fig. 2). Several studies have found that vegetation cover or productivity measured as NDVI explain large parts of the variation (~ 50%) associated with bird diversity and abundance (Lee et al. 2004, Foody 2005, Rowhani et al. 2008, Nieto et al. 2015, Bonthoux et al. 2018), Although the direction of the relation between variables can vary depending on the specific context. Our results agree with these studies although the variation explained by vegetation cover is less than 1 % for landbird diversity and 3 % for abundance (Fig 2. Table S1). The reason for having low levels of variation might be related to the fact that vegetation cover does not necessarily capture the specific needs of Galapagos landbirds, or its impact is still in early stages and is yet to be detected. Additionally, an increase in vegetation cover can directly increase the carrying capacity of the ecosystem and with it the numbers of certain populations (e.g generalists), whereas the affectation in species richness might be a rather slow process. This is probably why in our study bird diversity variation is less explained compared to abundance. Therefore, the use of NDVI would work better for species or trophic group-specific studies (Mcfarland et al. 2012). Additionally, high seasonality and inter-annual climate variation in the Galapagos can influence values of NDVI, therefore using a specific time frame for further studies of landbird diversity and abundance is suggested. Alternatively, other environmental variables related to vegetation cover and structure can be used. For instance, Geladi et al. (2021) used vegetation surveys in the agricultural zone of Santa Cruz Island, Galapagos and found that forest patch presence and native vegetation were the main predictors of landbird diversity and abundance, and that they were positively correlated. These findings also relate to our results since we found a positive correlation between NDVI and landbird abundance (Fig. 4), and studies have found that in Galapagos lush forest vegetation yield higher values of NDVI in Galapagos (Rivas-Torres et al. 2018, Herrera Estrella et al. 2021).

In our study, elevation also explained a large part of the variation in landbird diversity and abundance (Fig. 2), although it showed a negative correlation with abundance (Fig. 4). Global studies of bird diversity across mountain ranges have found that elevation is an important factor, with a decreasing number of species and individuals as elevation increases (reviewed in McCaine 2009, Quintero and Jetz 2018). This agrees with our results, yet elevation explained a larger part of the variation in abundance compared to species richness and evenness. Elevation, through changes in temperature and precipitation, has a direct impact on vegetation communities (e.g Bruun et al. 2006, Sundqvist et al. 2013), and thus on resource availability which would directly affect the abundance of landbirds rather than their richness.

Although responses of bird communities to agricultural practices might be often species and site-specific, several global patterns have been identified. Intensive agricultural practices that use extensive monocultures, and large amounts of pesticides and fertilizers are responsible for bird population declines around the world (Green et al. 2005, Staton et al. 2018, reviewed in Gil-Mendoza et al. 2024). In fact, agricultural expansion currently affects 73% of the total threatened bird species (BirdLife International, 2022). On the contrary, agricultural practices that include small field sizes (Zellweger-Fischer et al. 2018), reduced or absent use of fertilizer and/or herbicides (Smith et al. 2010, Jeliazkov et al. 2016), and diversity of plant and crop assemblages (Henderson et al. 2009, Pickett et al. 2011, Lengyel et al. 2016, Zellweger-Fischer et al. 2018) have shown positive results at increasing bird richness and abundance. In Galapagos, a farm census has identified conventional and organic farms (INIAP 2019), yet information on their specific practices, vegetation structures and biodiversity levels are still unknown. In Santa Cruz Island landbird diversity was higher in native forest and coffee sites in comparison to pastures (Geladi et al. 2021). In our study, there were no overall differences in landbird diversity and abundance across vegetation types nor agroecosystems, yet in San Cristobal Island there were significantly higher abundances in introduced vegetation patches and permanent crops (Fig. 3), and in native vegetation patches in Floreana. These results highlight the island-specific differences across agricultural zones.

San Cristóbal is the oldest island of the archipelago where first attempts of large-scale agriculture started in 1879 with sugar cane plantations that later set the example for agriculture activity expansion into other inhabited islands (Laso et al. 2019). Nevertheless, larger efforts from the Galapagos National Park have managed to preserve the native vegetation patches within the agricultural area, so today San Cristobal has the largest extension of native vegetation (Laso et al. 2019). The age of the agricultural zone along with conservational efforts to protect native plants might have contributed to structure the bird community on this island (e.g by providing more feeding and breeding niches) in a way that nowadays we see significant differences in landbird abundances. Additionally, larger bird abundances in permanent crops in San Cristobal or the lack of significant differences among agroecosystems for all the islands, can be related to the fact that most of the landbird community in the agricultural areas is composed of granivorous and insectivorous passerines, especially ground finches, who can adapt their diet from generalists to specialists during food scarcity periods (De León et al. 2014), in comparison with forest specialists with more strict requirements. Floreana, on the other site, although reporting the very first attempts of agricultural activity in Galapagos, its practice was more associated with survival of the first inhabitants of the archipelago rather than extensive agriculture, and even today its extension is smaller compared to the other islands. Finally, permanent crops in Galapagos are not entirely monocultures and often happen jointly with other crops (e.g coffee and guava) providing shape, structure and food to host several landbird species (Geladi et al. 2021).

In conclusion, landbird diversity and abundance is not explained by differences in vegetation and agroecosystem types (except for San Cristóbal) but rather for environmental factors such as vegetation cover and elevation mainly, followed by patch size, distance to closest native vegetation patch, patch size and heterogeneity. These results suggest that conservation purposes should focus on promoting practices that encourage vegetation cover, smaller patches, closeness to native vegetation patches and heterogeneity regardless of the type of agroecosystem. Additionally, our results highlight the importance of considering island-specific differences across agricultural areas since their anthropogenic history and environmental features are influencing the current landbird communities they have. Finally, we suggest further studies to focus on differences of landbird diversity and abundance between conventional versus organic farms to improve our understanding of the dynamics of these emblematic bird communities in human-dominated landscapes of the Galapagos islands.

