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RESEARCH ARTICLE

Environmental and geographic predictors of seed plant diversity across South American terrestrial coastal lomas

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Abstract

Understanding the predictors of plant diversity gradients remains a major challenge in biogeography, particularly in understudied arid ecosystems where water availability is highly constrained. Coastal lomas—isolated, fog-fed vegetation oases distributed across the Peruvian and Chilean coastal deserts of South America–provide a unique system for examining how climate, topography, and geography shape plant diversity under extreme aridity. Here, we evaluated the geographic variation and predictors of the taxonomic and phylogenetic diversity of seed plants in these environments. We compiled the most comprehensive data set to date of 71 coastal lomas and used generalized linear models to assess latitudinal diversity gradients. We also evaluated the relative importance of environmental, topographic, and geographic predictors of plant taxonomic and phylogenetic diversity. We found that mean phylogenetic distance (MPD) exhibited non-linear relationships with latitude, and standardized phylogenetic diversity (PD) showed a weak variation with latitude, with both peaking in the hyper-arid core of the Atacama Desert. In contrast, standardized mean nearest taxon distance (MNTD) and species richness (adjusted by area) showed no significant association with latitude. Our results suggest that current climate, environmental heterogeneity, and geographical factors are the primary predictors of seed plant diversity in these regions. Plant species richness (adjusted by area) increased with aridity and cloud cover, while standardized PD decreased with aridity and distance to the coast while increasing with human footprint and northness. Standardized MNTD also increased with human footprint and northness, and decreased with increasing aridity and temperature. Standardized MPD increased with slope, temperature, northness, and aridity, and decreased with cloud cover, isothermality, and distance to the coast. These results suggest that environmental filtering is not the only macroecological process acting on plant diversity across coastal lomas and is often counterbalanced at different points in evolutionary time by factors associated with environmental heterogeneity, possibly reflecting the presence of climate refugia and habitats that promote species coexistence. Over evolutionary time, these factors may have significantly contributed to shaping the current composition of coastal lomas.

Highlights

- Plant diversity did not follow a simple latitudinal gradient across coastal lomas.
- Aridity predominantly explains variation in diversity facets, underscoring the importance of water availability in shaping coastal lomas.
- Evolutionary diversity reached its peak unexpectedly in the hyper-arid Atacama Desert.
- Plant communities were clustered into distinct assemblages that correspond to geographic barriers along the coastal desert.
- Coastal lomas reflect multiple ecological and evolutionary processes rather than environmental filtering alone.

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PENSOFT

Keywords

drylands, environmental heterogeneity, incongruent latitudinal gradient, islands, MPD, phylogenetic diversity, species richness

Introduction

Despite their aridity, drylands are home to 20% of global plant diversity (White and Nackoney 2003) and provide critical ecosystem services to more than 38% of the world's human population (Reynolds et al. 2007; United Nations Development Programme [UNDP] 2014). Yet, the biodiversity of these ecosystems is highly vulnerable to global change drivers, principally desertification and land-use change (Maestre et al. 2012), which may have cascading effects across different taxa and ecosystem functions (Maestre et al. 2016). Understanding the macroecological and macroevolutionary processes that generate, and maintain, biodiversity in the most arid ecosystems globally may therefore provide insights into the potential impacts of aridification on other ecosystems (Tariq et al. 2024).

The geological history of many drylands is closely coupled with the history of its major plant lineages, with major dryland clades having diversified more or less in synchrony between the Late Miocene (11.63–5.33 Ma) and the Early Pliocene (5.3–3.6 Ma) (Maestre et al. 2021). Drylands show elevated recent diversification rates, as revealed by short phylogenetic branch lengths, resulting in a lower than expected number of plant species compared to extratropical moist biomes (Neves et al. 2021). An example of this can be seen in Caatinga dry forests, an important center of diversification of the Cactaceae family (Ortega-Baes and Godínez-Alvarez 2006). In contrast to other drylands (e.g., Ulrich et al. 2016; Wang et al. 2017; Saiz et al. 2018; Luebert 2021; Maestre et al. 2021), the biodiversity patterns of coastal lomas — isolated vegetation oases distributed within the Peruvian–Chilean coastal desert — and the underlying macroecological and macroevolutionary processes are not well understood (Gonzales et al. 2023).

Coastal lomas are sustained by advective fog deposition that occurs on steep coastal slopes (< 1000 m a.s.l) and occur at elevations between 200 and 1,200 meters within the hyper-arid coastal desert. In addition, coastal lomas are influenced by El Niño Southern Oscillation (ENSO) events, which trigger periods of rainfall (Dillon and Rundel 1990; Cereceda et al. 2002). Furthermore, ENSO events impact the occurrence of marine fog across the coastal desert. During strong to extreme ENSO events, marine fog becomes more frequent during the summer months at ~20°S (del Río et al. 2018), which have also been associated with the intrusion of fog with more precipitable water (Eichler and Lodoño 2013). Fog condensation increases with altitude until the upper limit reaches the regional temperature inversion (Schemenauer and Cereceda 1993), reaching its maximum at intermediate elevations (Rundel and Mahu 1976). However, it can vary considerably, depending on proximity to the ocean, elevation, local topographic relief, and aspect (Larrain et al. 2002). The vegetation of coastal lomas is dominated by a mixture of annual and perennial grasses, herbs, shrubs, and small populations of trees (Dillon et al. 2003). Tree species like *Myrcianthes ferreyrae* (McVaugh) are endemic to the coastal desert and occur in just a few coastal lomas (Gonzales and Villasante 2019). The extreme climate of the coastal desert is thought to have partitioned the flora of the coastal lomas into three distinct assemblages (Dillon et al. 2003; Gonzales et al. 2023), with the hyper-arid zone between 18° and 22 S° potentially acting as a dispersal barrier (Rundel et al. 1991; Dillon 2005).

Among the ecological factors that have been hypothesized to shape diversity patterns in drylands (see Li et al. 2013; Bergholz et al. 2017; Maestre et al. 2021), aridity is the most important and is typically quantified with the Aridity Index (AI), which is the ratio of annual precipitation (P) to potential evapotranspiration (PET) (Maestre et al. 2016; Liu et al. 2019; Berdugo et al. 2020; Wion et al. 2020). Generally, plant species richness in drylands is strongly influenced by water availability (Li et al. 2013), sometimes even increasing with a decrease in water availability (Wang et al. 2018). In coastal lomas, water supply comes from two main sources: (i) ENSO events, whose brief periods of heavy rains stimulate plant growth and increase recruitment and diversity (Dillon and Rundel 1990; Jiménez et al. 1999; Muñoz-Schick et al. 2001; Pinto et al. 2001; Rundel et al. 2007; Tovar et al. 2018), resulting in marked differences in species composition across the distribution of coastal lomas (Dillon 1997; Pinto and Luebert 2009; Manrique et al. 2014), and (ii) advective coastal fog, which creates vegetation bands that are associated with higher levels of humidity (Schemenauer and Cereceda 1993; Larrain et al. 2002). At local spatial scales, plant species richness exhibits a hump-shaped relationship with elevation in northern Chilean lomas (Rundel and Mahu 1976) and net primary productivity (NPP) increases with elevation, which is usually associated with higher levels of humidity in coastal lomas (Ávila and Guevara 2006; Sotomayor and Jiménez 2008; Muenchow et al. 2013; Cuya 2016). Distance to the coast is another proxy for water availability that may positively affect plant diversity (Moat et al. 2021), as proximity of hills to the coast implies higher water availability, with steeper coastal hills intercepting more fog than flatter areas, where the stratus layer of fog dissipates. Other environmental factors, such as soil conditions (e.g., soil C:N, soil pH) and temperature (e.g., mean annual temperature), may mitigate or exacerbate the effects of water availability on plant diversity (Nunes et al. 2019; Zhang et al. 2024). However, the joint impacts of environmental predictors on plant diversity patterns across coastal lomas have yet to be assessed, as previous efforts have been limited by data availability (Manrique et al. 2014).

