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Título

The role of inbreeding, kin competition, and environmental variability in the evolution of short- and long-distance dispersal in *Eriosyce* (Cactaceae)

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The irony is that science has served only to show how small human knowledge is.

—Masanobu Fukuoka

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ABSTRACT [EN]

Dispersal, the tendency of individuals to move away from parental patches, plays a critical role in determining patterns of gene flow, shaping the genetic structure of plant populations, and facilitating the colonization of novel habitats. Despite its eco-evolutionary importance, the mechanisms driving shifts in dispersal modes remain scarcely understood. Three major evolutionary drivers of dispersal evolution have been recognized: kin competition, inbreeding depression, and environmental variability. However, the evolution of dispersal cannot be understood by relying on single factors but on the synergistic interaction of various evolutionary drivers. These evolutionary drivers often operate with more intensity under extreme conditions, as in the case of arid environments. The patchy distribution of resources creates suitable limited-size microhabitats that favor reduced dispersal for their occupation and maintenance, although intensifying kin competition. Furthermore, reduced dispersal enables the occupation of suitable microhabitats, although it may enhance mating among relatives, leading to inbreeding, potentially compromising population viability in changing environments. On the other hand, the high spatio-temporal variability of deserts (characterized by severe droughts and brief resource pulses), creates strong selective pressures that may favor persisting in suitable local microhabitats or the long-distance escape to colonize distant suitable sites.

Although contrasting dispersal modes are relatively common in arid environments, the relative importance of these evolutionary drivers has not been explored yet. The genus *Eriosyce* (Cactaceae) provides a unique study system, as closely related taxa inhabiting the Huasco Valley of the Atacama Desert have evolved contrasting dispersal modes. The Atacama Desert represents one of the most extreme arid environments, characterized by hyperarid conditions that create distinct habitat types, such as coastal terraces and rocky outcrops. Long-distance dispersal taxa (dispersed by wind) inhabit coastal terraces, representing large, empty or sparsely vegetated habitats. Conversely, short-distance dispersal taxa (dispersed by animals) are microhabitat specialists occupying rocky outcrops, which constitute heterogenous, size-limited habitats. Therefore, I hypothesize that kin competition, inbreeding depression, and environmental variability operate simultaneously and complementarily to shape dispersal modes in *Eriosyce*, with their relative importance varying according to the distinct ecological conditions of coastal terraces versus rocky outcrops

Here, I employed a comprehensive methodological approach to examine how these evolutionary drivers have promoted the evolution of contrasting dispersal modes in six *Eriosyce* taxa from the Huasco Valley. In Chapter II, using population genomic analyses to assess genetic diversity and inbreeding, I found unexpected patterns that differed from theoretical expectations that long-distance dispersal reduces inbreeding. Genetic analysis revealed that long-distance dispersal taxa exhibit higher levels of inbreeding than short-distance dispersal taxa, while genetic diversity was similar between both groups. This pattern suggests that other ecological processes, such as historical demographic events (founder effects and population bottlenecks) have been more important than contemporary dispersal modes in shaping inbreeding and genetic diversity of these taxa. In Chapter III, relatedness analysis supports the role of kin competition as a major driver of dispersal evolution. Long-distance dispersal taxa showed a significant reduction of mean relatedness compared to short-distance dispersal taxa, besides exhibiting significant negative gradients of relatedness with geographic distance. Conversely, short-distance dispersal taxa maintained genetic similarity uniformly despite distance, evidencing localized gene flow restricted to nearby individuals within rocky outcrops.

Furthermore, Chapter IV employed a multi-dimensional characterization of environmental variability using four environmental indices to quantify resource availability, environmental stress, spatial heterogeneity, and temporal heterogeneity. This analysis revealed large differences in the habitats occupied by taxa with long- and short-distance dispersal. Coastal terraces exhibited high resource availability, defined by elevated soil water content, organic carbon, and total nitrogen, but also extreme environmental stress and spatial homogeneity, creating high-risk and high-reward environments. In contrast, rocky outcrops exhibited lower environmental stress and high spatial heterogeneity, providing multiple suitable microhabitats that serve as refugia from harsh environmental conditions. These results present strong evidence supporting that dispersal mode evolution results from the interaction among multiple evolutionary drivers. Specifically, I found that kin competition reduced genetic relatedness in long-distance dispersal taxa, while maintaining uniform similarity in short-distance taxa. Furthermore, environmental variability create distinct selective environments, with coastal terraces favoring wind dispersal through high resource availability but extreme stress, and rocky outcrops promoting animal dispersal through spatial heterogeneity and microhabitat diversity. This research contributes to a deeper understanding of dispersal evolution in arid environments, where the patchy occupation of suitable habitats may be a key mechanism promoting diversification in species-rich desert lineages such as *Eriosyce* and other diverse groups adapted to aridity conditions. The findings highlight the need for integrative approaches that include multiple temporal and spatial scales in the study of evolutionary adaptations.

RESUMEN [ES]

La dispersión, es decir, la tendencia de los individuos a alejarse de los parches parentales, tiene un rol clave determinando patrones de flujo génico, modelando la estructura genética de las poblaciones y facilitando la colonización de nuevos hábitats. A pesar de su importancia eco-evolutiva, los mecanismos que impulsan el cambio en los modos de dispersión permanecen escasamente comprendidos. Se reconocen tres principales impulsores evolutivos de la evolución de la dispersión: competencia entre parientes, depresión endogámica y variabilidad ambiental. Sin embargo, la evolución de la dispersión no puede entenderse basándose en factores únicos, sino en la interacción sinérgica de varios impulsores evolutivos. Estos impulsores operan con mayor intensidad bajo condiciones extremas, como en ambientes áridos. La distribución en parches de los recursos crea microhábitats adecuados de tamaño limitado que favorecen la dispersión reducida para su ocupación y mantenimiento, pero intensificando la competencia entre parientes. Aunque que la dispersión reducida permite la ocupación de microhábitats, puede incrementar el apareamiento entre parientes, llevando a endogamia, comprometiendo potencialmente la viabilidad poblacional en ambientes desafiantes. Por otro lado, la alta variabilidad espacio-temporal de los desiertos (sequías severas y pulsos breves de recursos), crea fuertes presiones selectivas que pueden favorecer el mantenimiento de microhábitats locales adecuados o el escape a larga distancia para colonizar sitios distantes.

Aunque los modos de dispersión contrastantes son relativamente comunes en ambientes áridos, la importancia relativa de estos impulsores evolutivos no ha sido explorada. El género *Eriosyce* (Cactaceae) provee un sistema de estudio único, ya que taxones cercanamente relacionados que habitan el Valle del Huasco del Desierto de Atacama han evolucionado modos de dispersión contrastantes. El Desierto de Atacama representa uno de los ambientes áridos más extremos, caracterizado por condiciones hiperáridas que crean distintos tipos de hábitat, como terrazas costeras y afloramientos rocosos. Los taxones con dispersión de larga distancia (mediada por viento) habitan terrazas costeras, representando hábitats grandes, vacíos o escasamente vegetados. Por el contrario, los taxones con dispersión de corta distancia (mediada por animales) son especialistas de microhábitat que ocupan afloramientos rocosos, los cuales constituyen hábitats heterogéneos de tamaño limitado. Por lo tanto, hipotetizo que la competencia entre parientes, la depresión endogámica y la variabilidad ambiental operan simultáneamente y de manera complementaria para modelar los modos de

dispersión en *Eriosyce*, con su importancia relativa variando según las condiciones ecológicas distintas de las terrazas costeras versus los afloramientos rocosos.

Aquí, empleé una aproximación integral para examinar cómo estos impulsores evolutivos han promovido la evolución de modos de dispersión contrastantes en seis taxones de *Eriosyce* del Valle del Huasco. En el Capítulo II, usando análisis genómicos poblacionales para evaluar diversidad genética y endogamia, encontré patrones que diferían de las expectativas de que la dispersión a larga distancia reduce la endogamia. El análisis genético reveló que los taxones con dispersión de larga distancia exhiben mayores niveles de endogamia que los taxones con dispersión reducida, mientras que la diversidad genética fue similar en ambos grupos. Este patrón sugiere que otros procesos ecológicos, como eventos demográficos históricos (efecto fundador y cuellos de botella poblacionales) han sido más importantes que los modos de dispersión contemporáneos en modelar la endogamia y diversidad genética de estos taxones. En el Capítulo III, el análisis de parentesco apoya el rol de la competencia entre parientes como un impulsor principal de la evolución de la dispersión. Los taxones con dispersión de larga distancia mostraron una reducción significativa del parentesco promedio comparado con los taxones con dispersión reducida, además de gradientes negativos significativos de parentesco con la distancia geográfica. Por el contrario, los taxones con dispersión reducida mantuvieron similitud genética uniformemente a pesar de la distancia, evidenciando flujo génico localizado restringido a individuos cercanos dentro de afloramientos rocosos.

El Capítulo IV empleó una caracterización multidimensional de la variabilidad ambiental usando cuatro índices para cuantificar disponibilidad de recursos, estrés ambiental, heterogeneidad espacial y heterogeneidad temporal. Esto reveló importantes diferencias en los hábitats ocupados por taxones con modos de dispersión contrastantes. Las terrazas costeras exhibieron alta disponibilidad de recursos, pero también estrés ambiental extremo y homogeneidad espacial, creando ambientes de alto riesgo-alta recompensa. En contraste, los afloramientos rocosos exhibieron menor estrés ambiental y alta heterogeneidad espacial, proporcionando múltiples microhábitats adecuados que sirven como refugios de condiciones ambientales severas. Estos resultados evidencian que la evolución de la dispersión resulta de la interacción compleja entre múltiples impulsores evolutivos. Específicamente, encontré que la competencia de parentesco redujo el parentesco genético en taxones de dispersión a larga distancia, mientras que mantenía una similitud uniforme en taxones de dispersión a corta distancia. La variabilidad ambiental creó hábitats selectivos distintivos: las terrazas costeras favorecieron la dispersión por viento debido a la alta disponibilidad de recursos, pero con estrés extremo, mientras que los afloramientos rocosos promovieron la dispersión animal debido a la heterogeneidad espacial y la diversidad de microhábitats. Esta investigación contribuye a un mayor entendimiento de la evolución de la dispersión en ambientes áridos, donde la ocupación de parches de hábitats adecuados puede ser un mecanismo clave promoviendo diversificación en linajes desérticos ricos en especies como *Eriosyce* y otros grupos diversos adaptados a condiciones de aridez. Los hallazgos destacan la necesidad de aproximaciones integrativas que incluyan múltiples escalas temporales y espaciales en el estudio de adaptaciones evolutivas.

1. CHAPTER I: THEORETICAL BACKGROUND AND HYPOTHESIS

1.1 INTRODUCTION

1.1.1 THE EVOLUTIONARY ECOLOGY OF DISPERSAL

Dispersal, the tendency for an organism to move away from parental patches (Levin, 2004) is central to ecology and evolutionary biology (Clobert et al., 2012). Dispersal shapes the regeneration dynamics of plants (de Almeida & Galetti, 2007), and determines establishment success and spatial distribution of plant populations (Muller-Landau et al., 2008). Furthermore, it plays a key role in the functioning and dynamics of communities, as well as in the maintenance of biodiversity (Corlett, 2017; Traveset & Richardson, 2006). Dispersal provides several advantages for plant species, such as spreading risks among offspring (Bach et al., 2006), facilitating persistence through changing habitats (Buoro & Carlson, 2014), avoiding inbreeding depression (Roze & Rousset, 2005), and enabling the colonization of suitable habitats (Salazar-Tortosa et al., 2019), particularly under harsh environmental conditions (Duputié & Massol, 2013). From an evolutionary perspective, dispersal influences population genetic structure by determining gene flow patterns (Bohrer et al., 2005), which may affect their potential for local adaptation to novel habitats (Willis et al., 2014).

Plants have developed multiple adaptations for effective seed dispersal, with strategies varying according to habitat characteristics, resource distribution patterns, and the spatial scale of environmental variability (Ronce, 2007). In most angiosperms, fruits and seeds (hereafter, diaspores) exhibit a set of morphological traits facilitating movement away from parental patches through biotic and abiotic vectors (Nathan & Muller-Landau, 2000). These traits are frequently linked with dispersal vectors and are widely recognized as “dispersal syndromes”, which are associated with either short-distance or long-distance dispersal modes. Syndromes include dispersal by animals (zoochory), wind (anemochory), water (hydrochory), and self-dispersal (autochory) (van der Pijl, 1982). Among these, anemochory typically enables long-distance dispersal, while zoochory can range from short-distance to long-distance dispersal depending on animal dispersal abilities and movement ranges (Chen et al., 2020; Correia et al., 2018; Gomes et al., 2021). These contrasting dispersal modes involve different ecological trade-offs, with each offering distinct advantages and costs depending on ecological context (Arjona et al., 2018). Therefore, the evolution of contrasting dispersal modes within plant lineages represents research opportunities to understand how different selective pressures shape dispersal and their ecological consequences.

1.1.2 EVOLUTIONARY DRIVERS OF DISPERSAL MODE SHIFTS

Morphological adaptive traits associated with dispersal modes can evolve as a response to multiple selective forces since dispersal provides several ecological functions (Matthysen, 2012). Long-distance dispersal is generally facilitated by diaspores with specialized structures, such as wings, bristles, or dense wool that enhance wind transport over hundreds of meters to kilometers (Nathan et al., 2002). Short-distance dispersal adaptations, on the other hand, involve fleshy fruits with bright coloration, nutritionally valuable seeds, or elaiosomes that attract animal vectors for targeted deposition, allowing diaspores to remain in suitable sites (Cordero et al., 2021; Gomes et al., 2021). Long-distance dispersal provides adaptive advantages in spatially homogeneous or temporally variable environments, enabling escape from local competition and the colonization of distant favorable sites (Duputié & Massol, 2013; Ronce, 2007). Conversely, short-distance dispersal favors establishment success in spatially heterogeneous environments through the precise deposition of diaspores in suitable microhabitats, reducing dispersal costs (Nathan & Muller-Landau, 2000; Schupp et al., 2002). Within plant communities, both dispersal modes can coexist as complementary strategies to exploit different spatial and temporal niches (Levin et al., 2003).

Dispersal evolution can be described as a balance between opposing forces selecting for and against dispersal (Ronce, 2007). Increased mortality or loss of diaspores during displacement and failure of seedling establishment by reaching unsuitable habitats are factors negatively selecting against dispersal (i.e., dispersal costs; Rousset & Gandon, 2002). Conversely, three main forces select for dispersal: i) kin competition, ii) inbreeding depression, and iii) environmental variability (Levin et al., 2003). Kin competition occurs when genetically related individuals compete for the same limited resources, thus promoting dispersal to reduce competition among relatives (Rousset & Gandon, 2002). Inbreeding, resulting from mating between relatives, increases population homozygosity and reduces genetic diversity; therefore, dispersal is selected to spatially segregate conspecific individuals (Cousens et al., 2008). Lastly, environmental variability creates sites with distinctive and variable characteristics, selecting for dispersal modes that enable movements from lower-quality to higher-quality habitats (Fresnillo & Ehlers, 2008). Therefore, the selection for reduced or increased dispersal influences critical plant aspects such as dispersal costs, distribution patterns, range sizes, population dynamics, and gene flow.

The influence of these selective forces may vary in time and space depending on different ecological contexts (Levin et al., 2003). In spatially heterogeneous environments, short-distance dispersal may be advantageous as it ensures the deposition of seeds in suitable microhabitats (Nathan & Muller-Landau, 2000). On the other hand, in temporally variable (where habitat quality fluctuates over time) or spatially homogeneous environments (where suitable patches are widely scattered), long-distance dispersal may provide advantages for escaping unfavorable conditions and colonizing distant suitable habitats (Ronce, 2007). Short-distance dispersal can reduce dispersal costs by maintaining populations within suitable habitats, but can also increase the probability of mating or competing with relatives (Duputié & Massol, 2013). In contrast, long-distance dispersal enables the colonization of novel habitats, allowing the escape from parental patches while expanding species' range boundaries (Willis et al., 2014). Furthermore, long-distance dispersal can effectively reduce both kin competition and inbreeding by spatially segregating related individuals and promoting gene flow among populations (Ronce, 2007). However, it can also increase dispersal costs due to high mortality of diaspores and establishment failure in unsuitable habitats (Rousset & Gandon, 2002). Arid environments are characterized by high spatio-temporal variability, with alternating wet and dry cycles and diverse microhabitats that create fragmented population structures and promote evolutionary processes (Axelrod, 1967). These contrasting selective pressures and their effects on dispersal evolution are summarized in Table 1.1.

Factor	Favors long-distance dispersal	Favors short-distance dispersal
Spatial heterogeneity	High heterogeneity (suitable microhabitats available locally)	Low heterogeneity (homogeneous landscapes)
Temporal variability	Low (stable conditions)	High (unpredictable quality)
Kin competition intensity	Low	High
Dispersal costs	Reduced	Moderated trade-off
Habitat predictability	High	Low

Table 1.1. Summary of selective pressures and environmental conditions that favor the evolution of short-distance versus long-distance dispersal modes in plant populations.

1.1.3 THE GENUS *ERIOSYCE* (CACTACEAE) AS A STUDY SYSTEM

The study of dispersal evolution requires analyzing multiple evolutionary drivers simultaneously (Bonte et al., 2012). Theoretical models have identified kin competition, inbreeding avoidance, and environmental variability as key evolutionary drivers contributing to shifts in dispersal modes, although empirical studies examining how these drivers interact in natural systems remain limited (Matthysen, 2012). Understanding how different selective pressures combine to drive dispersal evolution in natural populations requires study systems with contrasting dispersal modes inhabiting environments with clear differences in ecological conditions (Ronce, 2007). In this sense, *Eriosyce* (Cactaceae) represents an ideal study system for investigating the multiple evolutionary drivers driving dispersal evolution because species have evolved both short- and long-distance dispersal modes (Fig. 1.1). Also, they are habitat specialists occupying rocky outcrops and coastal terraces of the Atacama Desert with contrasting environmental characteristics (Fig. 1.2).

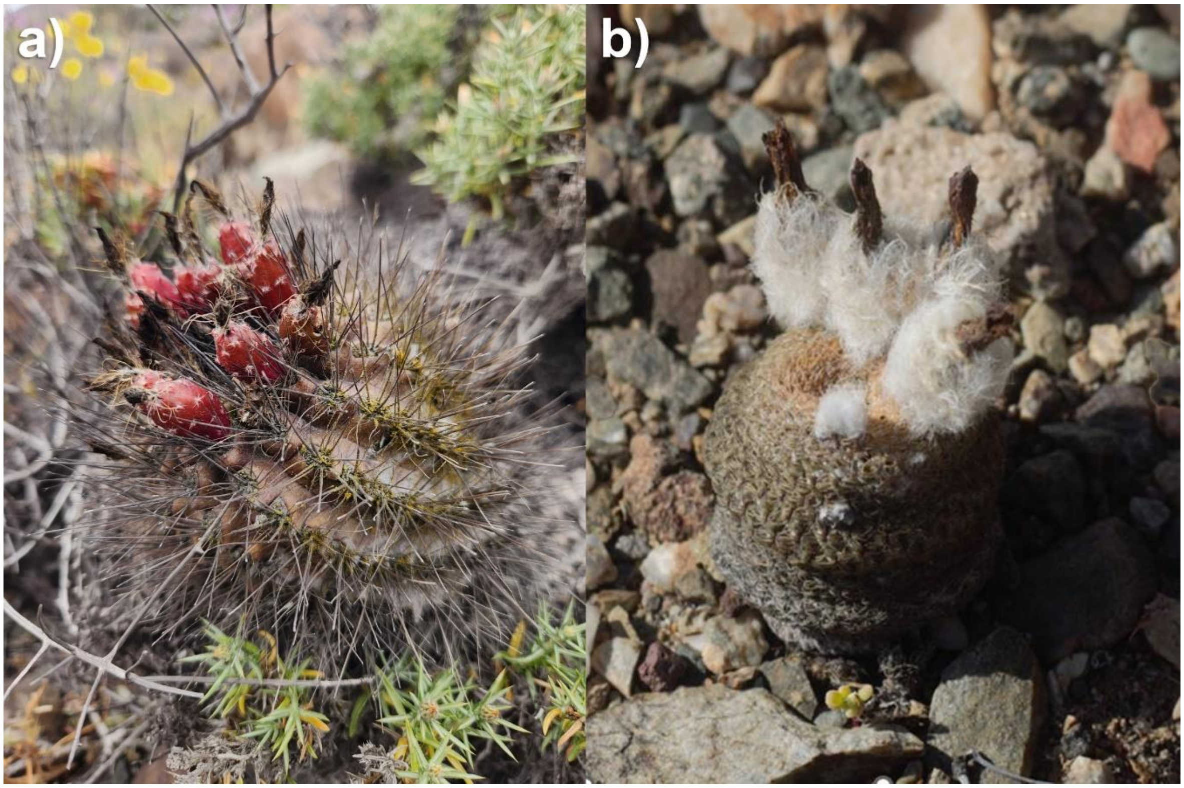

Figure 1.1. *Eriosyce* species with contrasting dispersal modes. a) Short-distance dispersal species (*E. villosa*), showing morphological features adapted for animal-mediated dispersal, including medium-size globular stems and fleshy colored fruits. b) Long-distance dispersal species (*E. napina*), with short stems buried or barely protruding above ground, deep taproots, and fruit adaptations for wind-mediated dispersal, such as bristles and dense wool.