4.6 Figures

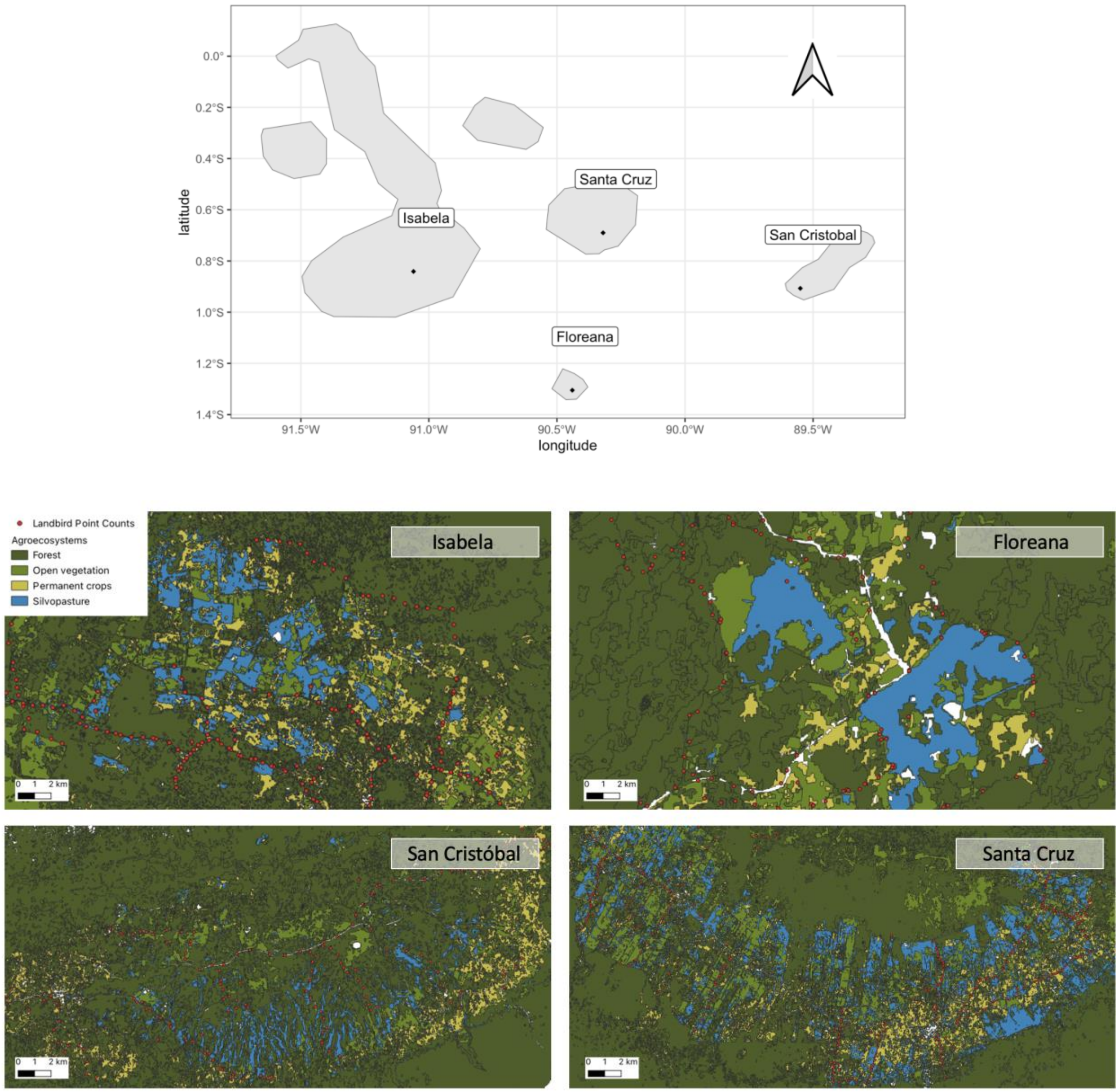


Fig 1. Agricultural areas in the Galápagos Islands. Top panel: location of agricultural areas in the Galapagos archipelago. Bottom panel: classification of agricultural areas based on landbird habitat preferences.

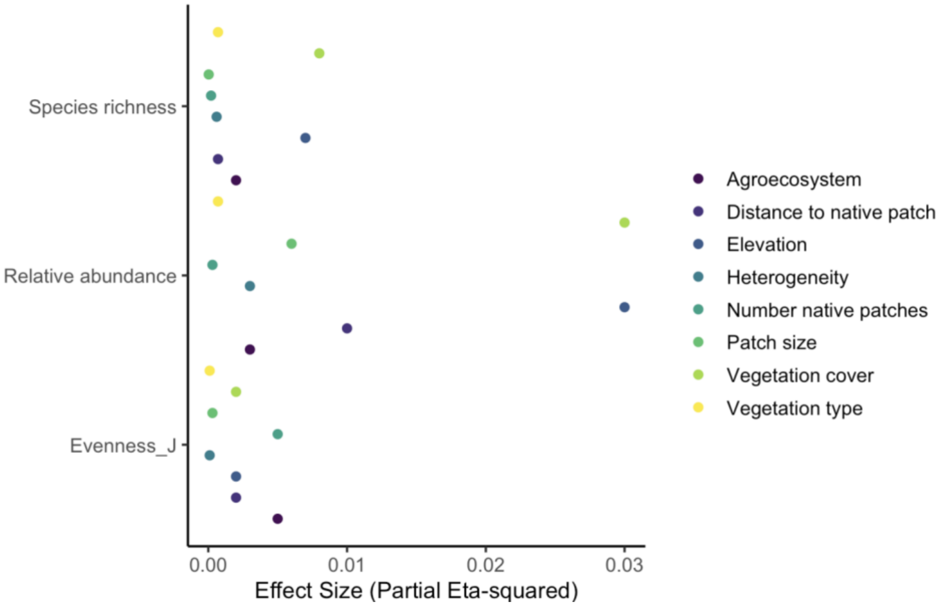


Figure 2. Effect sizes (partial eta-squared) for environmental variables associated with variation in diversity and abundance of landbirds in Galápagos islands.