In parallel with average environmental conditions, environmental heterogeneity can also influence biodiversity

patterns across coastal lomas. In particular, environmental heterogeneity is crucial for maintaining the diversity of rare species in drylands (Liu et al. 2019). Environmental heterogeneity resulting from small-scale topographic variability creates microclimatic conditions that buffer communities from the direct effects of aridity (e.g., Keppel et al. 2018), preventing the loss of less stress-tolerant individuals or species (Stotz et al. 2021). Moreover, the climate that plants directly experience can be mediated by nurse plants, highlighting the role of plant cover in facilitating species coexistence — and, indirectly, ecosystem functioning (Beugnon et al. 2024) — in extreme environments such as deserts (Bertness and Callaway 1994; Maestre et al. 2009; Sotomayor and Drezner 2019; Kéfi et al. 2024). Lastly, small-scale microclimate variability in dryland soils contributes to the maintenance of community evenness and the type of species distribution (Ulrich et al. 2016). Because average environmental conditions can fail to capture the effects of abiotic or biotic facilitation, it is crucial to also consider environmental heterogeneity to deepen current understanding of the predictors of biodiversity patterns in water-limited ecosystems such as coastal lomas.

As expected, the species-area relationship (Rosenzweig 1995) has been shown to hold in coastal lomas ecosystems (Arana 2019), and is primarily influenced by spatial aggregation, species evenness, and plant cover (DeMalach et al. 2018; McGlinn et al. 2019). Unlike in other ecosystems, latitudinal diversity gradients (LDGs) in drylands may be less pronounced due to harsh environmental conditions (e.g., higher aridity, low annual precipitation). In the case of coastal lomas, plant species richness does not vary linearly with increasing latitude, possibly due to high levels of endemism and climatic barriers that maintain diversity at similar levels across the distribution of coastal lomas (Manrique et al. 2014). However, the proximate predictors underlying the spatial variation in plant diversity across coastal lomas, and their relative importance, have yet to be explored within the frameworks of other relevant macroecological theories, particularly that of water-energy dynamics (Hawkins et al. 2003; Vetaas et al. 2019).

In coastal lomas, taxonomic diversity has been the most frequently used measure of diversity, particularly at local spatial scales (Gonzales et al. 2023). Yet, other components of biodiversity can provide complementary insights into ecological mechanisms shaping community assembly, such as phylogenetic diversity and structure metrics. These metrics include Faith's phylogenetic diversity (Faith's PD), which is the sum of the branch lengths of the phylogenetic tree (Faith 1992), mean pairwise distance between species (MPD), and the pairwise distance between the closest relatives in an assemblage (MNTD) (Webb et al. 2002). As phylogenetic diversity is usually strongly and positively correlated with species richness (Cadotte and Davies 2016), the use of null models that maintain species richness constant while randomizing phylogenetic relationships facilitates comparison across assemblages (Kembel and Hubbell 2006; Mazel et al. 2016). Consequently, negative values of standardized phylogenetic diversity and structure metrics reflect phylogenetic clustering (i.e., when species are more closely related than expected by chance), while positive values of these same metrics reflect phylogenetic overdispersion (i.e., when species are more distantly related than expected by chance; Mazel et al. 2016). Evaluating the phylogenetic structure of coastal lomas may yield new insights into underlying macroevolutionary processes by identifying the relative importance of environmental filtering, limiting similarity, and niche conservatism, along with how they may shift over evolutionary time (Hardy and Senterre 2007; Mazel et al. 2016; Tucker et al. 2017).

Phylogenetic clustering occurs when evolutionary distances between the species in a community are lower than expected by chance and can result from environmental filtering. This can indicate that environmental conditions act as a filter that selects for species with certain trait values, or that a particular region has rapid speciation rates or slow extinction rates (Wiens and Graham 2005; Kraft et al. 2015). In contrast, limiting similarity (or phylogenetic overdispersion) occurs where evolutionary distances between species are greater than expected by chance, and indicates that niche partitioning and biotic processes decrease the evolutionary similarity of co-occurring species (Webb et al. 2002; Burns and Strauss 2011). Because of the fundamental role played by aridity in shaping biodiversity patterns in other drylands (e.g., Maestre et al. 2021), we expect environmental filtering to be the dominant process in determining plant diversity patterns across coastal lomas over evolutionary time, largely due to the rapid diversification in some plant lineages since the Late Pliocene (Maestre et al. 2021; Neves et al. 2021).

Here, we examined the environmental, topographic, and geographic factors, along with evaluating the underlying ecological mechanisms, that influence plant diversity across coastal lomas in South America. We expected that taxonomic and phylogenetic diversity would not vary consistently with latitude, reflecting variation in energy (i.e., annual potential evapotranspiration (PET), actual evapotranspiration (AET)) (Currie 1991; Cerezer et al. 2022) and water availability. More specifically, we expected that standardized MNTD, a metric that captures phylogenetic structure at shallower evolutionary timescales, will exhibit a non-linear latitudinal gradient due to recent mid-latitude plant diversification along the coastal desert, and standardized MPD, a basal metric associated with phylogenetic structure at deeper evolutionary timescales, will exhibit a non-linear relationship with latitude due to increasing aridity between 18°and 22°S, and increasing humidity towards the northern distribution of coastal lomas (Rundel et al. 1991). We further expected that environmental filtering, likely associated with water availability, will constrain plant taxonomic and phylogenetic richness (species richness and Faith's PD) in more arid areas across the distribution of coastal lomas. We therefore hypothesized that taxonomic and Faith's PD will increase with area, mean annual precipitation (MAP), cloud cover, soil properties, and environmental heterogeneity (slope), and decrease

with elevation, mean annual temperature (MAT), aridity, and distance to the coast (Arana 2019; Moat et al. 2021). In coastal lomas far from the coast with higher MAT and aridity yet lower MAP, cloud cover, lower soil N and pH and environmental heterogeneity, we expected that standardized MNTD and MPD will exhibit phylogenetic clustering (i.e., negative standardized MNTD and MPD values) (Swenson and Enquist 2009), while those closer to the coast with lower MAT and aridity, and higher MAP, cloud cover, soil N and pH and environmental heterogeneity will exhibit phylogenetic overdispersion or divergence (i.e., positive standardized MPD and MNTD values) (Swenson and Enquist 2009). Also, we hypothesized that as elevation increases in coastal lomas, aridity tends to decrease due to changes in advective fog flux (see Rundel et al. 1991; Cereceda et al. 2002). That is, we expected that phylogenetic diversity patterns across coastal lomas would be determined by contrasting underlying ecological processes, i.e., limiting similarity or environmental filtering, largely due to shifts in aridity and its proxies over evolutionary timescales. Finally, we aimed to identify distinct species assemblages across coastal lomas. We expected that the extreme aridity in the areas between most of the coastal lomas would act as an abiotic barrier to plant exchange (e.g., Dillon 2005; Pinto and Luebert 2009), resulting in distinct floristic groups (Dillon et al. 2003).