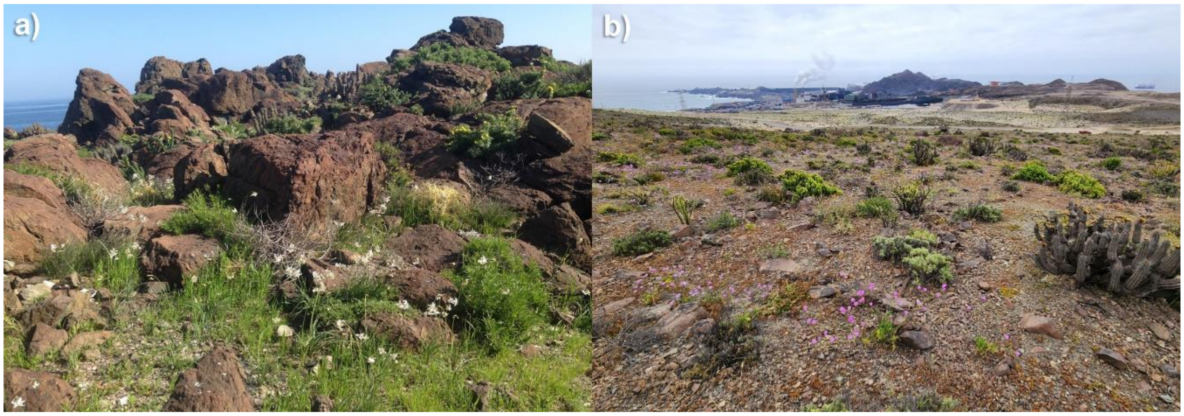

Figure 1.2. Habitat types occupied by *Eriosyce* species. a) Rocky outcrops with heterogeneous microhabitats and stable microclimatic conditions. b) Coastal terraces characterized by homogeneous, hyperarid environments with sparse vegetation cover.

According to the most up-to-date phylogeny (Guerrero et al., 2019) *Eriosyce* contains > 70 species belonging to 7 clades, showing a wide range of stem sizes, shapes, colors, and spine patterns as well as flowers, fruits, and root systems. Despite this morphological variation, *Eriosyce* species exhibit two distinct sets of adaptive traits corresponding to habitat specialization and dispersal modes. These contrasting sets of traits represent adaptations to the distinct environmental conditions imposed by the Atacama Desert. Species inhabiting rocky outcrops have evolved short-distance dispersal by animals, while those occupying coastal terraces have evolved long-distance dispersal by wind. Coastal terraces of the Atacama Desert represent large, homogeneous, empty habitats or sparsely vegetated, characterized by hyperarid conditions, sandy loam soils, and extremely high levels of surface ultraviolet irradiance (Cordero et al., 2018). Conversely, rocky outcrops represent limited-size habitats with stable microclimates, especially favorable in arid environments, since they provide moist conditions suitable for several plant species (Fitzsimons & Michael, 2017).

Eriosyce species inhabiting rocky outcrops benefit from favorable microclimatic conditions and rock fissures, since they provide physical support, enabling reduced root systems and medium- to long-size stems rising above the ground. These species produce bright-colored fruits with thick pericarps adapted for animal dispersal (Kattermann, 1994). Unlike other cactus genera, *Eriosyce* species are only dispersed through fruits and seeds, rather than vegetative structures. The high spatial heterogeneity of rocky outcrops favors short-distance dispersal that ensures seed deposition in suitable microsites (Nathan & Muller-Landau, 2000), but the discrete nature of these habitats may intensify local competition among individuals within patches (Gyllenberg et al., 2008). In contrast, species adapted to coastal terraces have short stems buried or barely protruding above ground since no physical support is available, with ribs dissolved into tubercles and taproot systems storing starch and water (Kattermann, 1994). Their fruits are elongated with thin pericarps, dense wool, and bristles that facilitate wind dispersal. The large, homogeneous nature of coastal terraces and their extreme environmental variability favor long-distance dispersal strategies that enable escape from both kin competition and unpredictable environmental conditions (Armijo et al., 2015). Notably, long-distance dispersal species belong to three different clades within *Eriosyce* (Horridocactus, Diaguita, and Unnamed clade; Guerrero et al., 2019), suggesting that this dispersal mode has evolved independently along the evolutionary history of the group. For these reasons, *Eriosyce* constitutes an ideal model system for studying the evolutionary drivers of dispersal evolution, since closely related species have evolved contrasting dispersal modes while inhabiting distinct but adjacent habitats within the same geographic region. This allows for direct comparisons of how different environmental pressures shape dispersal.

1.1.4 DISPERSAL MODES AND HABITAT SPECIALIZATION

Short-distance dispersal in rocky outcrop species likely represents an adaptive response to the spatial and temporal heterogeneity of these habitats (Spiegel & Nathan, 2010), where precise seed placement in suitable microsites is critical for establishment and survival (Schupp et al., 2002). Plant populations with reduced distribution ranges usually rely on short-distance dispersal mechanisms to prevent diaspores movement outside optimal habitats (Cheptou et al., 2008; Fresnillo & Ehlers, 2008). For microhabitat specialists like most *Eriosyce* species that depend on rocky outcrops, limited dispersal may reduce mortality of diaspores that would otherwise reach unsuitable habitats (Cheptou et al., 2008). Short-distance dispersal in these species is mediated by ants or lizards, similar to other habitat-specialist cacti (see Gomes et al., 2021 for examples). Animal-mediated dispersal ensures that seeds are deposited in suitable sites with a higher probability than expected by chance (Spiegel & Nathan, 2010), since animal movements are more finely structured and more predictable than the flow of abiotic vectors (Aukema & del Rio, 2002). In the Neoporteria clade of *Eriosyce* (comprising short-distance dispersal species), seed deposition within rock fissures is critical for seedling recruitment and survival. However, this dispersal mode may also increase kin competition and inbreeding risk by maintaining offspring in proximity to parental individuals and relatives.

1.1.5 ANCESTRAL STATE RECONSTRUCTION OF DISPERSAL EVOLUTION IN *ERIOSYCE*

To understand the evolutionary patterns that originated contrasting dispersal modes in *Eriosyce*, I reconstructed the evolutionary history of these traits across the phylogeny of the genus. First, I prepared a calibrated molecular phylogeny comprising 71 *Eriosyce* species, based on Guerrero et al. (2025), Guerrero et al. (2019), and Villalobos-Barrantes et al. (2022). Dispersal modes for each species were determined based on morphological assessments of diaspore characteristics. In this sense, the species were classified either as short- or long-distance dispersal based on fruit morphological adaptations. Then, I employed three methodological approaches to reconstruct ancestral dispersal states and assess the temporal evolution of long-distance dispersal. I used the rerooting method to provide estimates of ancestral state probabilities through the evaluation of alternative root positions. I also conducted a standard maximum likelihood ancestral character evolution (ACE) analysis under equal rates (ER), symmetric (SYM), and all rates different (ARD) evolutionary models, with model selection based on Akaike Information Criterion values. Furthermore, I employed stochastic character mapping, capturing uncertainty in evolutionary transitions and providing probabilistic estimates of character state changes along branches. Node ages were estimated from branch lengths, enabling the identification of specific time periods when long-distance dispersal capabilities emerged within the genus. In addition, a consensus analysis across the three methods was performed to identify those nodes with high probabilities of dispersal mode transitions (> 80% probability with low inter-method variance).

Model comparison supported the Equal Rates (ER) model as the best fit (AIC = 55.91), indicating symmetric transition rates between dispersal modes. Three complementary reconstruction methods revealed contrasting patterns of ancestral state probabilities for dispersal mode evolution, with the rerooting method identifying 62 nodes with high probability of dispersal transitions, ACE analysis detecting only 5 high-probability nodes, and stochastic mapping finding 17 nodes exceeding the 80% threshold (Fig. 1.3). Consensus analysis across methods identified five nodes with moderate support (>50% average probability) for dispersal transitions, with estimated ages concentrated in the late Pleistocene (0.31-0.90Ma). The temporal clustering of these transitions suggests multiple independent evolutionary shifts in dispersal modes during a relatively recent period of the evolutionary history of *Eriosyce*, coinciding with Pleistocene climatic oscillations.

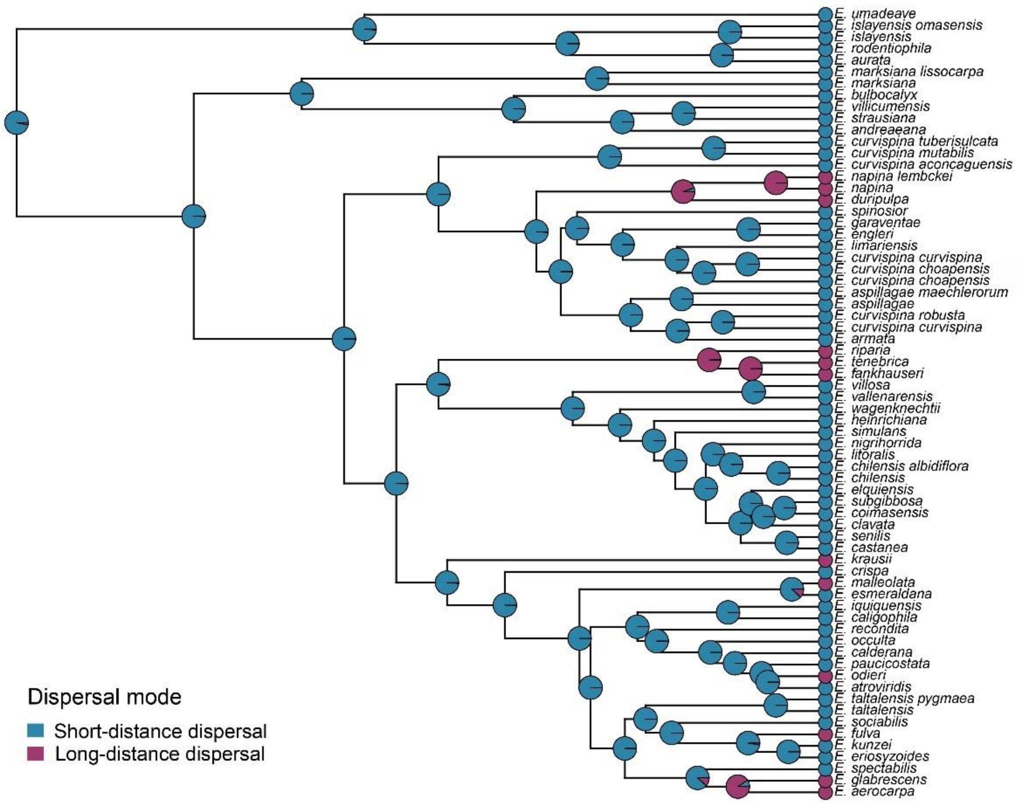

Figure 1.3. Ancestral state reconstruction for dispersal mode evolution in *Eriosyce*. Phylogenetic tree showing maximum likelihood estimates of ancestral dispersal states at internal nodes (pie charts) and observed states at terminal taxa. Pie chart sizes at nodes reflect the relative probability of each dispersal mode based on ACE analysis under the Equal Rates model.

These reconstruction results establish that dispersal mode evolution in *Eriosyce* involved transitions from ancestral short-distance to long-distance dispersal. Under this phylogenetic context, the following chapters test whether contemporary patterns of genetic diversity, relatedness, and environmental variation support the hypothesis that kin competition, inbreeding avoidance, and environmental variability drove these evolutionary shifts between contrasting dispersal strategies in *Eriosyce*.

1.1.6 MULTI-SCALE APPROACH TO EVOLUTIONARY DRIVERS OF DISPERSAL

To evaluate the role of multiple evolutionary drivers in dispersal evolution in *Eriosyce*, this thesis is structured into three experimental chapters. Chapter II examines the role of inbreeding through population genomic analyses, evaluating whether long-distance dispersal species exhibit lower inbreeding levels and higher genetic diversity compared to short-distance dispersal species, as predicted under the hypothesis that increased dispersal reduces mating among relatives. Chapter III analyzes kin competition through relatedness coefficients and spatial patterns of genetic structure, predicting that long-distance dispersal species will show lower mean relatedness and negative relatedness gradients with geographic distance due to effective spatial segregation of related individuals. Finally, Chapter IV characterizes the multidimensional environmental variability of coastal terraces and rocky outcrops using four environmental indices, evaluating whether these environmental contrasts have differentially selected for the observed dispersal modes.

1.2. SCIENTIFIC HYPOTHESIS

Dispersal ability is a key evolutionary trait in plants, balancing the costs of moving diaspores away from parental patches against the benefits of reducing kin competition, avoiding inbreeding, and tracking suitable environments. In arid systems, dispersal capability is particularly critical because resource availability is patchy in space and time. Within the Atacama Desert, *Eriosyce* species occupy two contrasting habitats. Coastal terraces are large, environmentally homogeneous landscapes with extreme aridity and highly unpredictable pulses of resource availability. Rocky outcrops, in contrast, are small, discrete habitats that provide spatial heterogeneity and relatively stable microclimatic conditions.

I hypothesize that the evolution of long-distance dispersal in *Eriosyce* inhabiting coastal terraces and short-distance dispersal in rocky outcrop specialists has been driven by the differential intensity of three evolutionary drivers. In coastal terraces, long-distance dispersal by wind is favored because it reduces kin competition arising from limited suitable microsites, mitigates the risk of inbreeding by spatially segregating relatives, and allows escape from temporally unfavorable conditions in homogeneous but unpredictable environments. Conversely, in rocky outcrops, short-distance animal dispersal is advantageous because environmental stress is buffered, microhabitat diversity provides many safe recruitment sites, and selective pressures for kin avoidance and long-distance escape are weaker. Under these conditions, precision in seed placement outweighs distance, selecting for short-range dispersal strategies.

1. 3. PREDICTIONS

I. Long-distance dispersal species (anemochorous) will exhibit reduced average relatedness among individuals and stronger negative isolation-by-distance compared to short-distance dispersal species (zoochorous).

II. Dispersal modes will show contrasting inbreeding patterns, with long-distance dispersal species showing lower inbreeding coefficients (F_{is}) than short-distance dispersal species, reflecting reduced mating among relatives.

III. Contrasting dispersal modes will be associated with distinct environmental conditions: coastal terraces (long-distance dispersal habitats) will show greater temporal variability and lower spatial heterogeneity than rocky outcrops (short-distance dispersal habitats).

1.4 OBJECTIVES

1.4.1 GENERAL OBJECTIVE

To evaluate the selective pressures of kin competition, inbreeding depression, and environmental variability that have driven the evolution of contrasting short- and long-distance dispersal modes in *Eriosyce* species inhabiting coastal terraces and rocky outcrops in the Atacama Desert.

1.4.2 SPECIFIC OBJECTIVES

I. Assess population genetic structure and diversity patterns using population genomic analysis to characterize the genetic consequences of contrasting dispersal modes in *Eriosyce* species.

II. Quantify spatial patterns of genetic relatedness using maximum likelihood estimation and spatial genetic analysis to evaluate the role of kin competition in dispersal evolution.

III. Characterize multidimensional environmental variation through the development of ecological indices measuring resource availability, environmental stress, spatial heterogeneity, and temporal heterogeneity to determine habitat-specific selective pressures.

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2. CHAPTER II: GENOMICS SIGNALS OF INBREEDING AND POPULATION STRUCTURE IN *ERIOSYCE* TAXA WITH CONTRASTING DISPERSAL MODES

2.1 ABSTRACT

Dispersal influences mating patterns and gene flow across populations. Reduced dispersal distance promotes high inbreeding, leading to increased homozygosity and the accumulation of deleterious mutations through genetic drift. Therefore, selection often favors long-distance dispersal, enabling the spatial segregation of conspecific individuals to avoid the costs of inbreeding. Conversely, short-distance dispersal may increase inbreeding risk by maintaining offspring in proximity to relatives. The genus *Eriosyce* provides an exceptional study model to examine the role of inbreeding as a selective pressure driving the evolution of dispersal modes. Within this genus, long-distance dispersal taxa (dispersed by wind) inhabit coastal terraces of the Atacama Desert, while short-distance taxa (dispersed by animals) are microhabitat specialists occupying rocky outcrops. Hence, I hypothesize that taxa with long-distance dispersal will exhibit reduced levels of inbreeding and increased population genetic diversity compared to short-distance dispersal taxa, since long-distance dispersal promotes gene flow between populations. Using genome-wide scanning, I identified 2,265 high-quality biallelic SNPs across 71 *Eriosyce* individuals of nine taxa with contrasting dispersal modes. I assessed genetic structure using Discriminant Analysis of Principal Components (DAPC) and Bayesian clustering (STRUCTURE), and estimated genetic diversity parameters (H_o, H_e, F_{is}) and linkage disequilibrium indices. Additionally, I explored spatial patterns of genetic variation through continuous maps of nucleotide diversity and observed heterozygosity. Contrary to expectations that long-distance dispersal reduces inbreeding, the results showed high inbreeding across all *Eriosyce* taxa, with the highest *Fis* values observed in long-distance dispersal taxa, while short-distance dispersal taxa showed lower inbreeding levels. Genetic structure was strong and mainly related to phylogenetic relatedness rather than dispersal modes. Furthermore, spatial genetic analysis revealed a north-south gradient of genetic diversity across the landscape, although no significant differences were observed for nucleotide diversity and observed heterozygosity between dispersal modes. These results suggest that other evolutionary drivers rather than inbreeding avoidance may have selected for long-distance dispersal in *Eriosyce*.

2.2 INTRODUCTION

Dispersal shapes the spatial distribution of plant species, therefore influencing mating patterns and gene flow (Gómez-Fernández et al., 2016). The distances that individuals move away from natal habitats determine not only the probability of mating with relatives, but also the distribution of genetic variation across landscapes (Baguette et al., 2013). Since dispersal spatially segregates conspecifics, it contributes to maintain high levels of heterozygosity within populations, consequently reducing inbreeding (Szulkin & Sheldon, 2008). Limited dispersal can facilitate local mating, leading to increased homozygosity and the accumulation of deleterious mutations through genetic drift (Jacquemyn et al., 2012; Spigler et al., 2017). This process is particularly important in small or isolated populations with limited mate availability and elevated risks of inbreeding (Hargreaves & Eckert, 2014). Hence, dispersal contributes to the genetic health of populations, as well as the maintenance of genetic variation necessary for adaptation to changing environments (Bijlsma & Loeschcke, 2012).

In plant populations, contrasting dispersal modes determine different patterns of genetic structure due to the inherent constraints and advantages of biotic and abiotic vectors. For example, wind dispersal enables individuals to move away from parental habitats, segregating relatives in space (Kling & Ackerly, 2021). As such, the probability of mating between relatives decreases as a function of distance, preventing inbreeding while promoting genetic homogenization among populations (Wójkiewicz et al., 2016). However, wind dispersal also implies higher ecological costs due to the stochasticity of wind fluxes (Cheptou et al., 2008), leading to increased diaspore loss and seedling mortality by reaching unsuitable habitats (Rousset & Gandon, 2002). Dispersal by animal species, on the other hand, is limited compared to wind dispersal, although it provides different ecological benefits. Since animal movements are spatially structured due to the specific habitat preferences of species, animal-mediated dispersal increases the probability of reaching suitable habitats more effectively (Aukema & del Rio, 2002; Spiegel & Nathan, 2010). These benefits, however, must compensate for the costs of short-distance dispersal, as the restricted spatial distribution of individuals may promote inbreeding within populations (Gelmi-Candusso et al., 2017). Therefore, wind and animal dispersal influence genetic structure of plant populations differently, ultimately leading to divergent evolutionary processes (Cain et al., 2000).