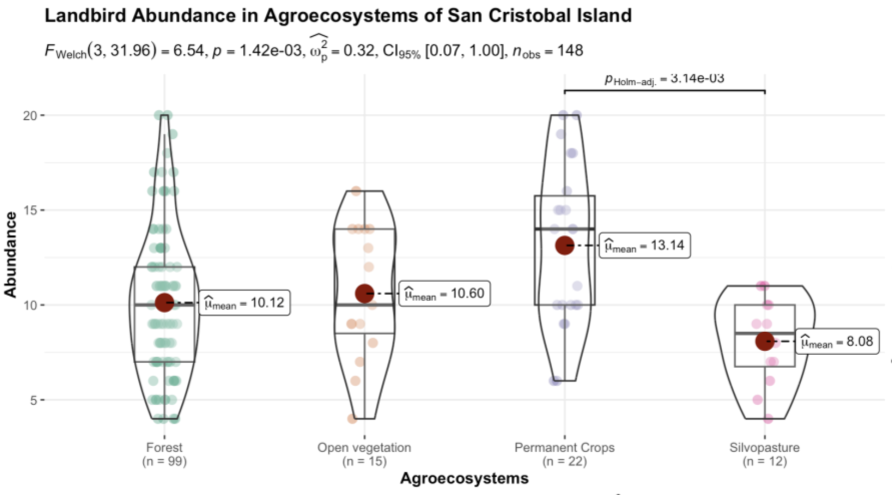


Figure 3. Landbird relative abundance across different agroecosystems in San Cristobal Island.

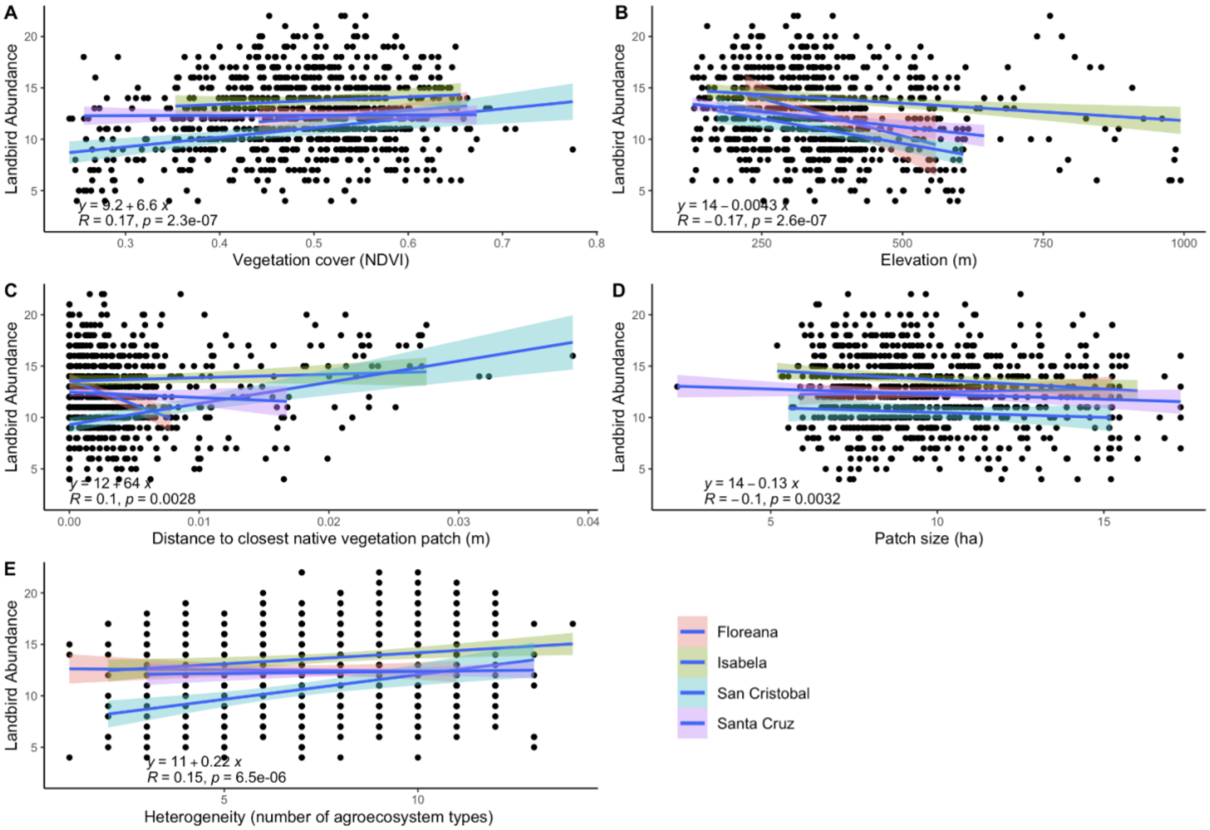
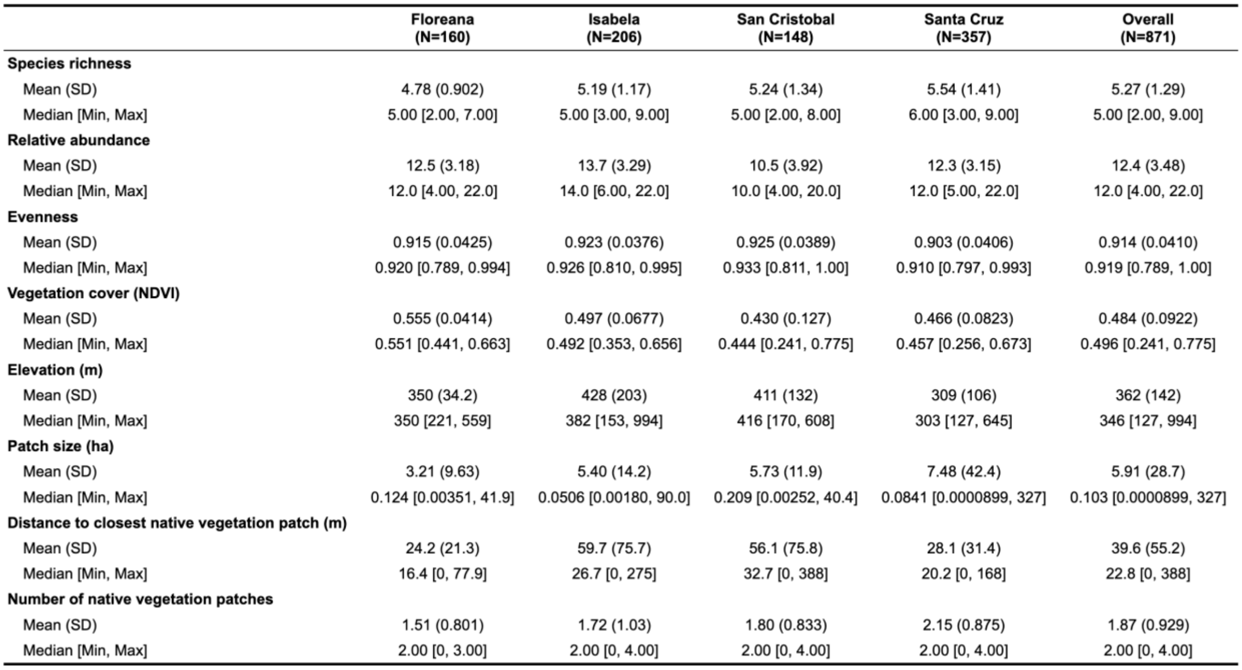