Methods

Study area

We evaluated 71 terrestrial coastal lomas, which extend through the Peruvian coastal desert and the Atacama Desert (hereinafter called coastal desert), extending continuously over 3,500 km from 7° to 30°S (Tago-Nakazawa and Dillon 1999) (Fig. 1, Suppl. material 1: fig. S1.3). The climate of the coastal desert is characterized by extreme aridity, short periods of heavy rainfall, and relatively high temperatures in the northern parts, bringing wet tropical conditions that are associated with ENSO events and remarkable temperature homogeneity along the entire latitudinal extent of the coastal desert (Rundel et al. 1991). According to the climatic classification of Köppen-Geiger, the study region belongs to a tropical and sub-tropical desert climate ("Bwh"; Beck et al. 2018). Coastal lomas have two distinct seasons, a dry season and a humid season that occurs mostly between May to October.

Floristic data

We compiled a comprehensive database of the flora of the 71 coastal lomas. We systematically reviewed the Peruvian and Chilean flora based on species records in herbaria

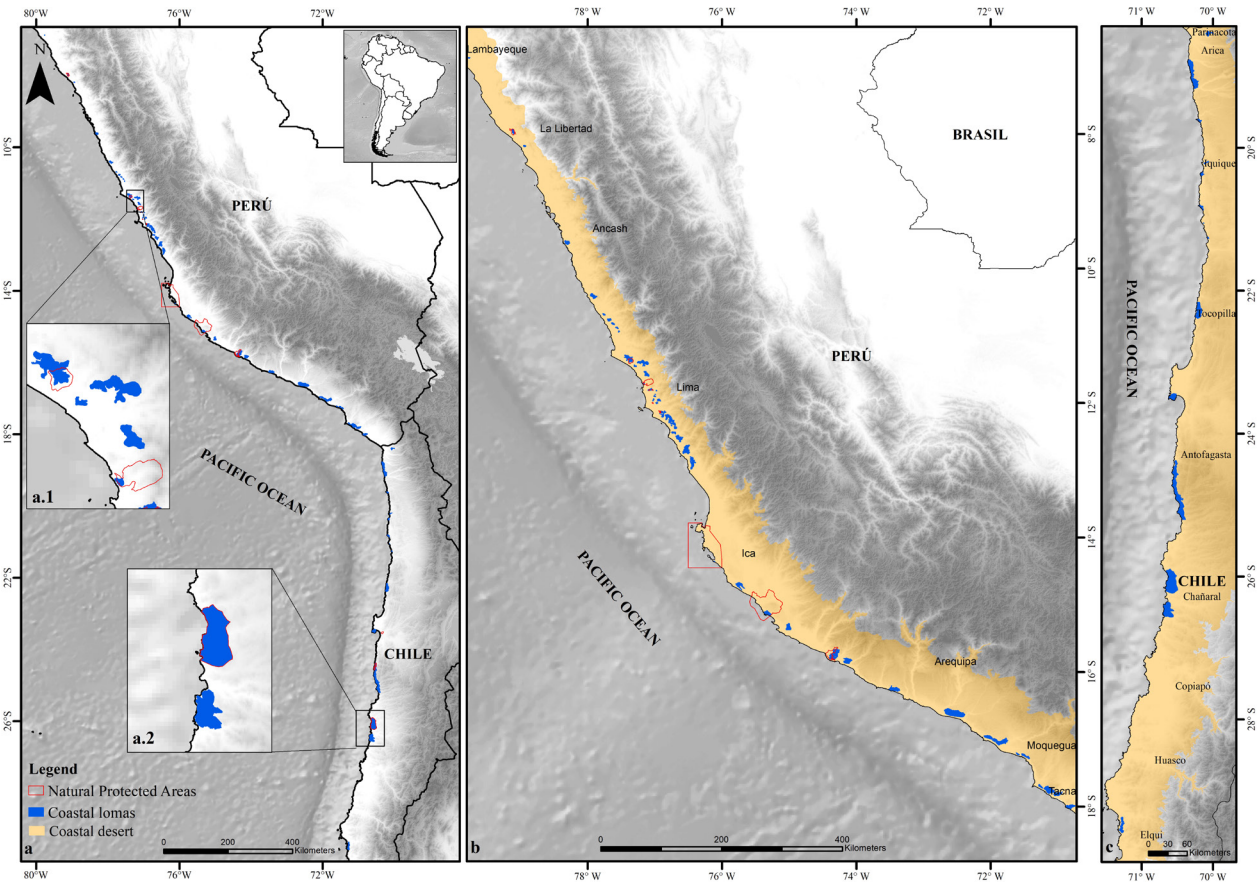

Figure 1. a. Locations of terrestrial coastal lomas (n = 71) across the Peruvian–Chilean coastal desert of South America. Examples of the coastal lomas in Lima, Peru (**a.1**) and in Antofagasta, Chile (**a.2**); **b, c.** The distribution of coastal lomas in Peru and Chile, respectively. Coastal lomas are indicated in blue, natural protected areas are indicated with red lines, and the coastal desert is indicated by orange.

(San Marcos Museum of Natural History UNMSM-Lima, Peru; Michael Owen Dillon Institute IMOD-Arequipa, Peru; Department of Botany of the University of Concepción CONC Concepcion, Chile). Additionally, we collected species checklists of natural reserves, scientific publications, theses, online data sets (http://sacha.org/), and personal observations, which we further complemented with species records obtained from the Global Biodiversity Information Facility (GBIF). In total, we recorded 1,460 plant species that occur in coastal lomas. We did not exclude exotic species. All data references are provided in Suppl. material 1: appendix S1.

Data preparation

Taxonomic standardization. To ensure compatibility of scientific names across our data set, we standardized species names based on the Taxonomic Name Resolution Service (Boyle et al. 2013), WFO (World Flora Online 2022), Tropicos (Missouri Botanical Garden 2023), USDA (United States Department of Agriculture 2022), and the World checklist of vascular plants (WCVP 2021) using the 'tnrs' function of the R package 'TNRS' (Boyle et al. 2021) and the 'tpl' function of the R package 'Taxonstand' (Cayuela et al. 2021). After taxonomic standardization, our data set had a total of 1,363 accepted plant species names.

Phylogeny. We constructed a phylogenetic tree for all plant species in our data set using the seed plant phylogeny of Smith and Brown (2018) as a backbone, using the functions 'read.newick' and 'congeneric.merge' of the R package 'phylotools' (Revell 2024). The 'congeneric.merge' function locates plant species that are not present in the phylogeny by assigning them to the branch of their genus or the closest available higher taxon, which may slightly underestimate phylogenetic diversity (Pearse et al. 2015). We placed a total of 1,305 species on the phylogeny, representing 95.7% of all species in our dataset.