The species of the genus *Eriosyce* (Cactaceae) inhabiting the Atacama Desert offer an ideal study system to examine how contrasting dispersal modes influence different patterns of population genetic structure. The genus includes both short-distance dispersal taxa (animal-mediated dispersal) and long-distance dispersal taxa (wind-mediated dispersal), which inhabit different habitats of the

Huasco Valley. This area, located in the northern Atacama Desert of Chile, encompasses distinct habitat types, including coastal terraces and rocky outcrops that may have provided contrasting selective environments for dispersal evolution. Short-distance dispersal taxa are microhabitat specialists inhabiting rocky outcrops, which rely on animal vectors with reduced dispersal abilities, such as rats and lizards (Kattermann et al., 1994). This dispersal mode enables rocky outcrop specialists to maintain the exploitation of suitable microhabitats (Gomes et al., 2021), but it may promote genetic structure among individuals and increase inbreeding within populations. Conversely, long-distance dispersal by wind enables these taxa to occupy coastal terraces, which represent large, empty or sparsely vegetated habitats (Kattermann et al., 1994). Therefore, this dispersal mode promotes gene flow, reducing genetic structure and inbreeding across broad spatial scales, but also increases dispersal costs due to the stochasticity of wind fluxes in the Atacama Desert (Schween et al., 2020). Since the genus *Eriosyce* comprises closely related taxa that have evolved contrasting dispersal modes, its study provides a testing ground to evaluate how the historical evolution of dispersal has influenced genetic patterns among contemporary populations.

Here, I aim to characterize genetic diversity and inbreeding patterns across *Eriosyce* taxa to evaluate the genetic consequences of dispersal modes in desert-dwelling plant populations. Since long-distance dispersal promotes gene flow between populations, I hypothesize that taxa with long-distance dispersal will exhibit lower inbreeding levels and higher genetic diversity than taxa with short-distance dispersal. These results could provide insights into the historical selective pressures that underpinned the evolution of contrasting dispersal modes in *Eriosyce*.

2.3 METHODS

2.3.1 STUDY AREA AND SPECIES SAMPLING

The study was conducted in the Huasco Valley, located in the Atacama Desert (northern Chile; 28°30'S - 29°40'S, 69°50'W - 71°10'W). This area encompasses two distinct habitats where *Eriosyce* species with contrasting dispersal modes inhabit: coastal terraces and rocky outcrops. The coastal terraces of the Atacama Desert represent large, empty or sparsely vegetated habitats characterized by hyperarid conditions, sandy loam soils, and extreme surface ultraviolet radiation (Cordero et al., 2018). These open environments provide ideal conditions for wind dispersal, with consistent wind fluxes and minimal physical barriers to seed movement across the landscape. In contrast, rocky outcrops constitute discrete habitats with stable microclimates that provide moisture conditions suitable for diverse plant species, despite the surrounding aridity (Fitzsimons & Michael, 2017).

Field sampling was conducted during the austral spring of 2022 and 2023. *Eriosyce* taxa were sampled from rocky outcrops and coastal terraces, encompassing 71 individuals belonging to the nine taxa inhabiting this area: *Eriosyce napina* subsp. *napina*, *E. napina* subsp. *lembckei*, *E. napina* subsp. *duripulpa*, *E. crispa* var. *crispa*, *E. crispa* var. *huascensis*, *E. crispa* var. *atroviridis*, *E. crispa* var. *carrizalensis*, *E. villosa*, and *E. vallenarensis*. Long-distance dispersal taxa were represented by the *E. napina* complex, while short-distance dispersal taxa encompassed the *E. crispa* complex as well as *E. villosa*, and *E. vallenarensis*. Since most of these taxa face important conservation threats and, in some cases, only one population has been reported, explicit spatial details have been deliberately omitted to protect these vulnerable populations.

2.3.2 DNA EXTRACTION AND GENOMIC DATA PROCESSING

Genomic DNA was extracted from root tissue samples collected from *Eriosyce* individuals. Plant tissue was transported to the laboratory using paper bags and stored at -60°C until DNA extraction. DNA was obtained based on the protocol described by (Edwards et al., 1991), optimized for succulent plants with high mucilaginous content. DNA quality and concentration were assessed using gel electrophoresis and spectrophotometry. Then, samples were sequenced using the DArTseq platform (Diversity Arrays Technology, Australia), which combines complexity reduction methods with next-generation sequencing technology. The DArTseq method identifies thousands of high-quality single nucleotide polymorphism (SNP) markers distributed throughout the genome. DArTseq does not require a reference genome, which is especially valuable for non-model organisms with complex genomes and limited genomic resources, as in the case of *Eriosyce* species.

The raw genomic data obtained from the DArTseq method was then processed using the ‘dartR’ package (Gruber et al., 2025) in R version 4.3.1 (R Development Core Team, 2025). I applied quality control filters sequentially to ensure data reliability. First, I filtered SNPs based on read depth, retaining only those with coverage between 5 and 50 reads to exclude potential sequencing errors and paralogs. Subsequently, I applied a minimum call rate threshold of 70% for loci, ensuring that each retained SNP had genotype calls for at least 70% of individuals. To remove rare variants that could represent sequencing errors or recent mutations, I implemented a minor allele frequency (MAF) filter of 5%. Finally, I filtered individuals based on their genotyping success rate, retaining only those with call rates exceeding 30% across all loci. After quality control filtering, the final dataset comprised 2,265 high-quality biallelic SNPs across 71 individuals.

2.3.3 GENETIC STRUCTURE AND DIFFERENTIATION OF *ERIOSYCE* POPULATIONS

To assess population genetic structure and evaluate the relation between dispersal modes and genetic differentiation, I employed a Discriminant Analysis of Principal Components (DAPC) using the R package '*adegenet*' (Jombart et al., 2025). DAPC is a multivariate method that maximizes between-group differences while minimizing within-group variation. This approach also facilitates addressing taxonomic uncertainties within the genus *Eriosyce*, as several phylogenetic relationships remain contentious, with intraspecific taxa likely representing independent evolutionary lineages that should be elevated to the status of species (Guerrero et al., 2019). First, I handled missing values of the genomic dataset employing the missForest algorithm ('*missForest*' package; Stekhoven, 2022) to impute missing data based on the observed pattern of variation using 10 maximum iterations, 100 trees per forest, and variablewise error estimates. Then, I implemented a cross-validation procedure to determine the optimal number of principal components (PCs) to retain for the DAPC analysis. This procedure was implemented with 30 replications and 90% of the data used as a training set, allowing the identification of the number of principal components that maximized the accuracy of membership assignment while avoiding overfitting. The optimal number of clusters was determined using k-means clustering and the Bayesian Information Criterion (BIC), which allow objective determination without prior assumptions. The BIC values for different numbers of clusters (K= 1 to 9) were plotted, and the k value that minimized BIC was selected as optimal. Subsequently, the DAPC was performed using the optimal number of principal components identified through cross-validation and retaining all discriminant functions. Furthermore, to examine fine-scale genetic structure within established phylogenetic lineages, I conducted hierarchical DAPC analyses for each major clade separately: i) the Horridocactus clade (*E. napina* complex), ii) Clade VII (*E. crispa* complex), and iii) the Neoporteria clade (*E. villosa* and *E. vallenarensis*) following the phylogenetic framework of Guerrero et al. (2019). This hierarchical approach allows for the detection of genetic structure that may be masked when analyzing all taxa simultaneously.

Additionally, populational structure and admixture among the populations were examined using the Bayesian clustering algorithm implemented in STRUCTURE 2.3.4 (Pritchard et al., 2000). SNPs were analyzed using the admixture model with correlated allele frequencies. Due to the presence of taxa with few individuals, the LOCPRIOR model was implemented to improve clustering performance (Hubisz et al., 2009). The analysis was performed with a burn-in length of 500,000 iterations followed by 1,000,000 MCMC iterations. Ten independent runs were conducted for each value of K ranging from 1 to 9. The optimal number of genetic clusters was determined using multiple statistical criteria: i) the elbow method, which identifies the inflection point where relative improvements become marginal; ii) the variance explained approach, determining the K value capturing ≥80% of genetic structure; and iii) second derivative analysis detecting maximum deceleration in likelihood improvements. STRUCTURE results were processed using the R package '*pophelper'* (Francis, 2017). Multiple independent runs for each K value were aligned and averaged to obtain consensus admixture proportions.

I analyzed genetic diversity across *Eriosyce* taxa using filtered SNPs obtained through DArT sequencing. Population genetic parameters were calculated for each taxa using the R packages '*poppr*' (Kamvar et al., 2024), '*hierfstat*' (Goudet et al., 2022), and '*pegas*' (Paradis et al., 2023). For each population, I calculated expected heterozygosity (H_{exp}) and observed heterozygosity (H_{obs}) as measures of genetic diversity. The inbreeding coefficient (F_{is}) was also calculated to assess deviations from Hardy-Weinberg equilibrium. Additionally, Simpson's diversity index (λ) was estimated as a measure of allelic dominance based on allele frequencies. To evaluate linkage disequilibrium, I calculated two related indices: i) the association index (I_A), which provides an absolute measure of multilocus linkage disequilibrium, and ii) the standardized index of multilocus linkage disequilibrium ($\bar{r}_d$), which accounts for the number of loci and allows for comparison between datasets with different numbers of markers. The statistical significance of these indices was assessed using 999 permutations.

2.3.4 SPATIAL GENETIC DIVERSITY MAPPING

To characterize the spatial distribution of genetic diversity across the Huasco Valley landscape, I employed the R package '*wingen*' (Bishop et al., 2023) to generate continuous maps of nucleotide diversity (π) and observed heterozygosity (H_{obs}). This approach facilitates the visualization of genetic diversity patterns across the geographic space, examining how dispersal modes influenced the spatial distribution of genetic variation. First, a study area raster was defined based on the geographic extent of sampling locations, with a resolution of 0.01 decimal degrees. Then, genetic diversity metrics were calculated based on a sliding window approach, using a window dimension of 5 grid cells. To obtain robust estimates, rarefaction was performed, using a minimum sample size of 3 individuals and 5 rarefaction iterations. Subsequently, kriging interpolation was applied to generate smooth, continuous surfaces of genetic diversity at higher spatial resolution (0.005 decimal degrees). This interpolation method estimates values at unsampled locations based on the spatial autocorrelation structure of the observed data, providing comprehensive coverage of the study area.

2.4 RESULTS

2.4.1 POPULATION STRUCTURE AND ADMIXTURE

The DAPC analysis showed clear genetic structure among the *Eriosyce* taxa analyzed. The Bayesian Information Criterion indicated that population structure was best explained by four genetic clusters (K=4), with three discriminant axes accounting for 90.1% of the total variance. The clustering pattern corresponded to taxonomic boundaries and dispersal modes (Fig. 2.1). Cluster 1 comprised taxa with sort-distance dispersal from the *E. crispa* complex: *E. crispa* var. *atroviridis*, *E. crispa* var. *crispa*, and *E. crispa* var. *huascensis*. Cluster 2 contained *E. vallenarensis* and *E. villosa*, both short-distance dispersal taxa. Cluster 3 was represented exclusively by *E. crispa* var. *carrizalensis*, a short-distance dispersal taxa. At last, cluster 4 included long-distance dispersal taxa from the *E. napina* complex: *E. napina* subsp. *duripulpa*, *E. napina* subsp. *lembckei*, and *E. napina* subsp. *napina*.

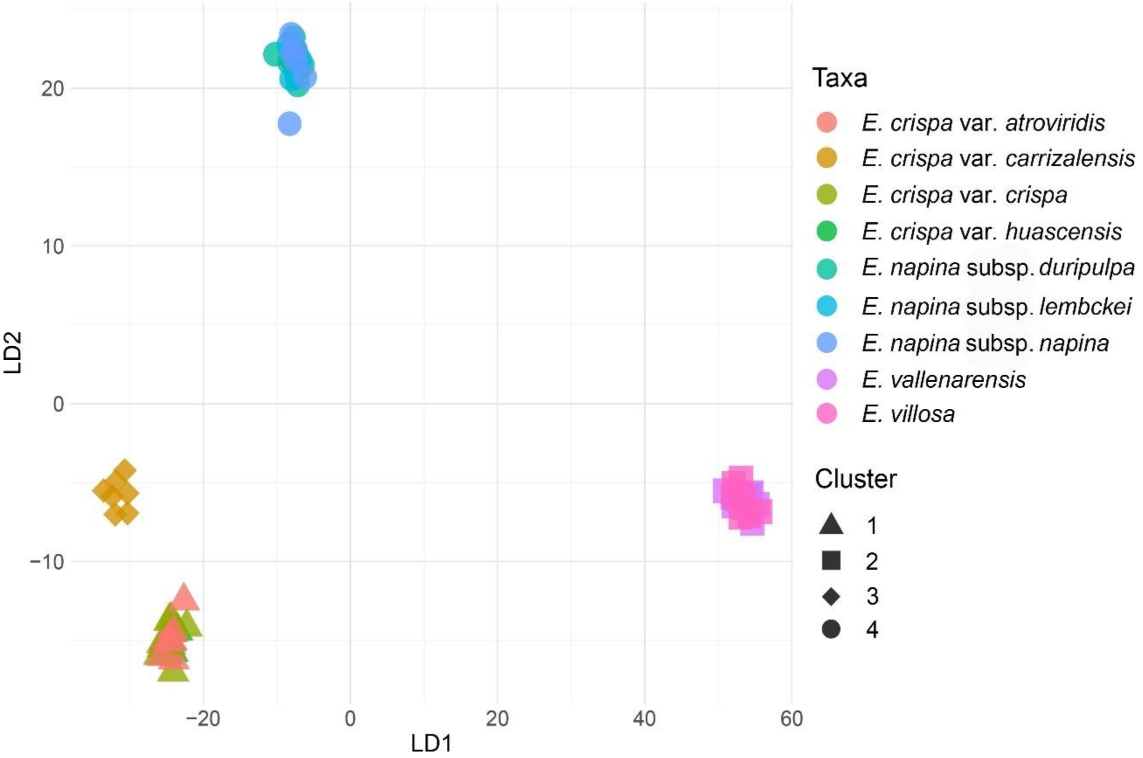

Figure 2.1. Discriminant Analysis of Principal Components (DAPC) of *Eriosyce* taxa. Scatter plot showing individual samples along the first two linear discriminants (LD1 and LD2).

Hierarchical DAPC analyses within major phylogenetic clades revealed additional fine-scale genetic structure. Within Clade VII (*E. crispa* complex), three genetic clusters were identified (Fig. 2.2), with *E. crispa* var. *carrizalensis* maintaining complete genetic isolation from other varieties, while *E. crispa* var. *atroviridis* and *E. crispa* var. *huascensis* clustered together, distinct from *E. crispa* var. *crispa*. The Horridocactus clade (*E. napina* complex) showed clear genetic subdivision into two clusters (Fig. 2.3), separating *E. duripulpa* individuals from *E. napina* subsp. *lembckei* and *E. napina* subsp. *napina*. The Neoporteria clade taxa (*E. villosa* and *E. vallenarensis)* demonstrated strong genetic differentiation (Fig. 2.4), confirming their distinct evolutionary trajectories despite sharing short-distance dispersal mode.

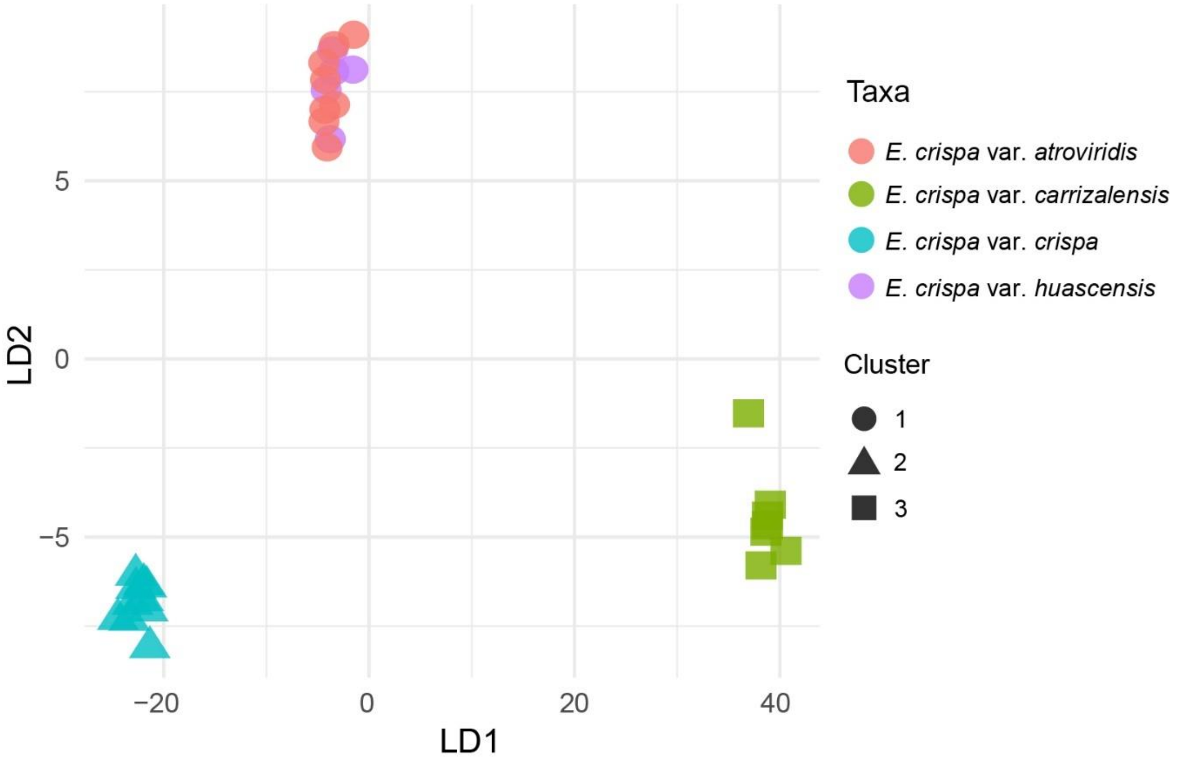

Figure 2.2. Discriminant Analysis of Principal Components (DAPC) of the *Eriosyce crispa* complex (clade VII). Scatter plot showing individual samples along the first two linear discriminants (LD1 and LD2).

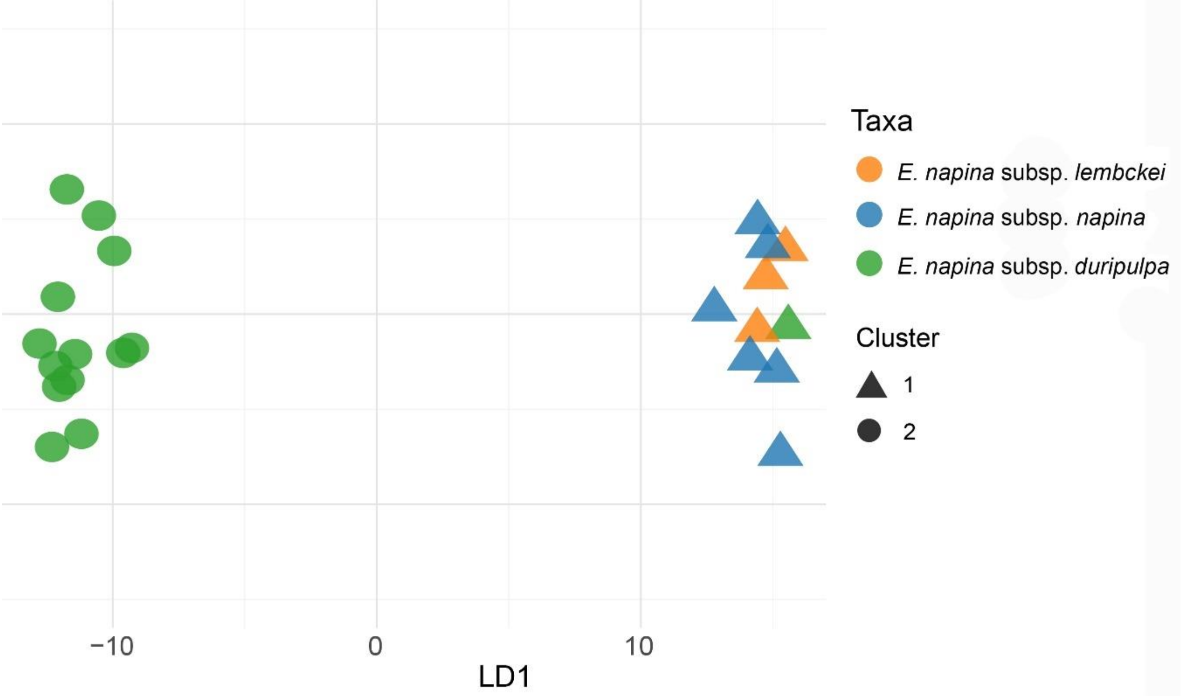

Figure 2.3. Discriminant Analysis of Principal Components (DAPC) of the *Eriosyce napina* complex (Clade Horridocactus). Scatter plot showing individual samples along the first linear discriminant (LD1).