Figure 4. Correlations between landbird abundance and different environmental factors of the agricultural areas of Galapagos. A) vegetation cover (NDVI), B) elevation (m), C) distance to the closest native vegetation patch (m), D) patch size (ha), and E) heterogeneity (number of agroecosystem types).

4.7 Tables

Table 1. Descriptive statistics of species richness, relative abundance, evenness and environmental factors across all the agricultural areas of Galápagos.



	Floreana (N=160)	Isabela (N=206)	San Cristobal (N=148)	Santa Cruz (N=357)	Overall (N=871)
Species richness					
Mean (SD)	4.78 (0.902)	5.19 (1.17)	5.24 (1.34)	5.54 (1.41)	5.27 (1.29)
Median [Min, Max]	5.00 [2.00, 7.00]	5.00 [3.00, 9.00]	5.00 [2.00, 8.00]	6.00 [3.00, 9.00]	5.00 [2.00, 9.00]
Relative abundance					
Mean (SD)	12.5 (3.18)	13.7 (3.29)	10.5 (3.92)	12.3 (3.15)	12.4 (3.48)
Median [Min, Max]	12.0 [4.00, 22.0]	14.0 [6.00, 22.0]	10.0 [4.00, 20.0]	12.0 [5.00, 22.0]	12.0 [4.00, 22.0]
Evenness					
Mean (SD)	0.915 (0.0425)	0.923 (0.0376)	0.925 (0.0389)	0.903 (0.0406)	0.914 (0.0410)
Median [Min, Max]	0.920 [0.789, 0.994]	0.926 [0.810, 0.995]	0.933 [0.811, 1.00]	0.910 [0.797, 0.993]	0.919 [0.789, 1.00]
Vegetation cover (NDVI)					
Mean (SD)	0.555 (0.0414)	0.497 (0.0677)	0.430 (0.127)	0.466 (0.0823)	0.484 (0.0922)
Median [Min, Max]	0.551 [0.441, 0.663]	0.492 [0.353, 0.656]	0.444 [0.241, 0.775]	0.457 [0.256, 0.673]	0.496 [0.241, 0.775]
Elevation (m)					
Mean (SD)	350 (34.2)	428 (203)	411 (132)	309 (106)	362 (142)
Median [Min, Max]	350 [221, 559]	382 [153, 994]	416 [170, 608]	303 [127, 645]	346 [127, 994]
Patch size (ha)					
Mean (SD)	3.21 (9.63)	5.40 (14.2)	5.73 (11.9)	7.48 (42.4)	5.91 (28.7)
Median [Min, Max]	0.124 [0.00351, 41.9]	0.0506 [0.00180, 90.0]	0.209 [0.00252, 40.4]	0.0841 [0.0000899, 327]	0.103 [0.0000899, 327]
Distance to closest native vegetation patch (m)					
Mean (SD)	24.2 (21.3)	59.7 (75.7)	56.1 (75.8)	28.1 (31.4)	39.6 (55.2)
Median [Min, Max]	16.4 [0, 77.9]	26.7 [0, 275]	32.7 [0, 388]	20.2 [0, 168]	22.8 [0, 388]
Number of native vegetation patches					
Mean (SD)	1.51 (0.801)	1.72 (1.03)	1.80 (0.833)	2.15 (0.875)	1.87 (0.929)
Median [Min, Max]	2.00 [0, 3.00]	2.00 [0, 4.00]	2.00 [0, 4.00]	2.00 [0, 4.00]	2.00 [0, 4.00]

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General Discussion and Conclusion

My thesis explores spatio-temporal factors that contribute to the variation in phenotypic traits, diversity and abundance in Darwin's finches as an example of how contemporary systems respond to changing conditions, especially those caused by human activities. Through this discussion I will review each chapter and compare my results with other similar systems while suggesting future topics for further research.

In chapter one, I explore the effect of site or *terroir* in the phenotypic variation of Darwin's finches. My findings showed that Darwin's finches phenotypic variation is mainly explained by site effect. Yet these results are driven by the presence of Daphne Major in the analysis. Thus, to be able to disentangle the independent effect of site from the effect of isolation, further studies should in this system should include more finch populations and species, particularly within the same islands and for a longer timeframe (more than 10 years). Looking for spatial and temporal effects in similar systems of contemporary evolution, we found that the effect of site is only slightly larger compared to the temporal effect. These results highlight the need to study the spatial and temporal factors that contribute to phenotypic variation from a broader perspective.

Siepielski et al. (2013) found that contributions of time and space to selection in natural populations are similar, yet more recent meta-analysis (Siepielski et al. 2018) has shown that precipitation is a major selection driver in natural populations. Further analyses on this topic are needed, given that environmental heterogeneity is expected to vary in time and space, especially under contemporary conditions of human impact, modifying the conditions the patterns to which populations adapt.

Furthermore, including additional information on some features of spatial variation such as biotic versus abiotic factors (e.g Urban 2011), the scale of spatial variation (Richardson et al. 2014, and the nature of the phenotypic variation (genetic versus plastic) (Hallsson and Björklund, 2012) would contribute to disentangle the patterns of local adaptation.

In birds, contributions of space and time to phenotypic variation depend on the type of trait that is studied. For instance, morphological diversity seems to be mainly driven by site, and it concentrates in the tropics, but even at regional scales can be very variable (Hughes et al. 2022). Dispersal variation is mainly driven by geographical and ecological differences, followed by seasonality features (Sheard et al. 2020). Finally, traits as body size mainly respond to the interaction between spatial and temporal factors in North American birds (Youngflesh et al. 2022).