Biogeographical characteristics of coastal lomas

We spatially delimited coastal lomas by combining geospatial files from the following sources: Map of Fragile Ecosystems (Peru; SERFOR 2019), National Map of Ecosystems (Peru; MINAM 2019), Map of Vegetation Cover (Peru; MINAM 2015), Map of Protected Natural Areas and Private Conservation Areas (Peru; SERNANP 2023; Arapa 2018), Map of Cloud Oasis Ecosystems (Chile; Moat et al. 2021), Vegetation Units (Chile; Luebert and Pliscoff 2017) and Protected Wilderness Areas (Chile; SNASPE 2019). For coastal lomas without geospatial information, we delimited them manually using ArcGis 10.8. To ensure the quality of the delimited areas, we checked them against plant species records that occur in coastal lomas with spatial coordinates and with the geospatial sources mentioned above. The map with all coastal lomas is available in Suppl. material 1: appendix S3. On average, the coastal lomas in our dataset cover 5,264.07 hectares, ranging from 77.26 to 44,862.44 ha.

Environmental conditions

Based on relevant literature (e.g., Kreft and Jetz 2007; Wilson and Jetz 2016; König et al. 2017; Testolin et al. 2021) and variables related to macroecological hypotheses that explain diversity patterns in drylands (Suppl. material 1: appendix S2), we selected an array of environmental predictor variables. We obtained mean annual daily mean temperature (bio1), isothermality (bio3), annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation of the driest month (bio14), mean monthly climate moisture index (cmi_mean), net primary productivity (NPP), and aridity, i.e. the ratio between annual precipitation and potential evapotranspiration, from CHELSA 2.1 (Karger et al. 2017). As cloud cover has been used previously as a proxy for fog (e.g., Eichler and Londoño 2013; Osses et al. 2017), which is an important source for sustaining coastal lomas (e.g., Weberbauer 1911; Ferreyra 1960), we used annual cloud cover and cloud cover for August, which is usually the wettest month across coastal lomas and best reflects seasonal differences in coastal lomas (e.g., Pinche 1996; Peréz 2019; Moat et al. 2021; Ruhm et al. 2022), which we obtained from Wilson and Jetz (2016). We derived mean soil pH and N for each coastal loma, using values estimated at a depth of 5 and 15 cm from SoilGrids at 1 km^2 resolution (Hengl et al. 2014) given the effects of soil properties on plant diversity patterns in drylands globally (Ulrich et al. 2014). We also included the human footprint index (Venter et al. 2018), because coastal lomas have been historically threatened by anthropogenic activities (Trinidad et al. 2012; Gonzales et al. 2023). All data sources had a spatial resolution of approximately 1 km^2. We calculated mean values for all climatic variables for each coastal loma.

Topographic and geographical factors

For each coastal loma, we calculated aspect (northness and easthness), roughness, and slope following Amatulli et al. (2018) as proxies for environmental heterogeneity, as they capture the structural complexity of the terrain (see Stein et al. 2014; Grobler and Cowling 2022). Additionally, we calculated elevation following Amatulli et al. (2018), as a proxy for the capacity to intercept coastal fog, which determines moisture availability in coastal lomas. As the species diversity of fragmented habitats such as coastal lomas is often associated with area and isolation (Arana 2019), we also calculated the area (km^2), distance to the coast (km), and geographic isolation using the surrounding mass area index following Weigelt and Kreft (2013) for each coastal loma. As for the environmental variables, we calculated topographic and geographic variables as the mean for each coastal loma.

Data analysis

Taxonomic and phylogenetic diversity. We estimated taxonomic species richness as the number of species that occur within each coastal loma. We estimated phylogenetic diversity using three indices that target different components of evolutionary history: (i) Faith's PD (PD; Faith 1992), which is the sum of all branch lengths and thus represents lineage diversity of an assemblage, while (ii) mean pairwise distance (MPD; Webb et al. 2002), and (iii) mean nearest taxon distance (MNTD; Webb 2000) emphasize different aspects of the phylogenetic structure of assemblages. MPD is the mean of the pairwise distances from each taxon to each other taxon within an assemblage and MNTD is the phylogenetic distance to the closest relative for each taxon and calculates the mean across all taxa (Webb et al. 2002). All PD metrics were calculated using the functions 'pd', 'mpd', and 'mntd' of the R package 'picante' (Kembel et al. 2010).

To control for differences in species richness across coastal lomas, we used null models to compare observed and randomized species assemblages to evaluate differences in phylogenetic diversity. We therefore generated 1,000 null communities for each coastal loma using the 'taxa.labels' null model of the R package 'picante'(Kembel et al. 2010). We then calculated standardized effect sizes for each metric of phylogenetic diversity using the functions 'ses.pd', 'ses.mpd', and 'ses.mntd' of the R package 'picante' (Kembel et al. 2010). Values above 0 indicate phylogenetic overdispersion, i.e. species are less related than expected by chance, and values below 0 indicate phylogenetic clustering, i.e. species are more related than expected by chance.

Statistical analysis. To evaluate the potential effects of the species-area relationship (SAR) on taxonomic and phylogenetic diversity, we fitted SAR models using the power-law relationship that is generally used for describing SARs (e.g., Connor and McCoy 1979; Dengler 2009). Only taxonomic diversity (richness) showed a significant relationship with area (Suppl. material 1: appendix S4). From here on, we used the residuals of the SAR model for further analysis instead of observed plant species richness (see Guilhaumon et al. 2008) but used the observed values of phylogenetic diversity.

To evaluate the relationship between species richness–expressed as the residuals of the SAR models–and standardized phylogenetic diversity with latitude, we fitted generalized additive models (GAMs). We used GAMs because they capture non-linear patterns and are less sensitive to outliers (Hastie and Tibshirani 1990) (Suppl. material 1: appendix S5). We then tested the influence of climatic conditions, soil properties, environmental heterogeneity, and geographical factors on the variation of taxonomic and phylogenetic diversity indices (PD, MNTD, MPD) across coastal lomas using generalized linear models (GLM). We restricted our analysis of phylogenetic diversity to standardized indices, because unstandardized phylogenetic diversity indices are strongly correlated with species richness, while standardized phylogenetic diversity indices provide insights into ecological processes underlying taxonomic diversity patterns (Webb 2000), such as environmental filtering while limiting similarity due to species richness patterns (see Suppl. material 1: appendix S6).

Except for latitude, we used a $\log_{10}(x+1)$ transformation to reduce skewness and visually assess model assumptions, i.e. homogeneity of variance and normality of model residuals (see Zuur et al. 2010). We tested multicollinearity using variance inflation factors (VIF) with the R package 'car' (Fox and Weisberg 2019).

We considered models with a ΔAIC value < 2.0 compared to the minimum AIC value to be the most parsimonious models (Burnham and Anderson 2004) using the R package 'MuMin' (Barton 2019). As we did not find significant differences between AIC values, we selected the best model using the 'stepAIC' function of the MASS package (Venables and Ripley 2002), which performs a stepwise procedure that iteratively adds or removes variables from the model, and selects the best model with the lowest AIC value (Venables and Ripley 2002). For model interpretation and for presentation we used the R package 'jtools' (Long 2022) and 'huxtable' (Hugh-Jones 2025).

We fitted SAR models using the R package 'sars' (Matthews et al. 2019), diversity-latitude relationships with GAMs using the R package 'mgcv' (Wood 2017), and GLMs using the "glm" function in the R packages 'stats' (R Core Team 2023), 'lm', and 'ggeffects' (Lüdecke 2018). To examine spatial autocorrelation, we calculated Moran's I for model residuals using the R package 'spdep' (Bivand 2022).