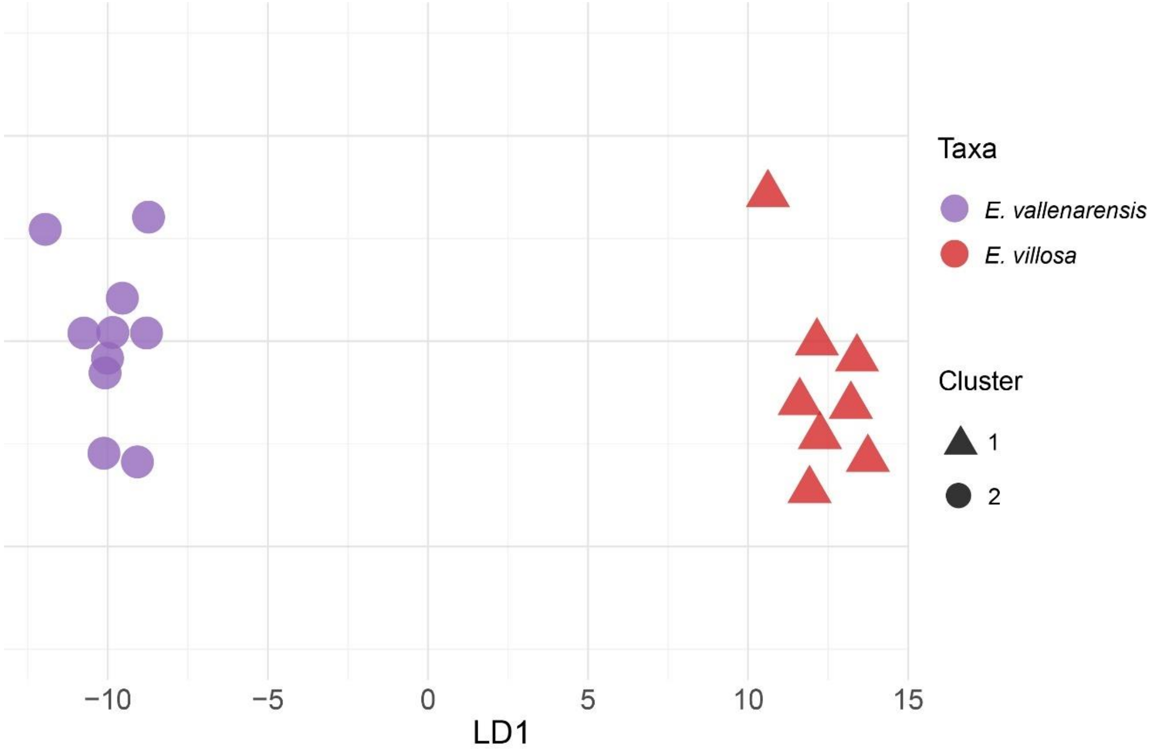

Figure 2.4. Discriminant Analysis of Principal Components (DAPC) of *E. vallenarensis* and *E. villosa* (clade Neoporteria). Scatter plot showing individual samples along the first linear discriminant (LD1).

On the other hand, statistical analysis of K optimization showed that different criteria provide similar solutions. The elbow method and variance explained approach indicated K=4 as optimal, while second derivative analysis suggested K=6. Given the marginal differences in statistical support and considering factors such as model stability and biological interpretability, K=6 was selected for further analyses. STRUCTURE analysis with K=6 revealed clear genetic differentiation among *Eriosyce* taxa, with most taxa showing high genetic coherence (Figure 2.5). Individual assignment strengths were notably high, with mean cluster assignments ranging from 0.78 to 0.99 across taxa. Seven of nine taxa showed complete genetic purity (100% of individuals with >80% assignment to main cluster), while *E. napina* ssp. *napina* and E. *napina* ssp. *lembckei* showed moderate admixture (66.7% pure assignments). Overall, 90% of individuals exhibited pure genetic assignments, indicating strong genetic differentiation with limited contemporary gene flow.

The genetic clustering patterns showed both concordance and divergence with DAPC results. STRUCTURE confirmed the genetic distinctiveness of *E. crispa* var. *carrizalensis* and the coherence of *E. crispa* vars. *atroviridis, huascensis, and crispa* (all assigned primarily to Cluster 1). However, STRUCTURE assigned *E. vallenarensis* and *E. villosa* to the same genetic cluster (Cluster 2), contrasting with their morphological differentiation. The *E. napina* complex maintained genetic unity consistent with DAPC patterns, while *E. duripulpa* formed a distinct genetic lineage (Cluster 3).

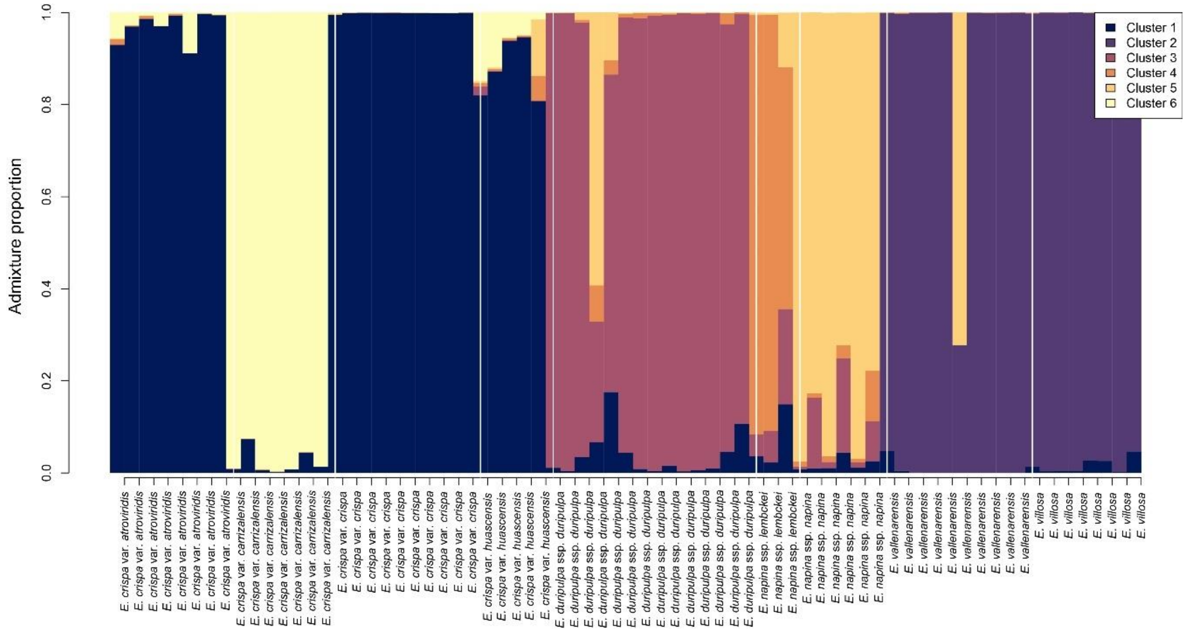

Figure 2.5. Population genetic structure of *Eriosyce* taxa revealed by STRUCTURE analysis. Barplot showing individual admixture proportions across four genetic clusters (K=6, with four populated clusters) for 71 individuals. Each vertical bar represents one individual, with colors indicating the proportion of genetic ancestry assigned to each cluster.

Based on the integrated evidence from both DAPC and STRUCTURE analyses, together with morphological and ecological criteria, I defined six operational taxonomic units for subsequent genetic diversity analyses: i) *E. crispa* var. *carrizalensis* as a distinct genetic entity; ii) *E. crispa*, combining vars. *atroviridis*, *huascensis*, and *crispa* based on their genetic affinity (*E. crispa* hereafter); iii) *E. duripulpa*; iv) *E. napina*, combining subspecies *napina* and *lembckei* that clustered together (*E. napina* hereafter); and v-vi) *E. vallenarensis* and *E. villosa* as separate units, prioritizing DAPC differentiation and morphological distinctions despite STRUCTURE genetic similarity (Figure 2.6-2.7).

Figure 2.6. *Eriosyce* taxa representing the six operational taxonomic units defined through DAPC and STRUCTURE analyses: a) *E. crispa*, b) *E. crispa* var. *carrizalensis*, c) *E. vallenarensis*, d) *E. villosa*, e) *E. duripulpa*, and f) *E. napina*.

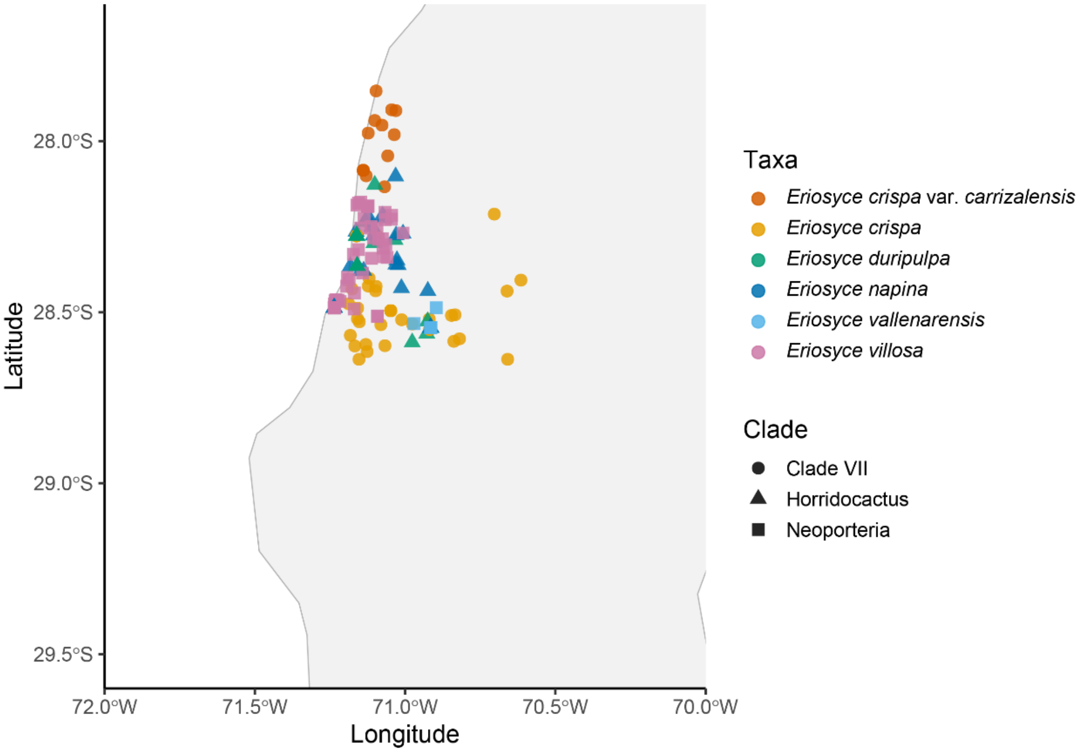

Figure 2.7. Geographic distribution of the six *Eriosyce* taxa included in this study along the Atacama Desert coast of northern Chile.

2.4.2 GENETIC DIVERSITY

The inbreeding coefficients revealed contrasting patterns between long- and short-distance dispersal taxa (Table 2.1). *Eriosyce napina* (long-distance dispersal) showed the highest F_{is} value at 0.56, while *E. duripulpa* (also long-distance dispersal) exhibited 0.43. Among short-distance dispersal taxa, values ranged from 0.49 in *E. crispa* var. *carrizalensis* to 0.28 in *E. villosa*, the lowest across all taxa. H_{obs} varied from 0.06 (*E. crispa* var. *carrizalensis*) to 0.11 (*E. vallenarensis*), with long-distance dispersal taxa showing intermediate values (*E. napina*: 0.06; *E. duripulpa*: 0.09). H_{exp} remained relatively similar across taxa (0.14-0.16), with no clear differentiation based on dispersal modes. Simpson's diversity index indicated high genetic diversity in all populations, ranging from 0.86 in *E. crispa* var. *carrizalensis* to 0.96 in *E. crispa*. Both long-distance dispersal taxa showed moderately high values (*E. napina*: 0.89; *E. duripulpa*: 0.92). Linkage disequilibrium measures were significant for all taxa ($p < 0.05$). The association index (I_A) was particularly high in *E. duripulpa* (47.48) and *E. napina* (37.64), while standardized linkage disequilibrium ($\bar{r}_d$) approached or equaled 1.00 for most taxa, except for *E. napina* (0.82).

Taxa	Group	*n*	H_{exp}	H_{obs}	F_{is}	λ	I_A	$\bar{r}_d$
E. crispa var. *carrizalensis*	Short-distance dispersal	7	0.12	0.06	0.49	0.86	28.65*	1.00*
E. crispa	Short-distance dispersal	23	0.16	0.07	0.47	0.96	17.34*	1.00*
E. duripulpa	Long-distance dispersal	13	0.16	0.09	0.43	0.92	47.48*	1.00*
E. napina	Long-distance dispersal	9	0.15	0.06	0.56	0.89	37.64*	0.82*
E. vallenarensis	Short-distance dispersal	10	0.16	0.11	0.37	0.90	19.05*	1.00*
E. villosa	Short-distance dispersal	8	0.14	0.10	0.28	0.88	1.43*	1.00*

Table 2.1. Genetic diversity parameters for *Eriosyce* taxa with long- and short-distance dispersal, displaying the number of sampled individuals (*n*); expected heterozygosity (H_{exp}); observed heterozygosity (H_{obs}); inbreeding coefficient (F_{is}); Simpson's diversity index (λ); association index (I_A); and standardized index of multilocus linkage disequilibrium ($\bar{r}_d$). *$p < 0.05$ indicates significance for linkage disequilibrium (I_A and $\bar{r}_d$).

2.4.3 SPATIAL PATTERNS OF GENETIC DIVERSITY

Spatial analysis revealed heterogeneous patterns of genetic diversity across the Huasco Valley landscape (Figure 2.8). Nucleotide diversity (π) ranged from 0.144 to 0.195 across 1,522 grid cells, with a mean value of 0.176 ± 0.012 (mean ± SD). Observed heterozygosity (H_{obs}) showed lower values, ranging from 0.049 to 0.105, with a mean of 0.081 ± 0.012. The spatial distribution of both diversity metrics exhibited a north-south gradient, with higher values concentrated in the central and northern portions of the study area. Comparative analysis between dispersal modes revealed no significant differences in spatial genetic diversity patterns. Long-distance dispersal taxa showed mean nucleotide diversity of 0.178 ± 0.011 and mean observed heterozygosity of 0.083 ± 0.008. Short-distance dispersal taxa exhibited similar values with mean nucleotide diversity of 0.174 ± 0.012 and mean observed heterozygosity of 0.081 ± 0.012. Statistical tests revealed no significant differences between dispersal modes for either nucleotide diversity (t-test, $p = 0.275$) or observed heterozygosity (t-test, $p = 0.570$). These results indicate that dispersal modes do not significantly influence the spatial distribution of genetic diversity in *Eriosyce* populations at the landscape scale.

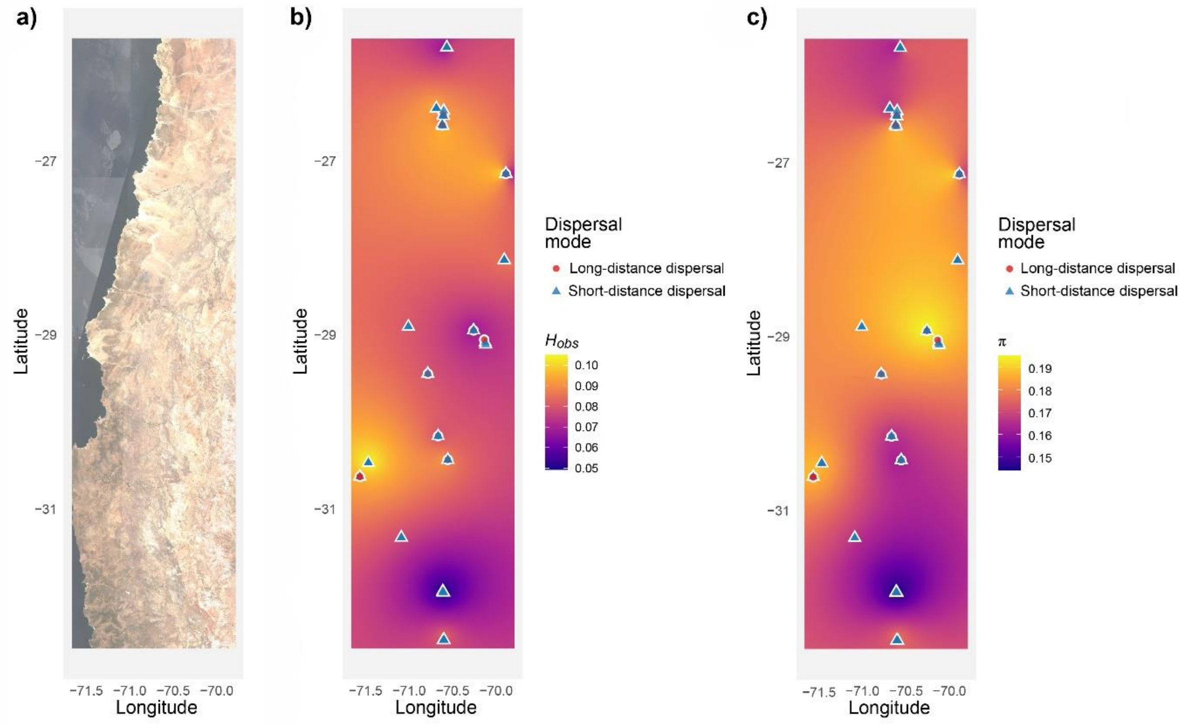

Figure 2.8. Spatial distribution of genetic diversity in *Eriosyce* populations across the Huasco Valley, Atacama Desert. a) Satellite imagery showing the study area topography and habitat distribution, b) nucleotide diversity (π), and c) observed heterozygosity (H_{obs}) interpolated using kriging across 1,522 grid cells. Red circles indicate long-distance dispersal taxa and blue triangles represent short-distance dispersal taxa. Both metrics show similar spatial patterns with a north-south gradient, and no significant differences between dispersal modes (π: $p = 0.275$; H_{obs}: $p = 0.570$).

2.5. DISCUSSION

Population genetic analyses revealed that dispersal modes have had less influence on genetic structure than expected in *Eriosyce*. Both DAPC and STRUCTURE analyses showed that *Eriosyce* taxa cluster mainly based on their phylogenetic relationships rather than dispersal modes, with strong genetic differentiation maintained between most taxa. The studied long-distance dispersal taxa of section Horridocactus form a cohesive group, while short-distance dispersal taxa are scattered among two clades: sections VIII (*E. crispa* complex) and Neoporteria (*E. villosa* and *E. vallenarensis*). Moreover, hierarchical DAPC analyses detected additional genetic structure within each dispersal mode: the *E. crispa* complex subdivided into three clusters with *E. crispa* var. *carrizalensis* maintaining complete isolation, the *E. napina* complex subdivided into two clusters separating *E. duripulpa* from the other subspecies, and Neoporteria taxa showed strong genetic differentiation despite sharing short-distance dispersal mode. STRUCTURE analysis revealed strong genetic differentiation among most *Eriosyce* taxa, with limited admixture patterns that were similar between short- and long-distance dispersal taxa, suggesting that dispersal modes have not generated important differences in historical genetic connectivity.

Contrary to expectations, taxa with long-distance dispersal from the Horridocactus clade exhibited higher levels of inbreeding compared to taxa with short-distance dispersal from clades VIII and Neoporteria. These results suggest that other selective pressures rather than inbreeding led to the evolution of long-distance dispersal in *Eriosyce* (Duputié & Massol, 2013). The observed genetic patterns suggest that other evolutionary drivers (specifically kin competition and environmental variability, as shown in Chapters III and IV, respectively) rather than inbreeding avoidance have been the primary selective pressures driving dispersal evolution in *Eriosyce*. The high levels of inbreeding in long-distance dispersal taxa are probably explained by historical demographic processes during the colonization of coastal terraces (Helsen et al., 2013; Maya-García et al., 2017). Long-distance dispersal may have facilitated the colonization of coastal terraces of the Atacama Desert by a reduced number of individuals due to the stochastic nature of wind fluxes (Schween et al., 2020), creating founder effects during the establishment of these small founding populations from ancestral lineages. Subsequently, population bottlenecks further reduced effective population sizes during extreme climatic fluctuations or habitat establishment challenges (Hewitt, 2004; Pierce et al., 2017). The combination of these demographic events presumably resulted in small populations where mating among relatives became inevitable, leading to the elevated inbreeding coefficients observed in contemporary populations of long-distance dispersal taxa.

The increased costs of wind dispersal may have also played an important role in influencing inbreeding patterns in long-distance dispersal taxa. In this sense, diaspore loss and seedling mortality by reaching unsuitable habitats are direct consequences of dispersal by spatially unpredictable abiotic vectors (Duputié & Massol, 2013). This increased dispersal costs with respect to short-distance dispersal taxa —whose dispersal is performed by animal vectors with predictable and directed movements (Cheptou et al., 2008; Nield et al., 2020)— could result in a lower number of reproductive individuals, causing higher levels of inbreeding within populations (Hidalgo et al., 2016). Since dispersal cost constitutes a continuous process, it may be precluding the overcoming of inbreeding caused by the historical demographic processes discussed before (Hidalgo et al., 2016; Ingvarsson, 2001). However, the geophytic nature of long-distance dispersal taxa largely constrains demographic assessments of their populations. Individuals are small in size, typically buried or barely protruding above the ground if not completely covered by soil, and stem colors are very similar to the surrounding soil, making visual detection highly challenging (Kattermann et al., 1994). Therefore, even though likely, the influence of dispersal costs on genetic population patterns is difficult to evaluate for these taxa.