In chapter two, my findings indicate that even when there is evidence of climate change presence in the Galapagos Islands, Darwin's finches seem to be resilient to it, likely because they are able to adapt to short-term weather changes. Although, there is increasing evidence on birds' phenotypic variation in response to climate change (e.g Delgado et al. 2019, McLean et al. 2022), yet studies often lack information on the nature of these changes (evolutionary versus plastic), whether they are adaptive, and the environmental drivers associated to them (Merilä and Hendry 2014) which are fundamental to understand the relation between climate change and species evolution.

In birds, evolutionary responses to climate change include the advancement of breeding seasons (Potti 2009, Fletcher et al. 2013, Halupka and Halupka 2017), yet this respond depends on the type of reproduction of species. Multi-brood species have increased their reproductive seasons, while single-brood species have shortened them (Halupka and Halupka 2017). Climate change has also caused changes in birds migration patterns. Birds have reduced their migration distances as temperature increases (Visser et al. 2009), but their migration time has been also influenced with advances in long-distance migrants and decreases in short-distance migrants (Jenni and Kéry 2003). Yet the trends in other adaptive traits such as body size are highly variable. In the Amazonian tropical rainforest, bird communities have shown reduction in mass over the past 40 years (Jirinec et al. 2021), and similar patterns were found in North American birds (Weeks et al. 2020). Yet across a 120-year study in Germany, results showed that only some species show a decrease in wing length (Saleweski et al. 2014). Meta-analysis to study body size variation in relation to climate change are limited by the variety of surrogates used to assess body size, the different analytical approaches used to analyse the data, and the rather short-term frames used in the studies (Saleweski et al. 2014).

Further impacts of climate change on birds' phenotypes include alterations in melanin-based colors as a thermoregulatory adaptation to increasing temperatures. A study on several species of snow finches over a 100-years period has shown an increase in saturation of their melanin-based colour (Delgado et al. 2019).

For these reasons, future studies investigating the impact of climate change on Darwin's finches could incorporate the following aspects: 1) investigate responses in other Darwin's finch species. Whereas ground finches seem to be insensitive to climate change, other species with more restricted feeding and reproductive requirements might react differently. For instance, parasitism by and introduced fly is exacerbated with increasing rainfall and affects more tree and woodpecker finches (Dudaniec et al. 2007). 2) Continue long-term monitoring. Less conspicuous selection events could be only identified after a 40-year monitoring of finch populations in Daphne Major (Grant and Grant 2002). This is particularly relevant since each year new limits in temperature are surpassed. 3) Incorporate collection of site-specific data on precipitation, humidity and temperature in long-term monitoring of finch populations, and if possible, data on vegetation since it is directly associated to finch diet and reproduction. Current remote sensing techniques allow data collection on several vegetation indexes (e.g Liang et al. 2022). 4) Finally, use other adaptive traits such as offspring number or survival, which can be seriously affected by climate change (McLean et al. 2022).

For chapter three, I explored parallel responses in the phenotypic variation of Darwin's finches in response to urbanization. My findings showed that although urbanization explains a small part in the variation in beak and body traits of Darwin's finches, parallel responses are seen within and across species. Small ground finches at urban sites present pointier beaks in all the studied populations, whereas in San Cristobal Island the small and medium ground finch present pointier and slightly larger beaks. These findings invite us to further investigate the specific drivers that influence the phenotypic variation in finches at urban sites.

Although cities can be considered good replicates to study parallelism since organisms are exposed to similar anthropogenic pressures (Santangelo et al. 2020), they can also present particularities. Thus, to further understand the drivers of urban evolution, and the level of consistency among adaptations, we should measure urbanization in a more specific way. In Galapagos, for example, urban places shared similar general features such as extension and building distribution, yet there is no specific information on other abiotic (e.g light, chemical, air pollution) factors that has the potential of changing the selection regimes in urban settings (Szulkin et al. 2020). Similarly, information is missing on biotic factors such as competition and predation that may influence species evolutionary responses in cities. In the case of Darwin's finches, further studies can introduce other measurements of urbanization that would potentially influence adaptive traits such as beak morphology, reproductive success, and survival. These include abundance of human food available for birds, exotic plant consumption, invertebrate diversity, impervious surface, and temperature variation in urban areas. For instance, an increase in impervious surface negatively affects the nestling condition and survival in the great (*Parus major*) and blue tit (*Cyanistes caeruleus*) (Corsini et al. 2020, Caizergues et al. 2021). Furthermore, food provisioning through bird feeders in urban sites can alter bird communities' composition, while increasing the abundance of introduced species and reducing the abundance of natives (Galbraith et al. 2015), and affect negatively their breeding performance (Plummer, et al. 2013). Moreover, food provisioning in interaction with increasing temperatures in cities, can accentuate changes in migratory behavior with further evolutionary consequences (Plummer et al. 2015).

Additionally, since the Galapagos Islands are home to various examples of contemporary evolution, future research on urban evolution can focus on other systems that are common in urban sites such as lava lizards (*Microlophus spp.)* to further explore parallel responses to urbanization. For instance, in several cities of Puerto Rico, Anolis lizards have adapted their limbs size and lamellae to better move through urban substrates (Winchell et al. 2016), while becoming less wary to predators when standing on trees (Avilés-Rodríguez et al. 2019). Finally, further studies on the impact of urbanization of phenotypic variation could include several phylogenetically similar species to explore parallelism, since responses to urbanization seem to have a phylogenetic sign as more related species tend to present the same responses to urbanization (Winchell et al. 2020). In conclusion, urbanization impact on species evolution and ecology is a relatively new topic in Galapagos, however it needs urgent attention given the rapid human population growth in the islands and the fragility of their ecosystems.