We performed cluster analysis to evaluate the spatial organization of communities across the coastal lomas. We used Hellinger distance to measure the similarity between localities, running 999 permutations using the "vegdist" function in the R package 'vegan' (Oksanen et al. 2020). To construct the dendrogram, we used the complete hierarchical clustering method ('complete linkage'), which optimizes clustering by minimizing the maximum distance between points of different clusters. We then calculated average silhouette widths using the R package 'cluster' (Hornik et al. 2009) that represented the degree to which a species typified its group (Legendre and Legendre 1998).

We performed all analyses and visualizations with R version 4.3.1 (R Core Team 2023), using the following packages: 'dplyr' (Wickham et al. 2020), 'tidyr' (Wickham and Henry 2019), 'stringr' (Wickham 2019), 'ggplot2' (Wickham 2016), 'cowplot' (Wilke 2019), and 'patchwork' (Pedersen 2020).

Results

Latitudinal diversity gradients

Our analysis revealed that plant species richness, expressed as the residuals of the species-area relationship (SAR), showed no significant association with latitude (effective degrees of freedom *edf* = 1, *F* = 0.006, *p*-value = 0.94, adj. R^2 = -0.014), indicating the absence of a latitudinal gradient in species richness. In contrast, phylogenetic diversity metrics varied linearly and non-linearly with latitude. Standardized PD showed a statistically significant non-linear trend (*edf* = 4.683, *F* = 2.417, *p*-value = 0.0415, adj. R^2 = 0.165). Standardized MPD (*edf* = 5.515, *F* = 4.182, *p*-value = 0.00087, adj. R^2 = 0.297) varied non-linearly and significantly with latitude, peaking at ~23°S (Fig. 2). Finally, standardized MNTD (*edf* = 1, *F* = 2.578, *p*-value = 0.113, adj. R^2 = 0.022) decreased linearly but not significantly towards the Equator (Fig. 2, Suppl. material 1: appendix S5). Across the entire latitudinal gradient, we observed an average of 86 (SE = 9.45) plant species. In terms of phylogenetic diversity, standardized PD averaged -0.40 (CI = -0.70, -0.09) and standardized MPD and MNTD averaged -0.137 (CI = -0.45, 0.17) and -0.49 (CI = -0.77, -0.21), respectively. Also, we found that none of the standardized phylogenetic diversity indices exhibited a statistically significant correlation with observed species richness (p > 0.05; Suppl. material 1: fig. S6.10).

Predictors of plant diversity patterns across coastal lomas

Our results show that current climate, environmental heterogeneity, and geographical factors are the principal predictors of plant taxonomic and phylogenetic diversity. Aridity was the only predictor retained in all models, suggesting a central role of water availability in structuring coastal lomas plant assemblages. We observed that plant species richness decreased with decreasing aridity (i.e., higher P/PET values) and was positively associated with cloud cover, suggesting that fog-related moisture contributes to maintaining higher plant richness in coastal lomas (Figs 3, 4, Suppl. material 1: table S6.8). We found that standardized Faith's PD increased with northness, and human footprint, yet decreased with aridity and distance to the coast (Figs 3, 4, Suppl. material 1: table S6.8). Standardized MNTD decreased with increasing MAT and aridity, yet increased with northness and human footprint (Figs 3, 4, Suppl. material 1: table S6.8); standardized MPD increased with aridity, slope, northness, and MAT, and decreased with increasing cloud cover, isothermality, and distance to the coast (Figs 3, 4, Suppl. material 1: table S6.8). Our models explained more variation for phylogenetic diversity (Pseudo R^2 = 0.27–0.44) than for taxonomic diversity (Pseudo R^2 = 0.07; Suppl. material 1: table S6.8, S6.9).

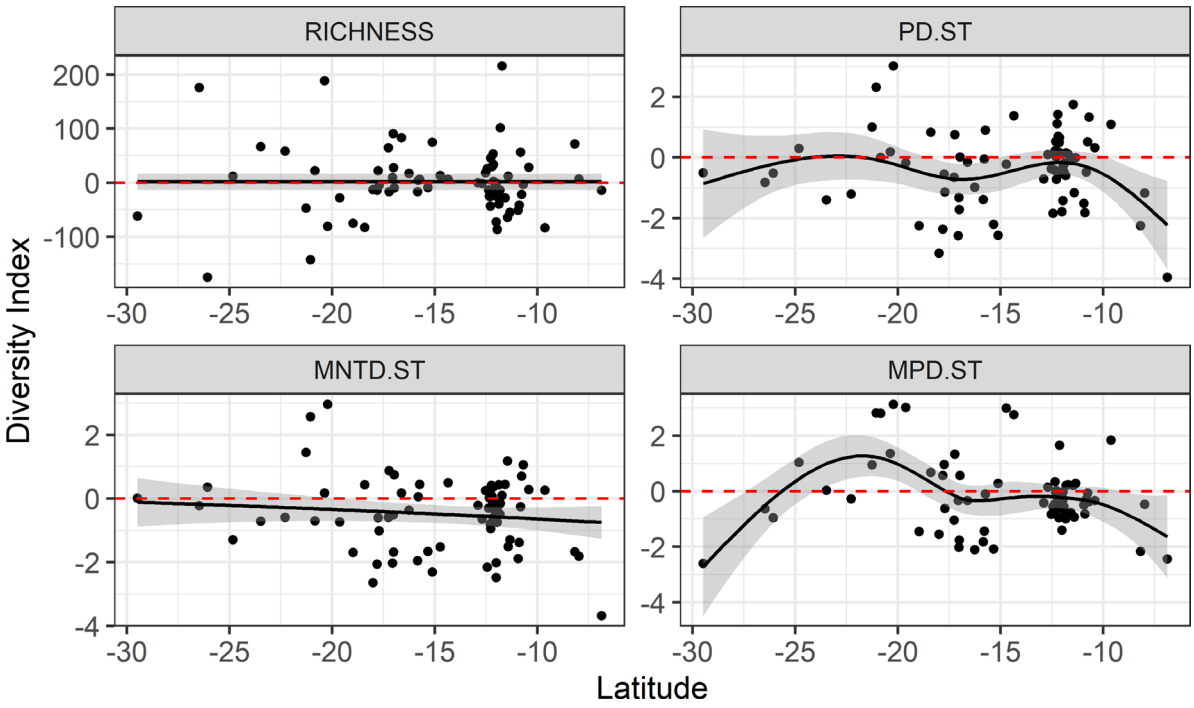

Figure 2. Relationships between latitude (South to North) and plant species richness or phylogenetic diversity across coastal lomas embedded within the Peruvian–Chilean coastal desert of South America (n = 71 coastal lomas). Species richness is expressed as the residuals of the species-area relationship (SAR). Phylogenetic diversity was calculated as MNTD, which is mean nearest taxon distance, MPD, which is mean pairwise distance, and PD, which is Faith's phylogenetic diversity. These indices were standardized with null models to identify assembly processes that structure communities. Lines are fitted with generalized additive models (GAM).