Although inbreeding avoidance is a major evolutionary driver of long-distance dispersal (Duputié & Massol, 2013), the results suggest this was not the case in *Eriosyce*. In plant species, pollination also plays a critical role promoting gene flow among populations, thereby reducing the risk of inbreeding (Breed et al., 2015). In *Eriosyce*, recent studies have demonstrated that pollination significantly influences population genetic patterns of rocky outcrop specialists, showing distinct effects depending on pollinator guilds (Guerrero et al., 2025; Meriño et al., 2024). Therefore, even if reduced dispersal fails to prevent inbreeding, alternative mechanisms such as pollination may promote gene flow, consequently influencing population connectivity (Gamba & Muchhala, 2023). This complementary gene flow strategy may be particularly important for short-distance dispersal taxa, especially for bird-pollinated species such as those of the Neoporteria clade (Guerrero et al., 2025), enabling the occupation of rocky outcrops while mitigating the genetic consequences of reduced dispersal via gene flow by pollination (Calviño-Cancela et al., 2012). However, in the case of long-distance dispersal taxa, the absence of pollinators in coastal terraces may have led to facultative autogamy as an alternative mechanism to cope with restricted pollination services (Martinell et al., 2011). Nevertheless, autogamy also implies a reduction in genetic diversity within populations, leading to increased levels of inbreeding (Shapcott et al., 2010).

Regarding genetic diversity, the observed patterns contradicted expectations on long-distance dispersal taxa exhibiting increased diversity. The expected heterozygosity and Simpson's Index showed similar values between taxa with long- and short-distance dispersal, despite differences in F_{is}. As such, the processes driving inbreeding may be different to those reducing total genetic diversity (Charlesworth & Willis, 2009). The observed levels of inbreeding and total genetic diversity can respond to different temporal scales and evolutionary processes (Petit & Excoffier, 2009). While inbreeding can be the result of both historical and contemporary demographic processes, total genetic diversity may represent the accumulative result of long-term evolutionary processes (Charlesworth & Willis, 2009; Excoffier et al., 2009). This apparent inconsistency between inbreeding levels and total genetic diversity suggests that the genetic structure of populations has been influenced by complex processes, affecting genetic patterns differently (Holderegger et al., 2006). On the other hand, significant linkage disequilibrium was higher for long-distance dispersal taxa, presumably as a consequence of demographic processes such as population bottlenecks (Slatkin, 2008).

The spatial patterns of genetic diversity revealed similar north-south gradient for both nucleotide diversity and observed heterozygosity that does not respond to dispersal modes in *Eriosyce* taxa. These results suggest that dispersal modes are insufficient to explain the spatial distribution of genetic variability in long- and short-distance dispersal taxa. Probably, other factors related to landscape characteristics or historical geological and climatic processes have been responsible for the genetic structure of populations. For example, tectonic uplifts created novel habitats for the colonization of long-distance dispersal taxa (Bentley et al., 2014; Hoorn et al., 2010), leading to founder events in recently exposed coastal terraces. Landscape fragmentation on the other hand, originated rocky outcrops, providing "islands" of suitable habitats (Clegg et al., 2025). These discrete units of habitat likely promoted the isolation of populations, resulting in the genetic differentiation of populations among rocky outcrops (Ferris et al., 2014). Similarly, climatic processes such as Pleistocene oscillations may have induced alternations between periods of population connectivity and isolation in refugia (Ortego & Knowles, 2022), thereby creating genetic patterns that persist despite current dispersal capabilities. This persistence of historical signals provides a parsimonious explanation for why spatial genetic patterns transcend contemporary dispersal differences.

2.6 CONCLUSION

These results contradict theoretical expectations about the role of inbreeding on the evolution of contrasting dispersal modes in *Eriosyce*, revealing unexpected genetic patterns. Long-distance dispersal taxa exhibited higher inbreeding levels than short-distance dispersal taxa, while the genetic structure of populations was mainly correlated with phylogenetic relationships rather than dispersal modes. These findings suggest that inbreeding has not driven the evolution of long-distance dispersal within the genus. Probably, the observed genetic patterns are explained by historical demographic processes such as founder effects and population bottlenecks during the colonization of coastal terraces, as well as the continuous ecological costs associated with the stochastic nature of wind dispersal in the Atacama desert. The absence of significant differences in the spatial genetic diversity between dispersal modes, along with the persistence of a north-south gradient, suggests that historical demographic and geological factors have been more important in determining dispersal modes. Therefore, it is critical to consider multiple temporal scales as well as the complexity of evolutionary processes in arid environments to understand the evolution of life-history traits in natural populations.

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3. CHAPTER III: CONTRASTING PATTERNS OF KIN COMPETITION IN *ERIOSYCE* TAXA WITH DIFFERENT DISPERSAL MODES

3.1 ABSTRACT

Kin competition, the competition among genetically related individuals, is a major evolutionary driver selecting for dispersal. Dispersal enables the spatial segregation of related individuals, reducing local competition while also facilitating the colonization of novel habitats. Contrasting dispersal modes, such as long-distance dispersal by wind and short-distance dispersal by animals, differentially influence genetic relatedness patterns among individuals, thereby determining kin competition intensity. Taxa within the genus *Eriosyce* (Cactaceae) inhabiting the Huasco Valley of the Atacama Desert provide an ideal study system to evaluate the role of kin competition in the evolution of dispersal. Long-distance dispersal taxa inhabit coastal terraces in the Atacama Desert, which represent large, empty or scarcely vegetated habitats. Short-distance dispersal taxa are micro-habitat specialists, occupying rocky outcrops, which constitute discrete and limited-size habitats. Since long-distance dispersal enables the escape from kin competition, I hypothesize that *Eriosyce* taxa dispersed by wind will exhibit reduced genetic relatedness compared to taxa dispersed by animals. I calculated pairwise relatedness coefficients among *Eriosyce* individuals using high-quality SNPs and Maximum Likelihood estimation. Spatial patterns of genetic relatedness were assessed using a neighborhood approach at multiple spatial scales and distance-relatedness gradient analysis to evaluate isolation by distance patterns between dispersal modes. Long-distance dispersal taxa exhibited significantly lower mean relatedness (0.004 ± 0.003; mean ± SD) than short-distance dispersal taxa (0.007 ± 0.005), representing a 43% reduction in genetic similarity. Moreover, long-distance dispersal taxa exhibited significatively decreasing relatedness with distance (slope = -0.006), whereas short-distance dispersal taxa maintained uniform genetic similarity across space (approximately 18 times weaker slope), indicating effective long-distance gene flow in wind-dispersed versus more localized genetic structure in animal-dispersed taxa. These findings support the hypothesis that kin competition has driven the evolution of long-distance dispersal in anemochorous *Eriosyce* taxa, with wind dispersal effectively reducing local genetic relatedness and promoting gene flow across the landscape.

3.2 INTRODUCTION

Kin competition —the competition among genetically related individuals— represents one of the main evolutionary forces driving the selection of dispersal (Rousset & Gandon, 2002). Individuals inhabiting parental patches generally compete with their relatives for the same limited resources, leading to reduced fitness and increased mortality (Ronce, 2007). Although reduced dispersal strategies enable the exploitation of suitable habitats (Gomes et al., 2021), they can also promote habitat crowding, increasing the probability of intraspecific competition (Duputié & Massol, 2013). The intensity of competition can be enhanced among highly genetically related individuals, as they tend to have similar resource requirements and competitive abilities (Violle et al., 2012). Therefore, kin competition drives the selection of mechanisms that spatially segregate conspecific individuals (Bach et al., 2006; Gyllenberg et al., 2008). As such, dispersal serves as an evolutionary solution to reduce the ecological costs associated with the competition for local resources (Ronce, 2007).

In plant species, natural populations with contrasting dispersal modes —such as long-distance dispersal by wind and short-distance dispersal by small animals— provide an opportunity to examine the role of kin competition in dispersal evolution. Based on theoretical predictions, long distance dispersal species (anemochorous) should experience reduced kin competition, since wind dispersal facilitates the colonization of new habitats, therefore reducing competition with relatives (Bohrer et al., 2005; North & Ovaskainen, 2007). Wind dispersal enables plants to escape from natal populations, while spatially segregating highly genetically related individuals (Kling & Ackerly, 2021). Conversely, zoochorous species with short-distance dispersal (e.g., dispersed by lizards, ants, rats) should exhibit increased kin competition, since animals with limited movement ranges can be expected to deposit seeds within or immediately around parental patches (Cordero et al., 2021; Gomes et al., 2021; Ronce & Promislow, 2010). Animal species usually generate aggregated seed deposits due to their habitat preferences, leading to the close spatial distribution of genetically related individuals (Schupp et al., 2002). This becomes particularly important for microhabitat specialists, as the exploitation of limited-size sites can increase local crowding and, consequently, the intensity of competition (Gyllenberg et al., 2008; Ronce & Promislow, 2010).

Kin competition is typically evaluated through fitness components (growth, survival, and reproductive success), phenotypic plasticity of functional traits, and measures of competitive responses and effects (Dudley et al., 2013). However, examining kin competition is also feasible by assessing the influence of historical dispersal events on genetic patterns of contemporary populations (Hendrickson & Cruzan, 2024; Soltis & Soltis, 2021). Dispersal shapes the genetic composition of plant populations, reflecting different patterns of genetic relatedness among individuals, which can be addressed through genomic approaches (Hamrick & Trapnell, 2011). This direct measure of local genetic similarity can evidence the effectiveness of dispersal in segregating relatives in space (Höhn et al., 2021). Furthermore, the spatial genetic structure of populations can also reveal the spatial extent over which kin competition operates, as well as the effectiveness of different dispersal modes in reducing local relatedness (Lara-Romero et al., 2016; Wells & Young, 2002). In this sense, populations with long-distance dispersal should exhibit reduced genetic relatedness with increasing geographic distances, reflecting weaker patterns of isolation by distance due to effective gene flow across landscapes (Bitume et al., 2013; Vekemans & Hardy, 2004).

The species of the genus *Eriosyce* inhabiting the Huasco Valley represents an ideal model system to examine the influence of kin competition as a driver of dispersal mode evolution. In this valley, long-distance dispersal taxa from the napina complex (*E. napina* subsp. *napina, E. napina* subsp. *lembckei, and E. napina* subsp. *duripulpa*) inhabit coastal terraces, which constitute large and empty or sparsely vegetated habitats (Armijo et al., 2015). These coastal terraces create conditions that may intensify kin competition, as suitable microsites are limited and scattered across the landscape, promoting related individuals to compete for the same favorable establishment sites. The increased dispersal capabilities of populations under selection could have facilitated the historical colonization of favorable sites across coastal terraces (Nathan et al., 2008), thus reducing genetic relatedness among individuals. On the other hand, short-distance dispersal taxa, including the *E. crispa* complex, *E. villosa*, and *E. vallenarensis*, are microhabitat specialists occupying rocky outcrops (Kattermann et al., 1994). Within the valley, these microhabitats represent discrete units with limited sizes that provide stable microclimatic conditions especially suitable for desert-dwelling plant species (Fitzsimons & Michael, 2017; Porembski & Barthlott, 2000). However, although these outcrops offer suitable microsites, they can concentrate related individuals within small areas, intensifying kin competition as relatives are maintained in proximity and must compete for the same limited local resources. Short-distance dispersal, therefore, becomes critical to maintain the exploitation of these microhabitats, relying on animal vectors with limited dispersal abilities (Gomes et al., 2021). However, short-distance dispersal can also increase genetic relatedness among individuals, leading to kin competition (Treep et al., 2021). These different selective pressures operating in the Huasco Valley may have driven the divergent evolution of dispersal modes, consequently shaping the genetic structure and relatedness patterns among species with contrasting dispersal capabilities.

Here, I evaluate whether patterns of genetic relatedness among *Eriosyce* taxa from the Huasco Valley are consistent with the hypothesis that kin competition selected for long-distance dispersal.

Specifically, I predict that *Eriosyce* taxa with long-distance dispersal will exhibit reduced genetic relatedness compared to taxa with short-distance dispersal, since increased dispersal enables the escape from kin competition. Furthermore, I predict that the genetic structure of populations will vary across spatial scales, with long-distance dispersal taxa exhibiting a negative correlation between relatedness and geographic distance. This model system could provide valuable insights into the role of kin competition underpinning the evolution of contrasting dispersal modes in desert-dwelling plants.

3.3 METHODS

3.3.1 RELATEDNESS ESTIMATION AND COMPARISON BETWEEN CONTRASTING DISPERSAL MODES

To assess whether kin competition promoted the evolution of dispersal modes in *Eriosyce*, I estimated pairwise relatedness coefficients among all individuals using the '*Relatedness*' package (Laporte & Mary-Huard, 2017). This package infers the relatedness distribution coefficients from a biallelic genotype matrix using a Maximum Likelihood estimation, without assumptions about Hardy-Weinberg equilibrium or linkage equilibrium. I used the same species sampling, DNA extraction protocols, and taxonomic treatment and genomic dataset described in Chapter II, which comprises 2,265 high-quality biallelic SNPs for 71 *Eriosyce* individuals. For quality control, I applied more stringent filtering criteria than Chapter II since the *Relatedness* package requires complete data matrices. Thus, I removed SNPs with >20% of missing data and individuals with >30% of missing data, resulting in a final dataset of 56 individuals and 2,071 high-quality SNPs. Subsequently, the remaining missing values were replaced with the most common genotype for each SNP by applying simple imputation, as Maximum Likelihood estimation requires complete data matrices.

SNP genotypes (coded as 0,1,2) were converted into the biallelic format (0,1) required by the *Relatedness* package. For each *Eriosyce* individual, I decomposed genotypes into two allelic columns as follows: homozygotes 0/0 were coded as (0,0), heterozygotes 0/1 as (0,1), and homozygotes 1/1 as (1,1). The resulting individual genotype matrix contained SNPs as rows and individuals × 2 as columns. Then, I calculated the allele frequencies for each SNP as the proportion of allele 1 in the total sample. Subsequently, I performed Maximum Likelihood estimation of relatedness coefficients using the following parameters: unphased data (since DArTseq data does not provide information about haplotype phase); five initial values for the EM (Expectation-Maximization) algorithm to enable convergence stability from multiple starting points; and convergence precision of 1×10^{-4} for likelihood optimization. The analysis generated nine relatedness coefficients (Delta1-Delta9), from which I extracted Delta1, as it represents the standard pairwise relatedness coefficient between individuals (Laporte et al. 2017).

At last, I assessed whether *Eriosyce* taxa with long-distance dispersal exhibit lower relatedness than short-distance dispersal taxa. First, I calculated the mean relatedness coefficients for each individual to avoid pseudoreplication, as the same individuals are contained in multiple pairwise comparisons. For this purpose, I averaged pairwise relatedness values with all other individuals (excluding self-relatedness values), obtaining an individual-level measure of average genetic similarity with conspecifics. Then, I evaluated the effect of dispersal modes on relatedness by using Welch's t-tests (normality of relatedness distributions were previously confirmed by Shapiro-Wilk tests). Additionally, I fitted a Linear Mixed Model (LMM) using the '*lme4'* package (Bates et al., 2025) to explore the contribution of taxa-specific effects. The model was built using the mean relatedness coefficients as response variable, while the dispersal mode was used as fixed effect and the taxa identity as random effect. At last, effect size was quantified using Cohen's d to assess the magnitude of observed differences.

3.3.2 SPATIAL PATTERNS OF GENETIC RELATEDNESS

To further examine the effects of kin competition at a spatial scale, I assessed whether dispersal modes influence genetic structure at multiple scales using a neighborhood approach to assess local relatedness. This approach allows the detection of genetic structure that could not be recognized at specific spatial resolutions, as genetic patterns can be affected differently across spatial scales. Hence, I calculated local relatedness coefficients for each individual within circular neighborhoods at multiple spatial scales: fine scale radii of 0.5-10 km, intermediate scale of 50 km, and landscape scale of 379 km (half the study area extent). As described above, local relatedness was estimated as the mean relatedness coefficient with all neighbors within the specified distances. Statistical differences in local relatedness between dispersal modes at each spatial scale were evaluated using Welch's t-tests, which account for unequal variances between groups.

I also conducted distance-relatedness gradient analysis using LMM to evaluate spatial patterns of genetic relatedness. Pairwise relatedness coefficients and geographic distances were calculated for all individual pairs, and then each pair was classified according to their dispersal mode: same dispersal mode pairs (both individuals sharing dispersal mode) or mixed pairs (individuals with different dispersal mode). Only pairs with the same dispersal mode were included in the model, for which a taxa-pair identifier was created by combining the name of the taxa of both individuals. Geographic distances were converted to kilometers and log-transformed, considering typical isolation by distance patterns. Then, I fitted LMM using pairwise relatedness coefficients as response variable, while the geographic distance, dispersal mode, and their interactions were used as fixed effects, and the taxa-pair identity as random effect. Statistical significance was evaluated using Satterthwaite's method for degrees of freedom calculation.

3.4 RESULTS

3.4.1 RELATEDNESS PATTERNS BETWEEN DISPERSAL MODES IN *ERIOSYCE*

Maximum likelihood estimation of pairwise relatedness coefficients showed clear differences between dispersal modes in *Eriosyce*. Simple relatedness coefficients (Delta1) ranged from 0 to 0.016 in all pairwise comparisons, with a mean of 0.006 ± 0.004 (mean ± SD). Long-distance dispersal taxa exhibited significantly lower mean relatedness (0.004 ± 0.003) than short-distance dispersal taxa (0.007 ± 0.005), with a 43% reduction in the average genetic similarity among individuals. This difference was statistically significant as shown by Welch's t-test (t = -2.91, df = 38.6, p = 0.006). Furthermore, LMM with taxa identity as a random effect confirmed the effect of dispersal mode (β = 0.003, SE = 0.002, t = 1.89) and showed that dispersal mode explained the variation in relatedness patterns (F = 3.55). Random effects variance among taxa was relatively small ($\sigma^2 = 2.29\times10^{-6}$), indicating consistent dispersal mode differences among taxa within the genus. The effect size was moderate to large (Cohen's d = -0.72, 95% CI: [-1.34, -0.10]).

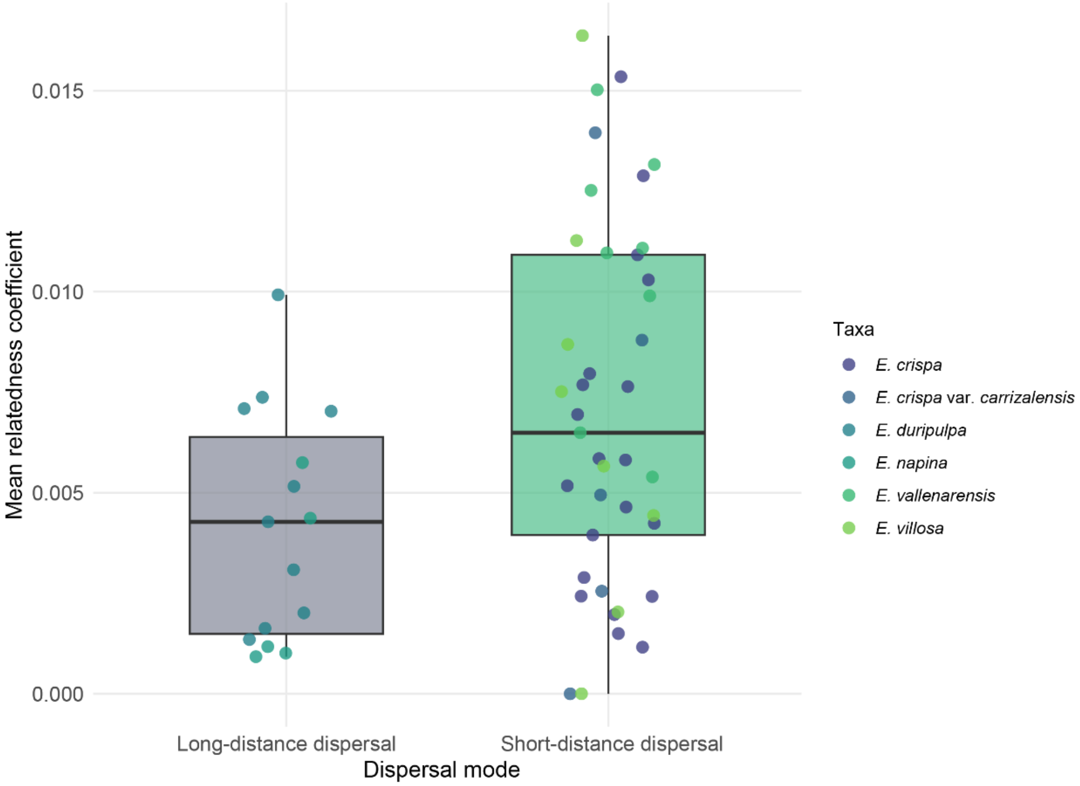

Figure 3.1. Relatedness by dispersal mode in *Eriosyce*. Box plots showing mean relatedness coefficients for long-distance dispersal (purple) and short-distance dispersal (green) taxa, based on maximum likelihood estimation. Points represent individual mean relatedness values, colored by taxa identity.