In chapter four, my results indicate that landbird diversity and abundance (including several species of Darwin's finches) in the agricultural areas of Galapagos are mainly driven by environmental factors such as vegetation cover and elevation rather than vegetation or agroecosystem type. Yet some island-specific results indicate that higher landbird abundances are found in permanent crops in comparison with forests, open vegetation and silvopastures. Further studies on this topic could incorporate data on other vegetation structures and ecological niche information of landbirds given their different breeding and feeding requirements. For instance, tree and warbler finches highly rely on forests since they build nests on trees canopy, and feed mostly on fruits and invertebrates that live there (Kleindorfer et al. 2022). Native forest cover has been seriously reduced in the agricultural zones of Galapagos, probably explaining why insectivorous birds are the most threatened species among all landbirds (Dvorak et al. 2012). Therefore, including in the analysis information on aspects of landbird ecological niche such as habitat preferences (e.g forest versus openland), or feeding preferences (granivorous versus insectivorous) would allow a more comprehensive view of the impact of agriculture on Galápagos biodiversity. For example, studies comparing habitat preferences in grassland and ground birds towards active or abandoned farmland found that species diversity and abundance in grassland birds was high in abandoned farmland but low in ground birds, who prefer active farmland (Kitazawa et al. 2021).

Additionally, current remote-sensing technologies can capture differences in canopy structures (Dutta et al. 2016), providing more detailed information on vegetation patterns to be analyzed alongside bird count surveys. This is useful given that several forests in Galápagos agricultural areas are nowadays dominated by invasive vegetation species such as guava than for native species (Walsh et al. 2008). For instance, using vegetation texture variables, Ribero et al. (2019) found that bird species richness varied between bird groups in that forest bird richness was mostly explained by tree cover availability rather than forest area, and open-land bird richness was mostly explained by patch size and presence herbaceous habitats. Finally, future research can combine the information on landbird point counts with citizen-science data to improve the available information on abundance and species diversity of landbirds in Galápagos, especially the less conspicuous and abundant species. In conclusion, this chapter contributes to understand biodiversity patterns in a little-known place in Galápagos such as their agricultural areas. Identifying the factors that promote landbird diversity and abundance contributes to improve the current conservation strategies to protect the emblematic endemic species that live there, and also provide relevant information to improve the agroecosystems services for human and environment benefit.

Conclusion

Human activities are rapidly changing our environment; therefore, it is pressing to understand the main factors that currently drive phenotypic variation, species diversity and abundance. In this sense, my thesis attempts to understand the spatio-temporal contributions of environmental factors known to highly influence phenotypes and biodiversity, or in other words the dynamics of today's *terroir* in determining different phenotypes and biodiversity patterns. My findings suggest that even when Darwin's finches seem resilient to human-related factors such as climate change, urbanization and agriculture, there are island-specific features (e.g vegetation structures) that influence their phenotypic variation, diversity and abundance. Consequently, my thesis set the ground to further research on Darwin’s finches-vegetation dynamics in face of anthropogenic impact and provide relevant information to improve current conservation strategies.

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Appendix

Supplemental material for Chapter 1

A.1 Supplemental tables

Table S1. Analysis of variance for spectroradiometric values testing for the effect of year, site, and interaction between Academy Bay and El Garrapatero, exclusively. P-values in bold mark significant effects. η2 quantifies effect size. EVI: enhanced vegetation index; NDVI: normalized difference vegetation index; LAI: Leaf Area Index; FPAR: Fraction of Photosynthetically Active Radiation.

Parameter	Effect	F	*p*	η2
EVI	Year	F (9,359) = 19.82	**< 0.0001**	0.34
	Site	F (1, 359) = 25.89	**< 0.001**	0.07
	Year * Site	F (9, 359) = 1.53	0.1344	0.04
NDVI	Year	F (9,359) = 12.84	**< 0.0001**	0.25
	Site	F (1,359) = 48.65	**< 0.0001**	0.13
	Year * Site	F (9,359) = 2.06	**0.03228**	0.05
LAI	Year	F (9,831) = 19.74	**< 0.0001**	0.18
	Site	F (1,831) = 176.55	**< 0.0001**	0.18
	Year * Site	F (9,831) = 4.01	**< 0.001**	0.04
FPAR	Year	F (9,831) = 17.50	**< 0.0001**	0.16
	Site	F (1,831) = 217.65	**< 0.0001**	0.21
	Year * Site	F (9,831) = 1.40	0.1808	0.02

Table S2. Analysis of variance (univariate ANOVAs and multivariate MANOVAs) for beak and body traits for *G. fortis* at the three study sites (AB: Academy Bay, EG: El Garrapatero, DM: Daphne Major) by year, site, and site-by-year interaction including MALES only. P-values in bold mark significant differences. Partial eta-squared (η^2) quantifies effect size.

		ALL POPULATIONS (AB, EG, DM)			ONLY AB vs. EG		
BEAK TRAITS	Term	F	*p*	η2	F	*p*	η2
PC1 (beak size)	Year	F (9, 2291) = 3.69	**< 0.0001**	0.01	F (9, 1399) =2.09	**< 0.01**	0.01
	Site	F (2, 2291) = 877.31	**< 0.0001**	0.43	F (1, 1399) = 3.84	**0.0501**	0.003
	Year * Site	F (18, 2291) = 3.71	**< 0.0001**	0.03	F (9, 1399) =2.00	**< 0.01**	0.01
PC2 (beak shape)	Year	F (9, 2291) = 10.92	**< 0.0001**	0.04	F (9, 1399) = 11.20	**< 0.001**	0.07
	Site	F (2, 2291) = 117.76	**< 0.0001**	0.09	F (1, 1399) = 2.42	0.119	0.002
	Year * Site	F (18, 2291) = 3.39	**< 0.0001**	0.03	F (9, 1399) = 2.18	**< 0.01**	0.01
Multi-trait	Year	F (9, 2291) = 17.76	**< 0.0001**	0.07	F (9,1399) =17.64	**< 0.0001**	0.10
(Beak length, beak depth,	Site	F (2, 2291) = 364.11	**< 0.0001**	0.32	F (1,1399) 10.97	**< 0.0001**	0.02
beak width)	Year * Site	F (18, 2291) = 7.01	**< 0.0001**	0.05	F (9,1399) = 3.85	**< 0.0001**	0.02
BODY TRAITS	Term	F	*p*	η2	F	p	η2
PC1 (body size)	Year	F (9, 2291) = 7.51	**< 0.0001**	0.03	F (9, 1399) = 3.79	**< 0.001**	0.02
	Site	F (2, 2291) = 958.90	**< 0.0001**	0.46	F (1, 1399) = 3.25	0.0713	0.002
	Year * Site	F (18, 2291) = 3.57	**< 0.0001**	0.03	F (9, 1399) = 2.00	**< 0.01**	0.01
PC2 (body shape)	Year	F (9, 2291) = 13.36	**< 0.0001**	0.05	F (9, 1399) = 9.18	**< 0.0001**	0.06
	Site	F (2, 2291) =109.47	**< 0.0001**	0.09	F (1, 1399) = 13.78	**< 0.0001**	0.01
	Year * Site	F (18, 2291) = 9.11	**< 0.0001**	0.07	F (9, 1399) = 10.65	**< 0.0001**	0.06
Multi-trait	Year	F (9, 2291) =8.09	**< 0.0001**	0.03	F (9, 1399) = 8.41	**< 0.0001**	0.05
(Mass, wing chord,	Site	F (2, 2291) = 363.84	**< 0.0001**	0.32	F (1, 1399) = 22.58	**< 0.0001**	0.05
tarsus length)	Year * Site	F (18, 2291) = 6.30	**< 0.0001**	0.04	F (9, 1399) = 5.46	**< 0.0001**	0.03