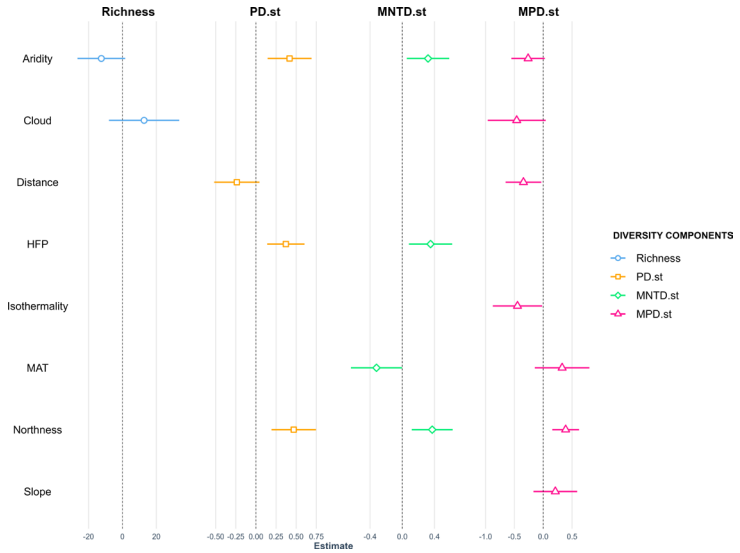

Figure 3. Effect sizes of abiotic and biotic predictors of plant diversity (taxonomic and phylogenetic) across coastal lomas in Peru and Chile. Richness is plant species richness but modeled as the residual of the species-area relationship, PD.st is standardized Faith's phylogenetic diversity, MNTD.st is standardized mean nearest taxon distance, and MPD.st is standardized mean (phylogenetic) pairwise distance. Fitted using generalized linear models (GLMs).

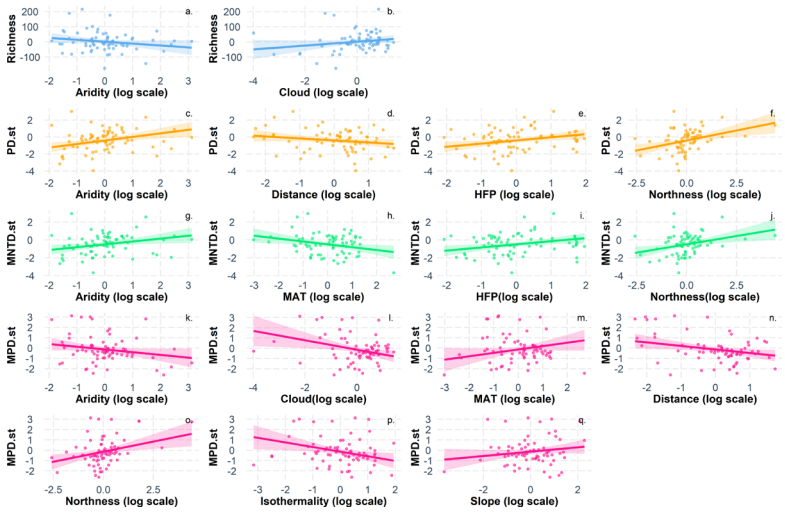

Figure 4. Estimated responses of taxonomic and phylogenetic diversity to environmental, topographic, and geographic factors across coastal lomas in Peru and Chile. Species richness was expressed as the residuals of the species-area relationship (SAR). Aridity is the ratio of mean annual precipitation to potential evapotranspiration, HFP is the human footprint, MAT is mean annual temperature, and Distance is the distance of each coastal loma to the coast. Explanatory variables were transformed using $\log_{10}(x+1)$ and subsequently centered and standardized. Fitted using generalized linear models (GLMs); solid lines are the fitted lines from generalized linear models and the shaded area represents the 95% confidence interval.

Finally, once accounting for the effects of climate, topography, and geography on taxonomic and phylogenetic diversity, we found no evidence of a latitudinal shift in taxonomic or phylogenetic diversity ($p > 0.05$; Suppl. material 1: figs S6.11–6.14).

Species assemblages

We found that the Chilean and Peruvian coastal lomas form separate assemblages, with a total of six distinct clusters (Fig. 5, Suppl. material 1: table S7). Differences in multivariate dispersion among assemblages were statistically significant ($F_{5,65} = 39.3, p < 0.001$). Within the coastal lomas of Chile (cluster 6), the northernmost loma (VLL: Villa Maria) is grouped with the southernmost one (TOF: Tofo). In Peru, coastal lomas are clearly divided latitudinally into clusters 1 and 3. Additionally, two coastal lomas (CRE: Cerro Reque and FLA: Flamenco) form independent branches.

Discussion

Our results reveal that plant phylogenetic diversity (standardized PD and MPD) of coastal lomas varies inversely and non-linearly with latitude, and is jointly shaped by water

availability, environmental heterogeneity, and distance from the coast. After accounting for these factors, we found no evidence that plant diversity of coastal lomas systemically shifts with latitude. The decline in standardized MPD toward lower latitudes has been documented for woody communities (excluding gymnosperms), whereas in herbaceous communities it decreases toward higher latitudes (Massante et al. 2019). Similarly, MPD has been shown to decline with latitude in other taxa, such as invertebrates (Grigoropoulou et al. 2021). Our finding supports the idea that latitude itself is not a direct, causal explanation for plant diversity in coastal lomas, but rather that the environmental predictors — principally water availability — that vary with latitude, in addition to faster diversification rates (see Neves et al. 2021), are likely responsible for the incongruent latitudinal diversity gradient in plants across coastal lomas.

Our results are consistent with those of Manrique et al. (2014), who did not find a latitudinal gradient in plant species richness across 13 coastal lomas. Also, a previous study found that plant cover increases non-monotonically with latitude in Tillandsia-dominated coastal lomas (Pinto et al. 2001), possibly in response to spatial variation in coastal fog and precipitation linked to ENSO events (Dillon 2005). While coastal fog productivity varies depending on proximity to the ocean, altitude, and local topography, it may not vary with latitude, at least in northern Chile (Larrain et al. 2002).