3.4.2 SPATIAL PATTERNS OF GENETIC RELATEDNESS

Local relatedness analysis at multiple spatial scales revealed patterns of genetic structure influenced by spatial scale. At fine spatial scales (0.5-10 km), local relatedness between dispersal modes showed no significant differences (Table 3.1). Similarly, no significant differences were found at the intermediate scale (50 km; Table 3.1). However, at the landscape scale (379 km), long-distance dispersal taxa exhibited significantly lower local relatedness (0.005 ± 0.004; mean ± SD) compared to short-distance dispersal taxa (0.008 ± 0.006; t = -2.073, p = 0.046) (Table 3.1). The number of neighbors within each radius was found to be relatively consistent between dispersal modes at fine scales (2.5-2.9 neighbors within 0.5-10 km), but increased considerably at larger scales (50 km: long-distance dispersal = 5.54, short-distance dispersal = 4.72 neighbors; 379 km: long-distance dispersal = 40.1, short-distance dispersal = 34.6 neighbors) (Table 3.1).

Radius (km)	**Long-distance dispersal**	**Short-distance dispersal**	**Mean neighbors**	**t**	**p**
	Mean ± SD	Mean ± SD	Long-distance dispersal / Short-distance dispersal		
0.5	0.001 ± 0.003	0.003 ± 0.006	2.89 / 2.52	-1.044	0.306
1	0.001 ± 0.003	0.002 ± 0.005	2.90 / 2.51	-0.935	0.357
2	0.001 ± 0.003	0.004 ± 0.014	2.90 / 2.54	-1.369	0.178
5	0.005 ± 0.012	0.004 ± 0.014	2.58 / 2.54	0.044	0.965
10	0.006 ± 0.013	0.004 ± 0.014	2.85 / 2.64	0.351	0.729
50	0.005 ± 0.007	0.007 ± 0.014	5.54 / 4.72	-0.698	0.489
379	0.005 ± 0.004	0.008 ± 0.006	40.1 / 34.6	-2.073	0.046*

Table 3.1. Local relatedness coefficients at multiple spatial scales in *Eriosyce* taxa with contrasting dispersal modes. Mean neighbors indicate the average number of individuals within each radius for focal individuals of each dispersal mode. Statistical comparisons between dispersal modes were conducted using Welch's t-tests at each spatial scale.

Furthermore, long-distance dispersal taxa showed effective genetic mixing across space, whereas short-distance dispersal taxa maintained more uniform genetic similarity regardless of distance (Fig. 4.2). Linear Mixed Models showed significant differences in distance-relatedness gradients between dispersal modes (interaction term: $F_{1,817} = 5.12$, p = 0.019). Long-distance dispersal taxa exhibited a strong negative slope of -0.006 (SE = 0.002, t = -2.49, p = 0.013), indicating that relatedness decreases substantially when geographic distance increases. On the other hand, short-distance dispersal taxa showed a much weaker slope of -3.26x10^{-4}, representing a slope approximately 18 times smaller in magnitude than that of long-distance dispersal taxa. The main effect of distance was significant ($F_{1,817} = 6.67$, p = 0.010), although the main effect of the dispersal mode was not significant ($F_{1,13} = 0.27$, p = 0.615), indicating that dispersal modes differ primarily in their spatial genetic patterns rather than overall relatedness levels. Moreover, the taxa-pair identity explained 86.9% of the total variance in the model (random effect variance = 0.003, residual variance = 4.26x10^{-4}). Despite the strong taxa structuring, the dispersal mode × distance interaction was statistically significant, evidencing differences in spatial genetic patterns between dispersal modes in *Eriosyce*.

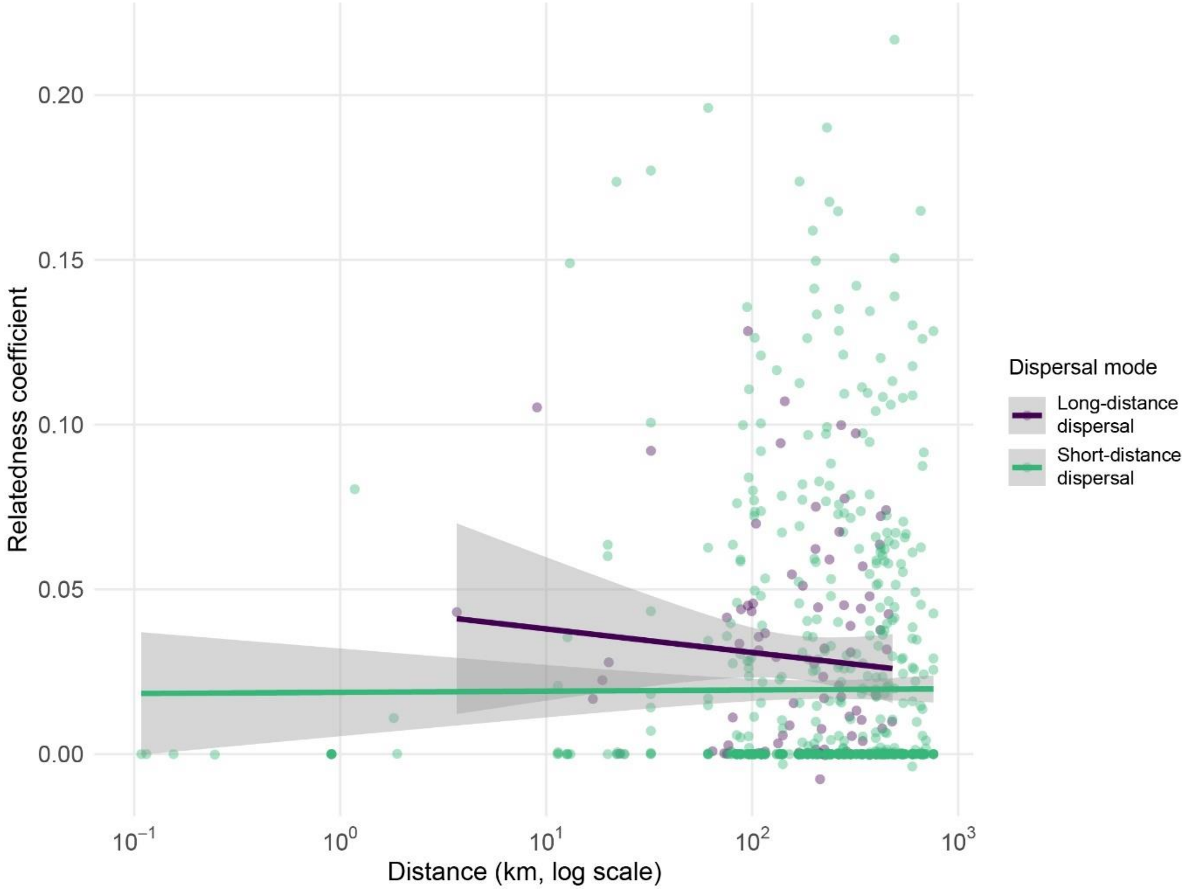

Figure 3.2. Distance-relatedness gradients for contrasting dispersal modes in *Eriosyce*. Long-distance dispersal taxa (purple) show declining relatedness with geographic distance, whereas short-distance dispersal taxa (green) maintain stable genetic similarity across space. Lines represent linear model predictions with 95% confidence intervals.

3.5 DISCUSSION

These findings supported the hypothesis of kin competition driving the evolution of long-distance dispersal in *Eriosyce*, with anemochorous taxa exhibiting a 43% reduction in the average genetic similarity among individuals compared to short-distance dispersal taxa. Significant differences in local relatedness were detectable at the landscape level, suggesting that the selection for escape from relatives operates at broader rather than finer scales. Furthermore, results revealed contrasting distance-relatedness gradients, with long-distance dispersal taxa showing a strong decrease in relatedness with distance, while short-distance dispersal taxa remained stable.

The specific mechanisms through which long-distance dispersal reduces kin competition in *Eriosyce* operate at multiple spatio-temporal scales that reflect both immediate ecological processes as well as long-term evolutionary processes. At an ecological scale, wind dispersal in the coastal terraces of the Atacama Desert takes advantage of the patterns of regular wind fluxes and the absence of topographic barriers (Schween et al., 2020). Wind enables diaspores to reach distances of several hundred meters to tens of kilometers (Nathan et al., 2002). These events of extreme dispersal can effectively spatially segregate related individuals, reducing the intensity of local competition for limited resources (Duputié & Massol, 2013). Since dispersal traits are highly heritable, individuals with increased dispersal abilities will be selected due to their ability to colonize areas with lower kin competition (Kubisch et al., 2013). This spatial segregation likely operates through repeated events of long-distance dispersal that result in genetic homogenization at landscape scales but not at finer scales (Kremer et al., 2012; Saladin et al., 2020). However, these contemporary patterns also reveal historic demographic factors, including possible bottleneck events during the colonization of coastal terraces and population fluctuations associated with climatic oscillations (Jangjoo et al., 2016). These historical processes have likely interacted with contemporary dispersal mechanisms to shape the genetic landscape (Wyatt et al., 2021), where long-distance dispersal provides enhanced capabilities that facilitate colonization of new habitats (Wu et al., 2023).

The existence of coastal terraces, representing large and empty or scarcely vegetated habitats, may have provided ecological opportunities for *Eriosyce* taxa. As such, the reduced competition in these habitats was likely more suitable for colonization (Yu & Wilson, 2001). Colonizing novel habitats often implies niche shifts enabling the adaptation to the new habitat conditions (Villaverde et al., 2017), which can be achieved by release from competitive pressures (Stroud & Losos, 2016). At decreased levels of competition —whether it be with relatives or no-relatives— the likelihood of survival increases during early stages of colonization, even for suboptimal individuals (Rey et al., 2017). Consequently, long-distance dispersal not only reduced kin competition but may also have facilitated adaptation to novel habitat conditions with reduced local competition (Ronce, 2007). Conversely, short-distance dispersal limits the ability to escape kin competition and colonize novel habitats, but enables the exploitation of suitable microclimatic conditions (Gomes et al., 2021). Since short-distance dispersal *Eriosyce* taxa are microhabitat specialists, this strategy enables the exploitation of stable microclimatic conditions. Therefore, the evolution of contrasting dispersal modes in *Eriosyce* can be understood as a fundamental trade-off between escaping local competition and maintaining specialized local adaptations. In this sense, both evolutionary strategies could be considered effective solutions to address kin competition under different ecological contexts.

Regarding the scale-dependency of the effects observed for relatedness relationships, results suggest that genetic patterns are more clearly manifested at broad spatial scales. These differences probably emerge at the landscape scale as they represent the accumulated effects of multiple dispersal events throughout the evolutionary time (Williams et al., 2016). At fine scales, individual variability and occasional dispersal events may mask differences between contrasting dispersal mode (McDevitt et al., 2013). Additionally, demographic noise such as founder effects and genetic drift can overcome dispersive signals (Hallatschek et al., 2007). As such, the net effect of these dispersal modes can only be revealed when considering the integration of different generations at the landscape level. The intrinsic differences between biotic and abiotic dispersal vectors can also account for this scale-dependent effect (Nathan & Muller-Landau, 2000). Wind dispersal can enable anemochorous taxa to reach distances of tens of kilometers in extreme dispersive events (Nathan et al., 2002), which are evident exclusively at a landscape scale. Animal vectors with reduced home ranges, on the other hand, rarely reach distances of hundreds of meters (Cordero et al., 2021; Wotton et al., 2016), explaining the homogeneity at every spatial scale analyzed.

The decrease in relatedness with distance in long-distance dispersal *Eriosyce* taxa evidences effective gene flow throughout the evolutionary time (Jin et al., 2024). Conversely, the absence of relatedness gradient in short-distance dispersal taxa indicates reduced gene flow and more localized genetic structure (Gelmi-Candusso et al., 2017). These gradients provide empirical evidence for the theoretical predictions on the different effects of contrasting dispersal modes. The negative correlation between relatedness and distance in long-distance dispersal taxa suggests effective connectivity among populations, also reducing risks of extinction (Sato et al., 2006). The absence of gradient in short-distance dispersal taxa, however, implies higher isolation among populations, potentially increasing the vulnerability to local perturbations (Gelmi-Candusso et al., 2017). Thus, these differences in connectivity can influence the ability of recolonization under scenarios of local extinctions. Dispersal promotes gene flow among habitat patches and is crucial for recolonizing suitable vacant habitat, maintaining genetic diversity, and mitigating extinction risk (Stevens et al., 2018; Van Schmidt & Beissinger, 2020). Additionally, these contrasting patterns of gene flow have opposing effects on local adaptation: while long-distance dispersal taxa may experience gene flow that constrains local adaptation, short-distance dispersal taxa may have evolved population-specific adaptations due to their genetic isolation.

Kin competition represents a fundamental ecological challenge as genetically related individuals compete for the same limited resources, reducing the fitness of all related individuals (Dudley et al., 2013). This selective pressure has driven the evolution of contrasting dispersal modes in *Eriosyce* as alternative solutions to the same ecological problem. According to classical dispersal theory, long-distance dispersal evolves when the benefits of escaping local competition outweigh the costs of colonization uncertainty (Ronce, 2007). The lower relatedness values observed in long-distance dispersal taxa demonstrate that wind dispersal effectively spatially segregates related individuals, representing an evolutionary solution to the kin competition problem. Conversely, short-distance dispersal taxa have evolved an alternative strategy where the costs of uncertain dispersal favor local retention and microhabitat specialization, despite maintaining higher levels of relatedness and potential competition.

3.6 CONCLUSION

Kin competition as a selective driver for dispersal evolution has important implications for understanding genetic diversity patterns in natural populations. The results suggest that different dispersal modes in *Eriosyce* represent alternative evolutionary solutions that balance the uncertainty costs of colonization against the benefits of escaping local competition. This balance may influence the adaptive capacity of populations, since long-distance dispersal promotes extensive gene flow, potentially limiting local adaptation. Conversely, short-distance dispersal may facilitate the evolution of specific adaptations to microhabitats, although increasing the risk of local extinction. Furthermore, the negative correlation between relatedness and distance in long-distance dispersal taxa revealed that increased dispersal effectively segregates relatives in space. The absence of this pattern in short-distance dispersal taxa suggests reduced gene flow and stronger local genetic structure. These contrasting patterns demonstrate how ecological context shapes the relative importance of kin competition in dispersal evolution.

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4. CHAPTER IV: MULTI-DIMENSIONAL ENVIRONMENTAL HETEROGENEITY DRIVES CONTRASTING DISPERSAL STRATEGIES IN ATACAMA DESERT HABITATS

4.1 ABSTRACT

The evolution of seed dispersal modes can be shaped by environmental variability across space and time, as different spatio-temporal patterns of resource availability and environmental stress select for contrasting dispersal strategies. In the coastal Atacama Desert, closely related taxa in the genus *Eriosyce* (Cactaceae) have evolved contrasting dispersal modes: long-distance dispersal taxa inhabit coastal terraces while short-distance dispersal taxa inhabit rocky outcrops. To examine whether these environmental differences have driven the selection of these different dispersal modes, I developed four environmental indices using edaphic, climatic, topographic, and vegetation variables that measured resource availability, environmental stress, spatial heterogeneity, and temporal heterogeneity for both habitat types. Coastal terraces showed significantly higher resource availability (elevated soil water content, organic carbon, total nitrogen), but also greater environmental stress (higher potential evapotranspiration, temperature extremes) compared to rocky outcrops, creating a high-risk, high-reward environment. Rocky outcrops exhibited much greater spatial variation, providing diverse microclimates within small areas. Although temporal variability was similar between habitats, it was the strongest organizing factor across the entire landscape. These environmental patterns explain the evolution of divergent dispersal strategies. Coastal terraces favor wind dispersal due to their homogeneous areas with unpredictable resource pulses, requiring long-distance escape from harsh conditions. Conversely, rocky outcrops promote short-distance dispersal through high spatial variation that provides nearby suitable microhabitats accessible via targeted dispersal.

4.2 INTRODUCTION

Spatial-temporal environmental variability is one of the main drivers of dispersal evolution, as the variability in resource availability and environmental stress creates trade-offs between local adaptation and dispersal, which influence demographic and evolutionary processes (Duputié & Massol, 2013; Levin et al., 2003). The interaction of climatic regimes, vegetation patterns, edaphic conditions, and topographic elements creates distinct microhabitats with varied quality (Franklin et al., 2000), imposing costs and benefits for different dispersal strategies (Schupp et al., 2010). Multiple environmental variables shape habitat variability: precipitation patterns influence water availability (Loik et al., 2004), soil properties mediate the retention of resources and their availability (McCarty et al., 2016), while topographic features determine both local climatic conditions and resource distribution (Baldeck et al., 2013; Niu et al., 2019). This environmental variability represents opportunities for the colonization of high-quality habitats, but may also imply high dispersal costs (Ronce, 2007). In this sense, the colonization of novel habitats often requires the development of specialized traits that enable both reaching and surviving in these habitats (Villaverde et al., 2017). Consequently, the selection of dispersal modes represents a trade-off between the risks of local extinction, colonizing novel habitats, and dispersal costs (Ronce, 2007). As such, those environments with a high degree of variability tend to promote long-distance dispersal, since increased dispersal facilitates the colonization of high-quality habitats, reducing the risks of local extinction, thereby compensating for dispersal costs (Duckworth, 2012).

From an evolutionary perspective, understanding the role of environmental variability implies analyzing how different environmental factors interact to create selective pressures that favor either precision dispersal in spatially complex environments or escape dispersal in temporally unpredictable landscapes. In the case of plants, different environmental dimensions —from edaphic and climatic conditions to vegetation patterns— influence habitat quality and its effects on dispersal modes (Nathan et al., 2002). However, the relationship between these environmental dimensions is usually not straightforward, requiring multi-dimensional approaches that consider both biotic and abiotic factors (Cadotte & Tucker, 2017; Kraft et al., 2015). The relative importance of different environmental factors can be different between species and ecological contexts, generating environmental gradients that favor different dispersal modes (Bullock et al., 2017).

Temporal variation in environmental conditions is another important dimension of habitat variability influencing dispersal evolutionary processes, particularly in arid ecosystems where resource availability can strongly vary across timescales (Chesson, 2000; Siepielski et al., 2009). This variability is influenced by predictable seasonal changes and stochastic events, such as variations in precipitation, temperature fluctuations, and changes in moisture availability over time (Sala et al., 2012). In arid environments, the interannual variability of precipitation, as well as extreme climatic events, lead to important fluctuations in the availability of resources that can influence dispersal selection (Angert et al., 2009; Jump & Peñuelas, 2005). This temporal variability can favor the evolution of different dispersal modes through the selection for strategies that optimize the responses to environmental unpredictability (Duputié & Massol, 2013). As such, more variable environments can promote dispersal modes that facilitate resource tracking and bet hedging (Ronce, 2007).

The genus *Eriosyce* (Cactaceae) provides an ideal study system to examine how the spatio-temporal variability of habitat quality drives dispersal evolution, since closely related taxa inhabiting the Huasco Valley of the Atacama Desert have evolved contrasting dispersal modes. Long-distance dispersal taxa inhabit coastal terraces, while short-distance dispersal taxa inhabit rocky outcrops (Kattermann et al., 1994). Coastal terraces constitute empty or scarcely vegetated habitats with variable environmental conditions (Armijo et al., 2015), whereas rocky outcrops represent discrete microhabitats with limited size that provide stable microclimatic conditions (Fitzsimons & Michael, 2017). These contrasting habitats exhibit different patterns of spatio-temporal variability that may have selected for different dispersal modes, since coastal terraces are large and open environments with higher exposure to climatic fluctuations, while rocky outcrops create mosaics of heterogeneous conditions (Nathan & Muller-Landau, 2000). The remarkable geological and climatic stability of the Atacama Desert since the Pleistocene makes it particularly valuable for evolutionary studies, as contemporary environmental patterns likely represent reliable indicators of the historical selective pressures that drove the evolution of short- and long-distance dispersal in *Eriosyce* (Hartley et al., 2005; Rodríguez et al., 2013).

Since habitat quality is determined by multiple environmental factors that vary across space and time, I hypothesize that spatio-temporal variability has driven the evolution of contrasting dispersal modes in *Eriosyce* through differential selective pressures: high temporal variability and spatial homogeneity favor long-distance dispersal to escape unfavorable conditions and track resources, while high spatial heterogeneity with lower temporal variability favors short-distance dispersal for precise microhabitat selection. Consequently, I predict that coastal terraces will exhibit higher temporal variability and environmental stress but lower spatial heterogeneity compared to rocky outcrops, favoring long-distance dispersal in coastal terraces and short-distance dispersal in rocky outcrops. Therefore, here, I aim to characterize and quantify environmental variables for coastal terraces and rocky outcrops where populations of *Eriosyce* taxa with contrasting dispersal modes inhabit.