Supplemental material for Chapter 2

B.1 Supplemental tables

Table S1. Number of finches captured and measured each year at two locations, AB (Academy Bay) and EG (El Garrapatero), in Santa Cruz Island, Galapagos between 1999 and 2022.

	G. fortis		*G. fuliginosa*	
Year	AB	EG	AB	EG
1999	44	0	31	0
2000	0	0	0	0
2001	27	0	8	0
2002	50	0	13	0
2003	76	44	27	14
2004	160	118	35	31
2005	676	222	4	16
2006	424	276	18	46
2007	8	64	5	68
2008	127	139	51	4
2009	63	214	42	69
2010	151	223	52	149
2011	112	201	60	194
2012	52	186	19	136
2013	123	235	66	211
2014	104	163	41	99
2015	39	36	25	26
2016	35	128	29	82
2017	57	113	17	70
2018	84	169	53	98
2019	23	300	4	149
2020	29	122	11	63
2021	0	0	0	0
2022	20	23	26	18
Total	2484	2976	637	1543

Table S2. Most extreme correlation values (CCF) and corresponding lags for analyses between time-series of environmental variables (precipitation and temperature), and beak (beak length, beak depth and beak width) and body (wing chord, tarsus length, mass) traits in *G. fortis*. AB: Academy Bay, EG: El Garrapatero

Environmental Variable	Location	Trait	CCF value	Correlation lag
Precipitation	AB	beak length	-0.411	4
		beak depth	-0.335	4
		beak width	-0.348	4
		wing chord	-0.289	1
		tarsus length	-0.131	4
		mass	-0.296	1
	EG	beak length	-0.417	1
		beak depth	-0.265	3
		beak width	-0.632	1
		wing chord	-0.35	3
		tarsus length	-0.459	2
		mass	-0.395	1
Temperature	AB	beak length	0.149	5
		beak depth	-0.349	2
		beak width	0.176	3
		wing chord	-0.513	2
		tarsus length	0.215	4
		mass	-0.442	1
	EG	beak length	0.365	4
		beak depth	-0.223	4
		beak width	0.121	5
		wing chord	-0.418	2
		tarsus length	0.368	3
		mass	-0.369	3

Table S3. Largest correlation values (CCF) and corresponding lags for analyses between time-series of environmental variables (precipitation and temperature), and beak (beak length, beak depth and beak width) and body (wing chord, tarsus length, mass) traits in *G. fuliginosa*. AB: Academy Bay, EG: El Garrapatero

Environmental Variable	Location	Trait	CCF value	Correlation lag
Precipitation	AB	beak length	-0.251	4
		beak depth	-0.451	4
		beak width	-0.312	5
		wing chord	-0.325	1
		tarsus length	-0.318	1
		mass	-0.217	3
	EG	beak length	-0.119	4
		beak depth	-0.345	1
		beak width	-0.502	1
		wing chord	-0.543	3
		tarsus length	-0.419	1
		mass	-0.219	3
Temperature	AB	beak length	0.337	5
		beak depth	-0.309	4
		beak width	0.313	5
		wing chord	-0.373	2
		tarsus length	0.405	4
		mass	-0.397	1
	EG	beak length	0.393	4
		beak depth	-0.413	2
		beak width	0.275	2
		wing chord	-0.212	2
		tarsus length	0.185	5
		mass	-0.495	5

Table S4. Medians, Lower 5th percentile (LCI), and Upper 95th percentile (UCI) intervals of the posterior distribution of persistence *r* (relation of current value with past values) of time-series corresponding to beak and body traits in *G. fortis* and *G. fuliginosa* at two sites of Santa Cruz Island, Galápagos. If the 95th percentile of the posterior distribution (UCI) is < 1, time-series is static, if not, is random walk.

Species	Site	Variable	Median	LCI	UCI	Pattern
G. fortis	AB	Beak length	0.991	0.940	1.042	Random walk
		Beak width	0.990	0.940	1.041	Random walk
		Beak depth	0.989	0.941	1.036	Random walk
		Tarsus length	0.586	0.302	0.874	Stasis
		Wing chord	0.585	0.298	0.882	Stasis
		Mass	0.583	0.302	0.874	Stasis
	EG	Beak length	0.988	0.934	1.044	Random walk
		Beak depth	0.988	0.936	1.040	Random walk
		Beak width	0.987	0.935	1.043	Random walk
		Tarsus length	0.597	0.288	0.913	Stasis
		Wing chord	0.596	0.276	0.909	Stasis
		Mass	0.590	0.271	0.899	Stasis
G. fuliginosa	AB	Beak length	0.985	0.917	1.058	Random walk
		Beak depth	0.981	0.909	1.049	Random walk
		Beak width	0.982	0.913	1.051	Random walk
		Tarsus length	0.514	0.203	0.825	Stasis
		Wing chord	0.522	0.202	0.837	Stasis
		Mass	0.523	0.211	0.841	Stasis
	EG	Beak length	0.983	0.909	1.061	Random walk
		Beak depth	0.980	0.906	1.055	Random walk
		Beak width	0.979	0.902	1.053	Random walk
		Tarsus length	0.521	0.193	0.858	Stasis
		Wing chord	0.519	0.179	0.860	Stasis
		Mass	0.521	0.197	0.860	Stasis

Supplemental material for Chapter 3

C.1 Supplemental tables

Table S1. Pairwise comparisons of beak traits phenotypic vectors between urban and non-urban sites in G. fortis and G. fuliginosa at three islands of Galápagos. *p*-values in bold indicate significant differences.