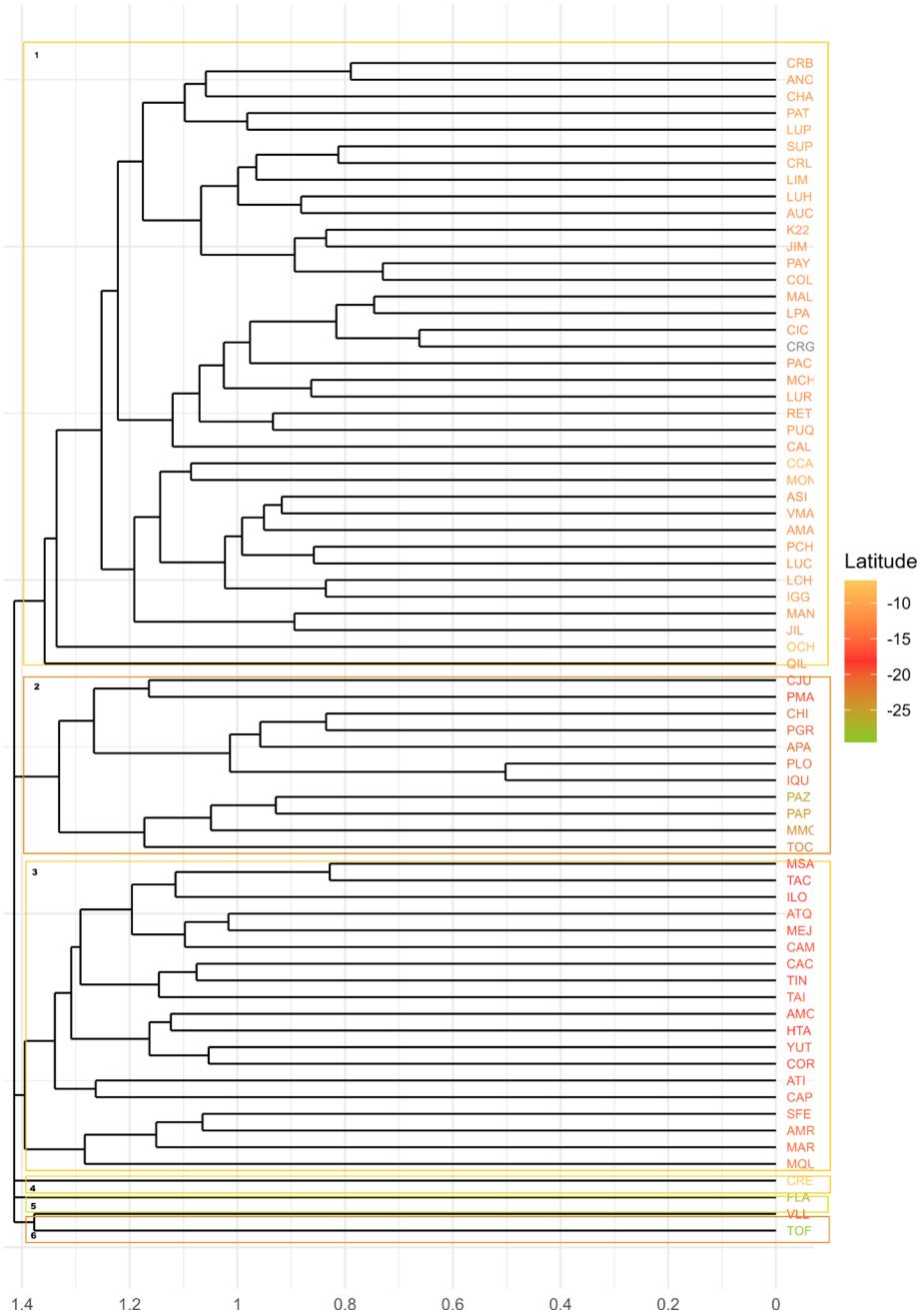

Figure 5. Dendrogram identifying floristic assemblages across the coastal lomas of Peru and Chile. We used Hellinger distances to assess the compositional similarity of 71 coastal lomas. The colors of the labels indicate the latitude of each location. The coastal lomas are separated into a total of six distinct clusters based on silhouette width.

Our findings therefore highlight the importance of environmental variation at local spatial scales — and not macroecological scales — in determining diversity patterns in coastal lomas, which may have generated the non-linear latitudinal gradient that we observed for standardized MPD and PD. Low standardized MPD and PD values at the extreme South and North of the coastal lomas' distribution appear to indicate stronger niche conservatism of coastal lomas plants. The contrasting latitudinal patterns for phylogenetic diversity indices associated with different evolutionary time scales therefore suggest that species diversification events, together with historical changes in climatic conditions, may have shaped plant diversity patterns across coastal lomas in South America.

Overall, we found low values of unstandardized PD, which coincides with values reported for other drylands such as the Sonoran Desert, large parts of Caatinga (Amaral et al. 2022), and the Atacama Desert (Scherson et al. 2017). This suggests that strong lineage clustering, i.e., neoendemism, has shaped the composition of the flora of coastal lomas at macroecological scales. For example, Tillandsia landbeckii (Phil.), a monospecific loma forming species in the Atacama Desert, is thought to have evolved only 2 Ma (Möbus et al. 2021). Because of their relatively recent origins, most deserts may have relatively lower phylogenetic diversity when compared to relatively more humid environments (Scherson et al. 2014; Neves et al. 2021). Yet, overall phylogenetic endemicity in seed plants reaches its peak in the tropical regions adjacent to the Peruvian–Chilean desert (Cai et al. 2023). Across coastal lomas, we found evidence of increasing phylogenetic clustering towards the North for standardized MNTD, yet only in the South for standardized MPD, which was phylogenetically overdispersed at ~22°S and 18°S. Together, these results suggest that different processes may have operated at different evolutionary times along coastal lomas distribution. However, we found that the 95% confidence intervals of standardized PD overlapped with zero, suggesting that either neutral processes (Vellend 2016) or weak niche partitioning and other biotic processes, such as competition (Cadotte and Davies 2016) may also shape community assembly at local scales.

Our models showed that current environmental conditions, particularly those associated with water availability, have a significant effect on phylogenetic diversity across coastal lomas. Species richness increased with aridity, contrasting with the dominant pattern of declining or hump-shaped species richness with increasing aridity (e.g., Berdugo et al. 2020; De Oliveira et al. 2022). Coastal lomas in highly arid regions may still support relatively rich plant communities when there is sufficient water in the form of advective fog to sustain plant growth.

Standardized Faith's PD and MNTD increased with decreasing aridity, which is broadly consistent with global and regional studies of drylands, desert scrub, and coastal lomas that have shown that phylogenetic diversity generally declines in response to increasing aridity (Xiao et al. 2018). In other words, less arid coastal lomas support assemblages composed of a broader range of evolutionary lineages. Moreover, the negative relationship between standardized MPD and aridity suggests that the diversity of older plant clades has not been constrained by water availability, contrary to what has been reported for arid ecosystems (Neves et al. 2021). Yet, plant diversification in the Atacama Desert could have happened after the increase in aridity, which is thought to have occurred in the late Pliocene after 5 Ma (Hartley and Chong 2002). This diversification may be associated with pluvial events during the Pleistocene that may have facilitated the long-distance dispersal of Andean species to the coastal desert (Díaz et al. 2012). Conversely, the inferred onset and expansion of hyper-arid conditions towards higher elevations in the Pre-Cordillera and Pre-Andean basins (Hartley and Chong 2002) likely restricted the distribution of plants in the Atacama Desert, such as species of the genera Nolana and Cristaria (Dillon et al. 2009; Boehnert et al. 2019). Additionally, the negative relationship between standardized MNTD and mean annual temperature (Fig. 4) indicates that warmer ecosystems such as deserts tend to be structured by recent radiations of closely related taxa, suggesting that environmental filtering at high temperatures favors clustering within lineages rather than coexistence of distantly related species. This result might suggest that environmental filtering due to aridification operates over longer evolutionary timescales (Qian et al. 2023). Further research on the dynamics of modern speciation events across coastal lomas is needed to strengthen our understanding of how temporal changes in aridity have impacted current diversity patterns.