4.3 METHODS

4.3.1 MULTI-DIMENSIONAL ENVIRONMENTAL CHARACTERIZATION

Although habitat characterization can be assessed through multiple approaches, most environmental indices focus on specific aspects (e.g., habitat suitability for individual taxa, fragmentation metrics, or productivity measures) rather than integrating the multiple environmental dimensions that can be relevant for dispersal evolution. Therefore, I employed a multi-dimensional approach to characterize the habitats occupied by long- and short- distance dispersal taxa and their role in the evolution of contrasting dispersal modes. I characterized environmental variability by developing four theoretical indices that represent different dimensions of habitat variation in deserts: i) Resource Availability, ii) Environmental Stress, iii) Spatial Heterogeneity, and iv) Temporal Heterogeneity. The Resource Availability Index integrated variables representing habitat productivity and resource conditions. The Environmental Stress Index comprised variables representing physiological limitations. The Spatial Heterogeneity Index quantified the environmental variation within habitats, while the Temporal Heterogeneity Index measured the environmental variability across timescales that affect plant establishment and survival.

For the construction of the indices, I considered edaphic, climatic, topographic, and vegetational variables. For each individual occurrence, environmental variable values were extracted at the exact geographic coordinates where the taxa were recorded. Edaphic variables were retrieved from the SoilGrids dataset (Poggio et al., 2021), considering coarse fragments, soil texture (percentage of sand, silt, and clay), and chemical properties (pH, cation exchange capacity, organic carbon, and total nitrogen). Additionally, I included water content at field capacity, recovering data from OpenLandMap (Hengl & Gupta, 2019) to determine baseline water availability. Since edaphic data contain multiple bands (different soil depths), I averaged values from bands over the top 60 cm soil depth. Furthermore, topographic variables (elevation and slope) were obtained from the Shuttle Radar Topography Mission digital elevation model (Farr et al., 2007), providing critical information on terrain configuration that influences solar radiation incidence, water runoff patterns, and microclimate conditions. On the other hand, the climatic variables were obtained from the CHELSA V2.1 database (Karger et al., 2017) for the period 1981-2010. I selected bioclimatic variables that represent both average conditions and climatic extremes: annual mean air temperature (bio1), mean diurnal air temperature range (bio2), temperature seasonality (bio4), mean daily maximum air temperature of the warmest month (bio5), mean daily minimum air temperature of the coldest month (bio6), annual precipitation amount (bio12), precipitation seasonality (bio15), and mean monthly precipitation amount of the driest quarter (bio17). Lastly, vegetation productivity patterns were characterized using 39-year Landsat time series (1984-2023) (Center, 2020a, 2020b, 2020c) to calculate NDVI metrics representing productivity baselines, temporal variability, and climate sensitivity.

Before the index construction, all the variables were standardized using z-score transformation. Multicollinearity within each index was assessed using Variance Inflation Factor (VIF) analysis with iterative variable removal until all VIF values were < 5. After VIF analysis, the final variables retained for each index were: Resource Availability Index (soil water content, soil organic carbon, and total nitrogen); Environmental Stress Index (potential evapotranspiration, bio5, bio6, and bio17); Spatial Heterogeneity Index (clay content, sand content, slope, and NDVI range); and Temporal Heterogeneity Index (seasonal amplitude, interannual variability, bio4, bio15, and NDVI coefficient of variation). The indices were calculated as arithmetic means of the standardized variables. Additionally, I evaluated the independence between the indices using correlation analysis (maximum $|r| = 0.47$), confirming that each index measured distinct environmental dimensions.

4.3.2 STATISTICAL ANALYSIS

I assessed environmental differentiation between coastal terraces and rocky outcrops using different complementary analytical approaches. Environmental differentiation between coastal terraces and rocky outcrops was assessed by comparing environmental indices between habitat types using Welch's t-tests (normality assumptions were previously evaluated via Shapiro-Wilk tests). For each case, I quantified the effect sizes for habitat comparisons using Cohen's d, employing the False Discovery Rate method for multiple comparisons. Furthermore, I evaluated overall environmental differentiation using Permutational Analysis of Variance (PERMANOVA) based on Euclidean distances (parametric assumptions were previously confirmed to be violated). This analysis was conducted to assess the overall distinction of coastal terraces and rocky outcrops as predicted by the hypothesis that these represent distinct selective environments.

Furthermore, I quantified the spatial structure of environmental indices using Moran's I statistic to detect clustering patterns in environmental conditions across the landscape, testing whether environmental variability creates the patched landscape structure predicted to favor different dispersal strategies. For this, I constructed spatial neighborhoods using k-nearest neighbors (k=6) based on geographic coordinates, using row-standardized weights to create spatial weights matrices. I calculated Moran's I for each environmental index and tested for significance using permutation tests (9,999 permutations). Values of Moran's I > E(I) indicate positive spatial autocorrelation (environmental clustering), while values < E(I) indicate negative autocorrelation (environmental dispersion).

Non-metric Multidimensional Scaling (NMDS) was conducted to explore how coastal terraces and rocky outcrops are segregated in the multidimensional environmental space and to identify the main axes of environmental variation. This approach enables testing the prediction that these habitats represent distinct environmental contexts that have shaped dispersal evolution. NMDS was performed based on Euclidean distances, which were calculated from the standardized environmental indices. The dimensionality was set to k=2 and maximum iterations were set to 100. Stress values < 0.15 were considered acceptable for interpretation. Environmental vectors were fitted to the ordination with 999 permutations to test significance, revealing which environmental dimensions were the most important organizing the environmental space.

At last, I employed Random Forest classification to validate the predictive capacity of the environmental indices for habitat discrimination, testing whether these environmental dimensions effectively capture the key differences that have driven dispersal evolution. The model was constructed with 1,000 trees, using habitat type as the response variable and the environmental indices as predictors. Variable importance was quantified using both Mean Decrease in Accuracy and Mean Decrease in Gini metrics. Model performance was evaluated using out-of-bag error rates and confusion matrices, which provide independent validation of the environmental framework's capacity to distinguish habitat types.

4.4 RESULTS

4.4.1 MULTI-DIMENSIONAL ENVIRONMENTAL DIFFERENTIATION BETWEEN COASTAL TERRACES AND ROCKY OUTCROPS

Significant environmental differentiation was detected between coastal terraces and rocky outcrops across multiple environmental dimensions, although patterns varied considerably among the four indices (Fig. 3.1). The Resource Availability Index demonstrated that coastal terraces exhibit significantly higher resource availability compared to rocky outcrops (coastal mean = 0.129 ± 0.37 SD, rocky mean = -0.108 ± 0.37 SD; t = 3.156, p = 0.002, Cohen's d = 0.637), representing a medium-to-large effect size. Furthermore, the Environmental Stress Index revealed that coastal terraces experience significantly greater environmental stress than rocky outcrops (coastal mean = 0.094 ± 0.33 SD, rocky mean = -0.078 ± 0.35 SD; t = 2.601, p = 0.011, Cohen's d = 0.496).

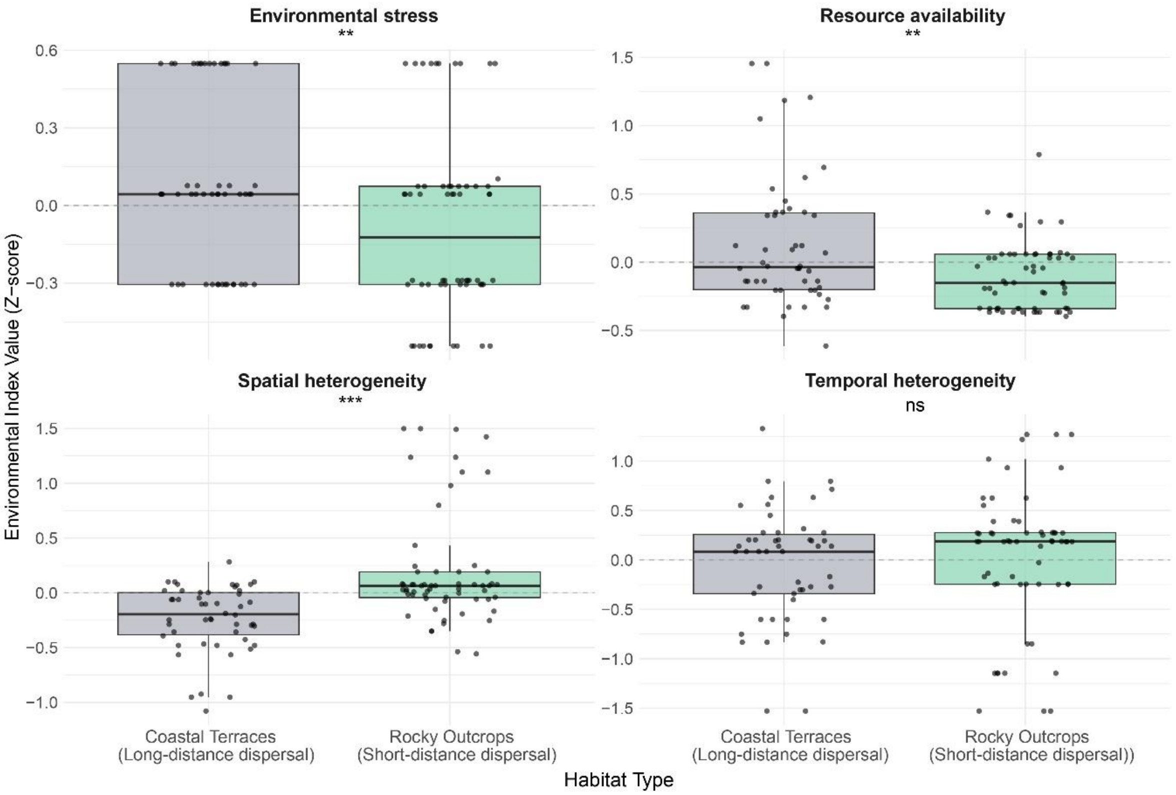

Figure 4.1. Environmental index values across habitat types. Boxplots showing standardized values (z-scores) for environmental indices. Gray boxes represent coastal terraces (long-distance dispersal taxa), green boxes represent rocky outcrops (short-distance dispersal taxa). Points show individual observations. Asterisks indicate statistical significance: ** $p < 0.01$, *** $p < 0.001$, ns = not significant.

On the other hand, the Spatial Heterogeneity Index indicated that rocky outcrops exhibit significantly greater spatial environmental variation than coastal terraces (coastal mean = -0.231 ± 0.43 SD, rocky mean = 0.193 ± 0.43 SD; $t = -5.404$, $p < 0.001$, Cohen's $d = -0.990$), representing a large effect size. Lastly, the Temporal Heterogeneity Index showed no significant differences between habitat types (coastal mean = -0.048 ± 0.60 SD, rocky mean = 0.040 ± 0.60 SD; $t = -0.732$, $p = 0.466$, Cohen's $d = -0.138$) (Fig. 3.2). Additionally, multivariate analysis revealed highly significant environmental differentiation between habitat types when all indices were considered simultaneously ($R^2 = 0.075$, $F_{1,108} = 8.800$, $p < 0.001$), confirming that coastal terraces and rocky outcrops represent environmentally distinct habitat types.

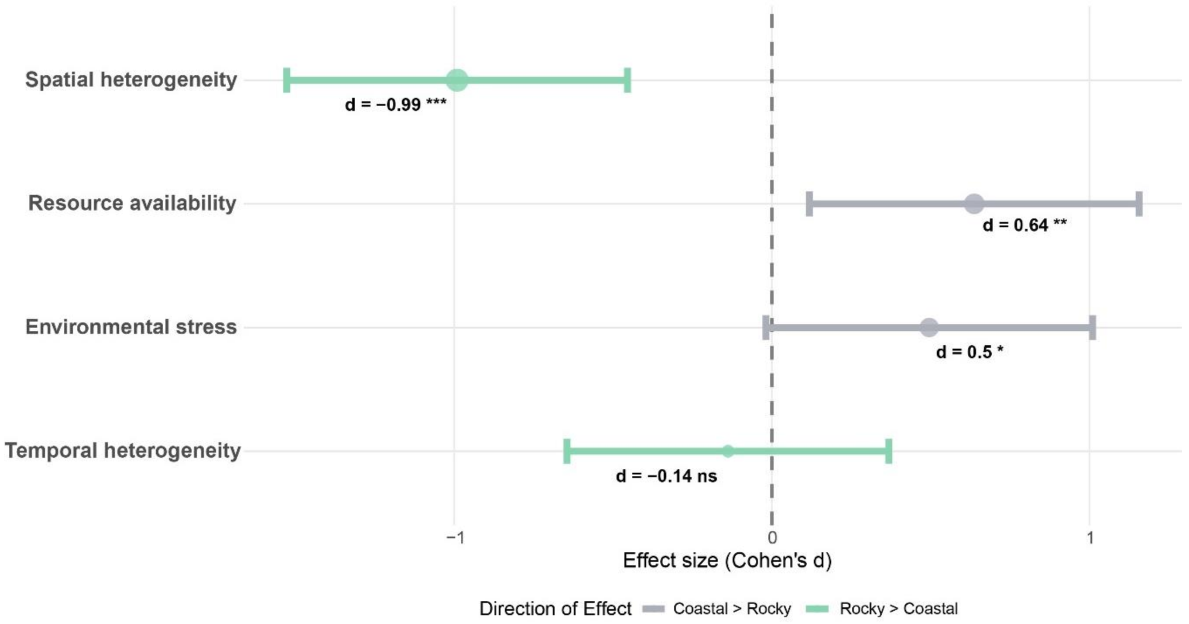

Figure 4.2. Environmental differentiation effect sizes between coastal terraces and rocky outcrops. showing Cohen's d values with 95% confidence intervals for the environmental indices. Positive values indicate higher values in coastal terraces; negative values indicate higher values in rocky outcrops. Significance levels: *p < 0.05, **p < 0.01, ***p < 0.001, n.s. = not significant.

4.4.2 SPATIAL CLUSTERING OF ENVIRONMENTAL CONDITIONS

Spatial autocorrelation analysis revealed highly significant clustering patterns for all the environmental indices ($p < 0.001$ for all cases). Environmental Stress showed almost perfect spatial clustering (Moran's I = 0.999), indicating distinct stress and favorable areas across the landscape. Spatial Heterogeneity showed strong clustering (Moran's I = 0.817), with heterogeneous and homogeneous areas forming discrete spatial units. Temporal Heterogeneity and Resource Availability indices showed moderate clustering patterns (Moran's I = 0.402 and 0.263, respectively).

4.4.3 ENVIRONMENTAL INDEX VARIATION AMONG *ERIOSYCE* TAXA

Environmental indices at the taxa level showed distinct patterns of habitat specialization within each dispersal mode (Table 4.1). Among long-distance dispersal taxa, *E. duripulpa* exhibited the highest resource availability (mean = 0.11 ± 0.53) and environmental stress (mean = 0.17 ± 0.11), occupying the coastal terrace sites with the highest resource availability, but at the same time the harshest conditions. *Eriosyce napina* showed more moderate environmental conditions across indices, with intermediate values for resource availability (0.14 ± 0.44) and environmental stress (0.12 ± 0.43), indicating occupation of intermediate coastal sites. Both taxa occupied spatially homogeneous environments as expected for coastal terraces.

On the other hand, short-distance dispersal taxa showed greater variation in environmental conditions despite sharing rocky outcrop habitats. *Eriosyce crispa* inhabited the most spatially heterogeneous environments (mean = 0.37 ± 0.67), occupying rocky outcrops with intermediate resource availability (-0.16 ± 0.30) and low environmental stress (-0.14 ± 0.29). *Eriosyce vallenarensis* occupied sites with moderate spatial heterogeneity (0.13 ± 0.07) but experienced the highest temporal variability among all taxa (0.72 ± 0.60). *Eriosyce villosa* showed the lowest resource availability (0.05 ± 0.15) and temporal heterogeneity (-0.95 ± 0.73), reflecting the occupation of microsites with stable conditions but also limited resources. Lastly, *E. crispa* var. *carrizalensis* exhibited an unusual pattern for a short-distance dispersal taxa, occupying sites with very low spatial heterogeneity (-0.02 ± 0.15) and the lowest environmental stress (-0.29 ± 0.00).

Taxa	**Resource availability (mean ± SD)**	**Temporal heterogeneity (mean ± SD)**	**Spatial heterogeneity (mean ± SD)**	**Environmental stress (mean ± SD)**
Long-distance dispersal / Coastal terraces				
E. duripulpa	0,11 ± 0,54	0,09 ± 0,44	-0,51 ± 0,26	0,05 ± 0,01
E. napina	0,14 ± 0,44	-0,14 ± 0,63	-0,05 ± 0,14	0,12 ± 0,43
Short- distance dispersal / Rocky outcrops				
E. crispa	-0,16 ± 0,30	0,28 ± 0,21	0,37 ± 0,67	-0,14 ± 0,29
E. crispa var. *carrizalensis*	0,04 ± 0,04	-0,37 ± 0,25	-0,02 ± 0,15	-0,29 ± 0

E. vallenarensis	-0,25 ± 0,10	0,72 ± 0,60	0,13 ± 0,07	-0,31 ± 0
E. villosa	0,05 ± 0,15	-0,95 ± 0,73	-0,05 ± 0,07	0,55 ± 0

Table 4.1. Taxa-level environmental index values showing mean ± standard deviation for each of four environmental indices. All values are z-score standardized.

4.4.4 VARIABLE IMPORTANCE HIERARCHY AND PREDICTIVE VALIDATION

Random Forest classification achieved an accuracy of 87.3% in differentiating habitat types. Variable importance analysis indicated a distinct hierarchy: Spatial Heterogeneity (importance = 56.142) was the most important discriminator, followed by Temporal Heterogeneity (42.074), Environmental Stress (41.641), and Resource Availability Index (38.283). The confusion matrix showed that rocky outcrops were classified with 90% accuracy, while coastal terraces attained 84% accuracy. All four environmental indices showed substantial importance for habitat classification (all > 38). The high overall accuracy demonstrates effective habitat discrimination using the environmental framework.

4.4.5 ENVIRONMENTAL SPACE ORGANIZATION AND MULTIVARIATE PATTERNS

NMDS ordination successfully represented environmental relationships with acceptable stress (0.123) and significant habitat differentiation (PERMANOVA: $R^2 = 0.075$, $F = 8.800$, $p < 0.001$). Environmental vector analysis showed that Temporal Heterogeneity was the strongest organizational axis of environmental space ($R^2 = 0.984$, $p < 0.001$), followed by Spatial Heterogeneity ($R^2 = 0.6785$, $p < 0.001$), Resource Availability Index ($R^2 = 0.483$, $p < 0.001$), and Environmental Stress ($R^2 = 0.339$, $p < 0.001$).