BEAK TRAITS					
Pairwise Comparison	**Distance (mm)**	**p-value**	**r**	**Angle**	**p-value**
Floreana_fortis:Floreana_fuliginosa	0.075929115	0.71	0.3213318	71.256514	0.53
Floreana_fortis:San Cristobal_fortis	0.552659673	0.055	-0.7110601	135.321236	0.27
Floreana_fortis:San Cristobal_fuliginosa	0.121582277	0.585	-0.6644219	131.63799	0.28
Floreana_fortis:Santa Cruz_fortis	0.05738334	0.85	-0.891598	153.074737	**0.045**
Floreana_fortis:Santa Cruz_fuliginosa	0.001981773	0.985	0.3353793	70.404395	0.565
Floreana_fuliginosa:San Cristobal_fortis	0.476730559	0.115	-0.7476565	138.387784	0.185
Floreana_fuliginosa:San Cristobal_fuliginosa	0.045653162	0.68	-0.3030215	107.639171	0.435
Floreana_fuliginosa:Santa Cruz_fortis	0.133312455	0.2	-0.6763954	132.562607	0.11
Floreana_fuliginosa:Santa Cruz_fuliginosa	0.077910888	0.315	0.9974022	4.130783	0.99
San Cristobal_fortis:San Cristobal_fuliginosa	0.431077396	0.14	0.8506539	31.717135	0.805
San Cristobal_fortis:Santa Cruz_fortis	0.610043014	0.075	0.9426943	19.490934	0.945
San Cristobal_fortis:Santa Cruz_fuliginosa	0.554641447	0.08	-0.7844766	141.672294	0.115
San Cristobal_fuliginosa:Santa Cruz_fortis	0.178965617	0.2	0.7710607	39.550766	0.69
San Cristobal_fuliginosa:Santa Cruz_fuliginosa	0.12356405	0.295	-0.3637608	111.331339	0.305
Santa Cruz_fortis:Santa Cruz_fuliginosa	0.055401567	0.34	-0.6990788	134.35314	0.085

Table S2. Pairwise comparisons of body traits phenotypic vectors between urban and non-urban sites in *G. fortis* and *G. fuliginosa* at three islands of Galápagos. *p*-values in bold indicate significant differences.

BODY TRAITS

Pairwise Comparison	Distance (mm)	p-value	r	Angle	p-value
Floreana_fortis:Floreana_fuliginosa	0.07441754	0.895	-0.53471984	122.324914	0.235
Floreana_fortis:San Cristobal_fortis	0.56378288	0.43	0.87137246	29.381478	0.785
Floreana_fortis:San Cristobal_fuliginosa	0.1157205	0.82	0.88752557	27.436061	0.75
Floreana_fortis:Santa Cruz_fortis	0.26538591	0.625	0.03732843	87.860741	0.33
Floreana_fortis:Santa Cruz_fuliginosa	0.43764652	0.435	0.31629178	71.561185	0.415
Floreana_fuliginosa:San Cristobal_fortis	0.48936534	0.345	-0.88053024	151.706392	0.11
Floreana_fuliginosa:San Cristobal_fuliginosa	0.04130296	0.91	-0.86393198	149.760975	**0.02**
Floreana_fuliginosa:Santa Cruz_fortis	0.33980345	0.19	-0.86440071	149.814345	**0.005**
Floreana_fuliginosa:Santa Cruz_fuliginosa	0.51206406	0.085	-0.97077474	166.113901	**0.005**
San Cristobal_fortis:San Cristobal_fuliginosa	0.44806238	0.385	0.99942362	1.945417	0.975
San Cristobal_fortis:Santa Cruz_fortis	0.82916879	0.18	0.52280712	58.479263	0.46
San Cristobal_fortis:Santa Cruz_fuliginosa	1.0014294	0.13	0.74104246	42.179707	0.545
San Cristobal_fuliginosa:Santa Cruz_fortis	0.38110641	0.145	0.49356728	60.424681	0.24
San Cristobal_fuliginosa:Santa Cruz_fuliginosa	0.55336702	**0.05**	0.71782107	44.125124	0.36
Santa Cruz_fortis:Santa Cruz_fuliginosa	0.17226062	0.39	0.95980746	16.299557	0.525

Supplemental material for Chapter 4

D.1 Supplemental tables

Table S1. Variance analysis and effect sizes of environmental factors contributing to the variation of diversity and abundance of landbirds in the agricultural areas of Galapagos.

Trait	**Explanatory Variable**	**F**	**df**	***p***	**Effect size (ηp2)**
Species richness	Vegetation type	0.587	1	0.443	0.0007
	Agroecosystem	0.546	3	0.65	0.002
	Elevation	5.728	1	**< 0.05**	0.007
	Vegetation cover	4.27	1	**< 0.05**	0.008
	Distance to native patch	0.617	1	0.432	0.0007
	Patch size	0.023	1	0.878	0.00003
	Heterogeneity	0.544	1	0.461	0.0006
	Number native patches	0.171	1	0.67	0.0002
Evenness J	Vegetation type	0.024	1	0.874	0.0001
	Agroecosystem	1.477	3	0.219	0.005
	Elevation	1.844	1	0.174	0.002
	Vegetation cover	2.858	1	0.09	0.002
	Distance to native patch	1.331	1	0.249	0.002
	Patch size	0.221	1	0.638	0.0003
	Heterogeneity	0.069	1	0.792	0.0001
	Number native patches	4.713	1	**< 0.05**	0.005
Relative abundance	Vegetation type	0.606	1	0.436	0.0007
	Agroecosystem	0.791	3	0.499	0.003
	Elevation	25.077	1	**< 0.0001**	0.03
	Vegetation cover	23.431	1	**< 0.0001**	0.03
	Distance to native patch	11.622	1	**< 0.0001**	0.01
	Patch size	5.005	1	**< 0.05**	0.006
	Heterogeneity	2.793	1	0.095	0.003
	Number native patches	0.225	1	0.635	0.0003