Our results clarify the impacts of the dynamic interplay between environmental conditions and topography (e.g., slope and northness) on diversity patterns in coastal lomas. Environmental heterogeneity, such as slope, is frequently associated with diversity patterns (Stein et al. 2014; Heidrich et al. 2020), and also co-varies with climatic conditions, such as temperature and precipitation. Across the coastal lomas, standardized MPD exhibited a statistically significant positive relationship with slope. Moreover, northness emerged as an important predictor of phylogenetic diversity. Standardized PD, MPD, and MNTD all increased towards north-facing slopes, which are drier (Badano et al. 2005), suggesting that slope orientation plays a primary role in shaping the evolutionary structure of coastal lomas plants. While variation in northness reflects variation in slope aspect, slope itself modulates the interception of oceanic fog by vegetation. At local scales, both slope and elevation are related to the availability of coastal fog (see Rundel and Mahu 1976; Muenchow et al. 2013) and have been found to influence taxonomic diversity (Moat et al. 2021). Furthermore, topographically heterogeneous areas should provide more possibilities for shelter and refuge, enabling species to persist in extreme conditions such as those found in deserts (e.g., Keppel et al. 2012).

We also found evidence that diversity patterns across coastal lomas depend on their biogeographical context. Species richness followed the expected species-area relationship (Rosenzweig 1995; DeMalach et al. 2018), indicating that plant species richness consistently increases with the area of coastal lomas (Arana 2019). In contrast,

standardised phylogenetic diversity did not follow this pattern, suggesting that the accumulation of evolutionary lineages is shaped by environmental or historical factors. We also found that human activity does not always have a predictable impact on plant diversity, observing an increase in standardized PD and MNTD with the human footprint index (HFP), which may be due to the introduction of exotic species that can increase plant diversity.

We also observed that standardized MPD peaked at ~22.5 and ~13.5°S and reached its lowest values at ~17.5°S, which coincides with distinct geographical barriers: the hyperarid core of the Atacama Desert, Lima Chillon, and Lurin hydrographic basins in central Peru, and the Abancay deflection in central Peru (Lima and Apurimac departments). These geographical barriers could have influenced species dispersion and divergence, resulting in coastal lomas with a mixture of distantly related taxa (Mazel et al. 2016). Moreover, we found that standardized PD and MPD decreased with increasing distance from the coast, again highlighting the importance of coastal fog for maintaining species coexistence.

Our floristic similarity analysis suggests that some clusters represent compositionally more heterogeneous communities than others, supporting the hypothesis proposed by Rundel et al. (1991), Dillon and Hoffmann (1997), Dillon (2005), Pinto and Luebert (2009), Ruhm et al. (2022), and Ruhm et al. (2020) in revealing the presence of a climatic barrier near the Chilean–Peruvian border. Notably, this barrier coincides with the separation of clusters 2 (northern Chile) and 3 (southern Peru) at ~18.21°S. Also, three major clusters (1, 2, and 3) are similar to the floristic regions proposed by Dillon et al. (2003). Additionally, the separation between northern (cluster 1) and southern (cluster 3) Peruvian lomas near 13.5°S coincides with the Abancay deflection, a prominent geomorphological feature in the central Andes of Peru (Marcocco 1978), that likely functions as a dispersal barrier between these regions. Finally, two localities, Cerro Reque (CRE, Peru) and Flamenco (FLA, Chile) are presented as independent branches, suggesting that their singular floristic composition may be driven by site-specific environmental conditions or local evolutionary differentiation processes.

Limitations of the present study

Although we compiled the most comprehensive dataset of coastal lomas to date, we acknowledge the potential presence of spatial, phylogenetic, taxonomical, and historical biases (Hortal et al. 2008; Meyer et al. 2016; Hughes et al. 2021) that may have affected our results. First, at least 30% of coastal lomas had no published species checklist, reflecting collection bias. To complete our data set, we therefore used species records from other data sources, e.g., herbaria, online check lists, and GBIF (see Methodology). Using only GBIF data can lead to an underestimation of species diversity; for example, in the coastal lomas of Atiquipa, GBIF reports only 168 species, which we increased to 346 species by consulting additional sources. Second, most plant diversity data of coastal lomas is limited to conservation areas (Gonzales et al. 2023). By not including less protected coastal lomas, we may have underestimated human activity impacts on the taxonomic and phylogenetic diversity patterns of coastal lomas. On the other hand, the separation of clusters 2 and 3 along the political border between Peru and Chile could reflect a biogeographic discontinuity shaped by climate and topography acting as a historical barrier to plant dispersal (Rundel et al. 1991). Third, the lack of high-resolution climate data on fog and low clouds along the South American coast limits our understanding of the role that both factors play in shaping the plant diversity of coastal lomas (del Río et al. 2021). More precise environmental indicators (e.g., remotely-sensed fog frequency) are likely to reveal ecologically significant variation otherwise missed by standard climate data. Lastly, we used a relatively coarse-scale resolution (1 km^2) to estimate environmental conditions and environmental heterogeneity in coastal lomas. This may be particularly relevant for small lomas, where environmental estimates could be influenced by edge effects arising from the inclusion of adjacent desert areas within the same grid cell. Nevertheless, this resolution remains appropriate for characterizing broad-scale environmental gradients, which was the primary focus of this study. A higher resolution Digital Elevation Model (DEM) may better capture the environmental heterogeneity and micro-climate of coastal lomas, which have been found to improve predictions of species distributions in other ecosystems (Lembrechts et al. 2019). Finally, global climatic data sets used in regional studies may fail to capture local climatic conditions, particularly in regions with a low density of climate stations and sharp climatic gradients in topographically complex areas (Bedia et al. 2013).

Conclusions

By compiling the most comprehensive dataset of coastal lomas to date, our study provides a broad-scale assessment of the environmental, topographic, and geographic factors shaping plant taxonomic and phylogenetic diversity across the Peruvian and Chilean coastal deserts. Among the diversity metrics evaluated, only species richness followed the expected species-area relationship across coastal lomas. We found that, rather than conforming to a simple latitudinal gradient, phylogenetic diversity was associated with spatial variation in climate, topography, and geography. We provide evidence that predictors of biodiversity differ markedly among phylogenetic diversity indices, revealing how the phylogenetic structure of coastal lomas has shifted over evolutionary time. Aridity predominantly explains variation in diversity facets to varying extents, indicating that water availability is a key predictor shaping both taxonomic and phylogenetic diversity patterns. However, our understanding of the potential impacts of land-use change on plant diver-

sity of coastal lomas remains incomplete, as there is little data on coastal lomas not in conservation areas in Peru and Chile. In light of our results, future research should focus on coastal lomas without checklist data (Hortal et al. 2008) to increase our ability to predict their response to global change drivers, particularly climate and land-use change. Furthermore, adaptation and planning strategies should be developed in response to the increasing aridification and land degradation occurring in coastal lomas to conserve their unique biodiversity.

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Additional information

Conflict of interest
The authors have declared that no competing interests exist.

Ethical statement
No ethical statement was reported.

Artificial Intelligence (AI) use
The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
AI was not used in the production of this manuscript, other than assistance disentangling coding errors.

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Conceptualization FNG, DC and HK; methodology FNG, DC, HK and LA; formal analysis FG; data curation FG and LA; writing -original draft preparation FNG; writing- review and editing, FNG, DC, LA and HK. All authors have been involved in developing, writing, commenting, editing, and reviewing the manuscript.

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Data availability
All data supporting the findings of this study are available in the Suppl. material 1. The spatial dataset of the coastal lomas is available on Zenodo (https://doi.org/10.5281/zenodo.21886215).

Supplementary materials

Supplementary material 1

Supplementary Information (.docx)
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