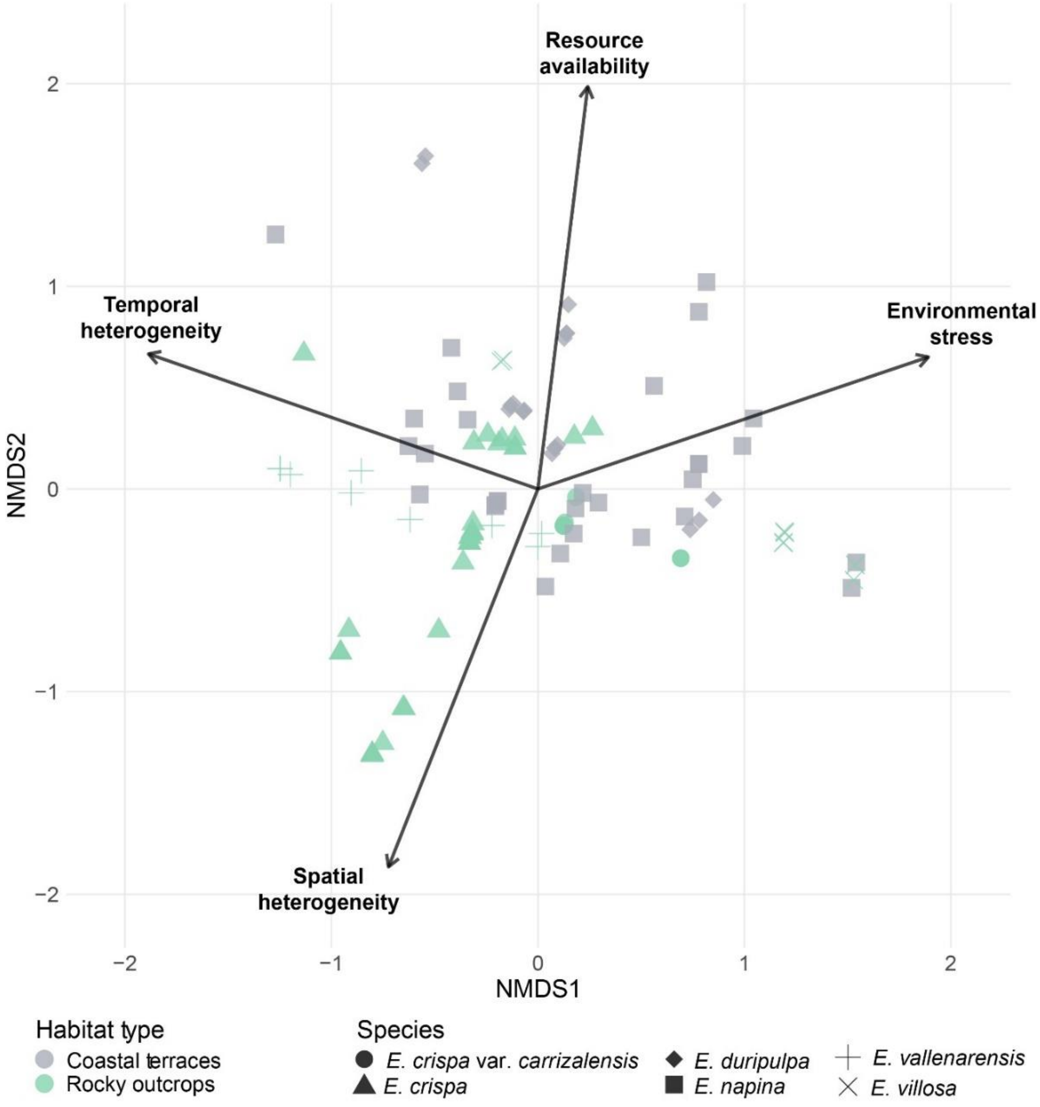

Figure 4.3. NMDS ordination of the environmental space organization, showing two-dimensional representation of environmental relationships among *Eriosyce* individuals (stress = 0.123). Arrows indicate significant environmental vectors ($p < 0.001$).

4.5 DISCUSSION

These findings indicate that coastal terraces and rocky outcrops from the Atacama Desert represent ecologically different habitats that differ in multiple environmental dimensions simultaneously. Multivariate analysis confirmed this differentiation, indicating that these differences are not explained by a single variable but involve complex patterns of environmental variation. This multi-dimensional differentiation suggests that both habitats have been subject to different selective pressures throughout the evolutionary time. Given the magnitude of these differences and the geologic stability of the Atacama Desert over millions of years (Hartley et al., 2005), contemporaneous environmental patterns likely reflect the historical conditions that have influenced the evolution of dispersal modes in *Eriosyce*.

The environmental indices captured different dimensions of habitat variation between coastal terraces and rocky outcrops. The Resource Availability Index showed that coastal terraces have significantly higher productivity capacity than rocky outcrops. This result reflects the geomorphological processes where fog and precipitation accumulate in terraces, creating periodic resource pulses. On the other hand, the Environmental Stress Index revealed that coastal terraces exhibited significantly higher stress levels despite their resource abundance, creating the high-risk, high-reward conditions. Furthermore, the Spatial Heterogeneity Index showed that rocky outcrops are subject to significantly more environmental variation within small areas, creating microhabitat mosaics. Finally, the Temporal Heterogeneity Index showed no significant differences between habitat types, indicating that both experience similar regional-scale temporal variability driven by climatic cycles. These patterns have also been observed in other arid ecosystems. For example, in deserts of North American (Sonora, Chihuahuan, Mojave), resource pulses generally concentrate in geomorphological catchments such as alluvial terraces and ephemeral channels, due to localized moisture accumulation (Noy-Meir, 1973; Reynolds et al., 2004; Schwinning & Sala, 2004). Similarly, in deserts of Israel, temporal variability in precipitation and localized water availability generates episodic pulses of resources that influence plant establishment and growth (Tielbörger & Kadmon, 2000). These patterns are similar to those observed in the Atacama Desert, where coastal terraces concentrate resources episodically, while rocky outcrops generate fine-scale microhabitat mosaic.

These common environmental patterns across geographically different arid regions provide insights into how resource distribution and stress–heterogeneity trade-offs operate.

The most notable pattern revealed was the simultaneous occurrence of increased resource availability and environmental stress in coastal terraces relative to rocky outcrops. This suggests a trade-off where more productive environments also impose the highest physiological costs (MacTavish & Anderson, 2020). Coastal terraces undergo intense resource pulses from occasional precipitation and fog accumulation (Cáceres et al., 2007; Larraín-Barrios et al., 2018); nonetheless, their extreme exposure generates elevated evapotranspiration, severe hydric stress during dry periods, and pronounced thermal fluctuations (Lobos-Roco et al., 2021). Thus, coastal terraces constitute high-risk, high-reward ecosystems wherein plants exploit abundant resources intermittently, while enduring harsh environmental conditions predominantly. This selective environment has favored geophytic life-history traits that enhances the ability of plants to uptake and store water through deep taproots during precipitation pulses, while reducing exposure to stressful conditions through minimally exposed or buried stems (e.g., Howard et al., 2019; Ofir & Kigel, 2003). Such specialized morphology in coastal *Eriosyce* taxa enables survival during prolonged dry periods and complements long-distance dispersal for the temporal escape of harsh conditions. Therefore, wind dispersal represents an adaptive solution to the environmental variability of coastal terraces, enabling both escape from adverse conditions and colonization of distant sites during favorable periods.

Complementing the resource-stress trade-off, spatial patterns reveal that rocky outcrops exhibited significantly higher spatial variation compared to coastal terraces. The irregular topography of rocky outcrops creates gradients of solar radiance, differential water retention capacities, soil accumulation, and microsites offering wind protection (Fitzsimons & Michael, 2017). This spatial variability enables the existence of multiple microsites with different microclimatic conditions within relatively small areas (García et al., 2020). In contrast, coastal terraces are relatively large and flat, generated by uniform processes of marine erosion, which result in edaphic and topographic conditions that are more homogeneous at the local scale (Armijo et al., 2015). Therefore, the higher spatial variability in rocky outcrops favors short-distance dispersal to suitable microhabitats in zoochorous taxa, while the lower spatial variability of coastal terraces enables stochastic movements by wind-mediated long-distance dispersal in anemochorous taxa.

At the landscape scale, the autocorrelation analysis revealed an extreme clustering of environmental stress, which indicates that the landscape is organized in discrete patches with well-defined boundaries between favorable and stressful areas. This spatial organization is the consequence of geomorphological, climatic, and topographic processes that have created a highly organized spatial mosaic (Bolliger et al., 2003; Temme & Veldkamp, 2009). The extreme clustering implies that similar conditions tend to spatially aggregate, creating "islands" of suitable conditions separated by areas with adverse conditions (Altermatt & Holyoak, 2012). This patchy landscape structure has important implications for dispersal selection (Lohmus et al., 2014; Vittoz & Engler, 2007), since plants must disperse over large distances to reach habitats with similar or better conditions in the case of long-distance dispersal taxa, or colonize nearby suitable microhabitats in the case of short-distance dispersal taxa (Green et al., 2022).

The NMDS ordination indicated that environmental space is organized along multiple independent gradients, confirming the multidimensional nature of the environmental differentiation between habitats. Despite the extreme spatial clustering of environmental stress, temporal heterogeneity was identified as the strongest organizational axis across the entire landscape, even though it showed no significant differences between habitat types. This suggests that while spatial clustering creates discrete patches of suitable conditions, temporal variability operates as a predominant environmental filter that structures variation throughout the landscape regardless of habitat type (Collins et al., 2018). This temporal dominance has important implications for dispersal evolution since long-distance dispersal taxa in coastal terraces must cope with unpredictable temporal fluctuations across large homogeneous areas (de Pedro et al., 2023; Snyder, 2011), while short-distance dispersal taxa in rocky outcrops can exploit spatial refugia that buffer against temporal variability (Buschke et al., 2020; Keppel et al., 2012). The multidimensional nature of environmental space indicates that habitat differentiation results from the interaction of several environmental factors rather than single environmental drivers, supporting the evolution of contrasting dispersal strategies as adaptive responses to different combinations of spatial and temporal environmental variability.

Although temporal heterogeneity showed no significant differences between habitat types, the remaining three environmental dimensions revealed clear differentiation patterns. By incorporating these environmental dimensions, these findings provide insight into the evolution of contrasting dispersal modes in *Eriosyce* as adaptive responses to different patterns of environmental variability. Coastal terraces, characterized by abundant resource availability and high environmental stress with spatial clustering of stress conditions, have favored wind-dispersal. Long-distance dispersal facilitates rapid escape under adverse conditions (Snyder, 2011) and the colonization of distant favorable habitats during resource pulse events (Chesson et al., 2004). In this sense, wind dispersal is especially advantageous in environments where conditions involve high resource-stress trade-offs (Chesson et al., 2004), requiring the capacity to colonize various distant sites during favorable opportunities (Hidalgo et al., 2016). In contrast, rocky outcrops, characterized by high spatial heterogeneity and more moderate resource and stress conditions, have promoted short-distance dispersal, enabling the precise deposition of seeds in suitable microhabitats within a heterogeneous mosaic (Gomes et al., 2021). This targeted dispersal strategy enhances the effective establishment and survival of local populations by optimizing microhabitat selection instead of depending on stochastic colonization events (Schupp et al., 2002).

4.6 CONCLUSION

These findings indicate that environmental variability is strongly associated with contrasting dispersal modes in *Eriosyce,* suggesting its potential role as an important selective pressure driving their evolution. Coastal terraces represent a high-risk, high-reward habitat characterized by abundant but unpredictable resource availability and severe environmental stress. The association between these environmental conditions and long-distance dispersal suggests that these large, homogeneous areas with extreme temporal fluctuations may have favored the evolution of long-distance dispersal, which would enable plants to escape adverse conditions and colonize distant favorable sites. Additionally, the spatial clustering of environmental conditions across the landscape implies that suitable habitats are separated by large distances, potentially making long-distance dispersal essential for survival and reproduction. In contrast, rocky outcrops provide spatially heterogeneous environments with diverse microclimates within small areas. The correspondence between this spatial variability and short-distance dispersal modes suggest that these multiple suitable microsites can be reached through short-distance, targeted dispersal by animals. Therefore, the lower environmental stress and more predictable resource availability in these refugia-like habitats reduce the need for long-distance escape, potentially favoring precision in microhabitat selection.

Notably, temporal heterogeneity was identified as the most important organizing factor across the landscape, despite showing no differences between habitat types. This reveals that while both habitats experience similar temporal variability, they differ fundamentally in how this variability can be managed. Long-distance dispersal taxa must cope with temporal fluctuations across homogeneous landscapes through dispersal, whereas short-distance dispersal taxa can use spatial refugia that mitigate temporal variability. These results highlight the importance of considering multiple environmental dimensions for the study of dispersal evolution. The complex interactions between resource availability, environmental stress, spatial heterogeneity, and temporal variability create different selective environments that cannot be understood by examining single variables.

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5. CHAPTER V: CONCLUDING REMARKS

This research revealed that dispersal evolution is influenced by multiple evolutionary drivers that operate simultaneously at different ecological and evolutionary scales (Figure 5.1). As such, the evolution of different dispersal modes in desert-dwelling taxa cannot be understood by relying on single factors but on the synergistic interaction of various selective pressures. These findings contradict initial theoretical predictions about the role of long-distance dispersal in inbreeding avoidance, suggesting that other evolutionary drivers have been more important in selecting for increased dispersal capabilities in *Eriosyce*. However, the results demonstrated that kin competition and environmental variability have played a critical role underpinning the evolution of contrasting dispersal modes in *Eriosyce* taxa inhabiting distinct habitat types.

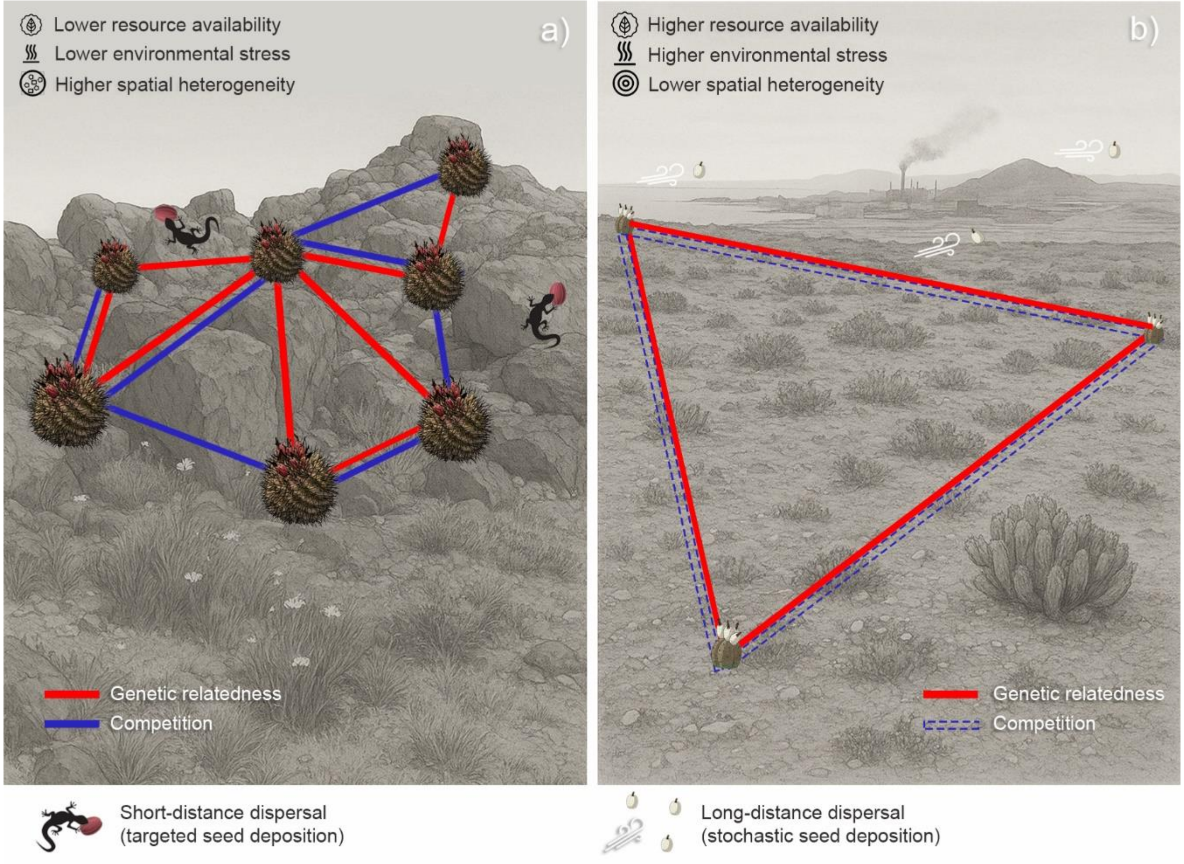

Figure 5.1. Conceptual framework of contrasting ecological and evolutionary patterns between *Eriosyce* dispersal strategies in the Atacama Desert. a) Rocky outcrops support zoochorous taxa with short-distance,

targeted seed dispersal by animal vectors, characterized by lower resource availability, reduced environmental stress, and higher spatial heterogeneity. These conditions promote intense kin competition (solid blue lines) and strong genetic relatedness networks (red lines). b) Coastal terraces harbor anemochorous taxa with long-distance, stochastic wind dispersal, experiencing higher resource availability, increased environmental stress, and lower spatial heterogeneity. This environment results in reduced kin competition (dashed blue lines) while maintaining genetic relatedness patterns.

Although unexpected, I observed interesting genetic patterns in *Eriosyce* taxa, providing insights into the possible mechanisms underlying the differences between contrasting dispersal modes. Due to the role of wind dispersal in spatially segregating related individuals, long-distance dispersal taxa were expected to exhibit reduced inbreeding levels and increased genetic diversity compared to short-distance dispersal taxa. However, long-distance dispersal taxa showed higher inbreeding levels than short-distance dispersal taxa, while genetic diversity was similar between these groups. This suggests that historical demographic processes may have influenced contemporary genetic patterns in anemochorous taxa, such as population bottlenecks and repeated founder effects. The effects of these historical processes are probably maintained by the ecological costs associated with the stochastic nature of wind dispersal in the Atacama Desert. Conversely, inbreeding in short-distance dispersal taxa has been likely reduced through complementary mechanisms of gene flow via pollination, representing an evolutionary solution to the genetic risks associated with the maintenance of suitable microhabitats.

Kin competition had an important role in driving dispersal evolution in *Eriosyce*, aligning with the initial theoretical predictions. Long-distance dispersal taxa exhibited lower mean relatedness compared to short-distance dispersal taxa, representing a significant reduction in genetic similarity. Moreover, long-distance dispersal taxa showed a significant decrease in relatedness with distance, while short-distance dispersal taxa maintained uniform genetic similarity. These results show that kin competition has driven the evolution of long-distance dispersal in *Eriosyce*, reducing local relatedness by increasing gene flow, although these effects were only detected at the landscape scale. Contrasting dispersal modes in *Eriosyce* taxa may constitute different evolutionary solutions, representing a trade-off between the benefits of escaping from local competition and the ecological costs associated with colonizing novel distant habitats. However, the apparent contradiction between reduced relatedness and high levels of inbreeding is noteworthy. Reduced relatedness evidences the historic effectiveness of long-distance dispersal in spatially segregating individuals, while increased inbreeding reflects severe demographic limitations during the colonization and establishment in coastal terraces. These demographic processes, associated with stochastic dispersal, likely led to the successful establishment of few genetic lineages, resulting in the mating between relatives within these limited founder populations. In this sense, long-distance dispersal taxa may successfully escape from parental patches, but the small number of individuals colonizing novel habitats promotes mating among themselves.

The multi-dimensional approach employed to characterize environmental variability of coastal terraces and rocky outcrops also confirmed the role of this selective pressure on the evolution of dispersal modes in *Eriosyce*. These findings revealed that coastal terraces represent high-risk but high-reward habitats that have favored the selection of long-distance dispersal. Anemochorous taxa must cope with severe extreme environmental conditions and abundant but unpredictable resource availability imposed by coastal terraces. However, their geophytic adaptations along with their increased dispersal capability enable the occupation of these homogeneous habitats. Conversely, rocky outcrops represent heterogeneous environments with diverse microclimatic conditions within small areas. These environments create suitable microhabitats that can be reached by zoochorous taxa due to the targeted deposition of seeds by animal species. Therefore, the lower environmental stress and more predictable resource availability have selected for short-distance dispersal in taxa inhabiting rocky outcrops. These results highlight the remarkable importance of ecological contexts in determining the selection of different dispersal modes.

The results derived from these different approaches provide a direct test of the main hypothesis that kin competition, inbreeding avoidance, and environmental variability have driven the evolution of contrasting dispersal modes in *Eriosyce*. From the evolutionary drivers examined, two of them received strong support. Kin competition was clearly supported, with long-distance dispersal taxa showing reduced mean relatedness and negative isolation-by-distance patterns, demonstrating effective spatial segregation of relatives. Environmental variability was also supported, with coastal terraces and rocky outcrops differing significantly in resource availability, environmental stress, and spatial heterogeneity, as predicted by theoretical models. However, inbreeding avoidance was not supported. Long-distance dispersal taxa showed higher inbreeding levels than short-distance taxa, opposite to theoretical predictions. This pattern appears to result from historical demographic processes during habitat colonization rather than contemporary dispersal benefits.

The differential support for these three drivers indicates that dispersal evolution in *Eriosyce* has been shaped primarily by ecological pressures (i.e., kin competition and environmental conditions) rather than genetic pressures (i.e., inbreeding avoidance). In the extreme conditions of the Atacama Desert, the benefits of escaping local competition and tracking favorable environments may outweigh the genetic costs of founder effects and population bottlenecks. Therefore, this research demonstrates that the relative importance of evolutionary drivers varies with ecological context, and that understanding dispersal evolution requires considering multiple selective pressures simultaneously rather than focusing on single factors.

Although the evolution of contrasting dispersal modes in *Eriosyce* was approached based on contemporary measures, they succeed in revealing both historical and contemporary processes. All empirical data collected represent contemporary observations that integrate evolutionary processes operating across multiple temporal scales. As such, the observed genetic patterns reflected historical demographic processes as well as contemporary patterns of gene flow. Environmental measurements were based on current habitat conditions but represent stable selective pressures that have operated continuously over the evolutionary time in this geologically stable area. Similarly, relatedness patterns integrate both historical colonization events and contemporary gene flow, while spatial genetic structure preserves signatures of both historical demographic bottlenecks and contemporary dispersal effectiveness. This temporal integration within contemporary data allowed the reconstruction of evolutionary processes that would otherwise remain undetectable in more dynamic environments.