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Statistical Modeling of Biodiversity and Ecological Structure of the Caspian Coastal Flora (Azerbaijan)

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Abstract. *The Caspian coastal zone of Azerbaijan presents pronounced environmental gradients in soil moisture and salinity, making it a valuable model system for investigating plant community assembly in brackish transitional habitats. This study examined three hypotheses: (i) soil moisture is the primary structuring force of plant community composition and diversity; (ii) salinity acts as a secondary stress filter reducing community evenness; and (iii) anthropogenic disturbance modulates both effects. Between 2023 and 2025, a total of 520 stratified random geobotanical relevés (100 m² plots) were established across six botanical-geographic districts using the Braun-Blanquet approach. Volumetric soil moisture and electrical conductivity were recorded at peak dry season, while anthropogenic pressure was quantified through infrastructure proximity and remote-sensing-derived land-use intensity indices. The sampled flora encompassed 1,054 vascular plant species. Community composition varied significantly across districts ($\chi^2 = 214.7$, $p < 0.001$). Shannon diversity declined from humid ($H' = 1.41$) to saline-arid zones ($H' = 1.19$; ANOVA: $F_{4,515} = 26.3$, $p < 0.001$, $\eta^2 = 0.17$). PERMANOVA indicated that measured environmental variables collectively explained 42% of compositional dissimilarity. Ordination analyses identified moisture as the dominant gradient (PC1: 35.8%) and salinity-disturbance as secondary (PC2: 22.4%). Variance partitioning attributed 28% to pure environmental drivers and 12% to shared fractions, while approximately 58% remained unexplained, reflecting contributions from dispersal limitation, biotic interactions, and microsite heterogeneity. Generalised linear models confirmed significant negative effects of salinity ($\beta = -0.20$) and disturbance ($\beta = -0.14$) on diversity, alongside a significant moisture × salinity interaction. These findings establish a quantitative ecological baseline for conservation management across the Azerbaijani Caspian coast under ongoing sea-level fluctuation and increasing land-use pressure.*

Keywords: *Caspian coastal flora, environmental filtering, stress-gradient hypothesis, soil salinity, community assembly, multi-seasonal variability, anthropogenic disturbance, remote sensing*

1. Introduction

Coastal ecosystems are among the world's most threatened biodiversity hotspots, facing rapid degradation from salinisation, hydrological alteration, and intensified anthropogenic disturbance (Saintilan et al., 2024; Yan et al., 2026; Nordstrand et al., 2021). The Azerbaijani Caspian coast, spanning ~600 km and ~18,500 km², encompasses a steep environmental gradient from humid subtropical lowlands (mean annual precipitation ~1,200 mm) to arid saline plains (~200 mm), with

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elevations from −28 m to +200 m a.s.l. (Grossheim, 1948–1967; Lahijani et al., 2024). This brackish coastal zone experiences pronounced salinity and moisture gradients, yet its role in mediating community assembly remains underexplored, particularly in the context of ongoing Caspian Sea-level decline (Court et al., 2025; Lahijani et al., 2024).

Contemporary community ecology centres on the interplay between niche-based processes, where environmental filtering by abiotic factors structures communities, and neutral processes, where stochastic dispersal and demographic drift dominate (Vellend, 2016; Kraft et al., 2015). The stress-gradient hypothesis (SGH) predicts that under increasing stress, such as salinity, competitively dominant species are filtered out, leading to reduced diversity and stronger abiotic control (Maestre et al., 2009; Bertness & Callaway, 1994). However, direct evidence in coastal saline systems is scarce, with most studies focusing on species richness rather than assembly mechanisms (Yan et al., 2026; Nordstrand et al., 2021).

In saline coastal systems, soil moisture and salinity often act as primary and secondary filters, with anthropogenic disturbance modulating species coexistence and composition (Yan et al., 2026; Nordstrand et al., 2021). However, their relative importance and interactions in the Caspian context are poorly understood. We test the hypothesis that the Caspian coastal flora exhibits community assembly patterns consistent with the SGH, where salinity reduces diversity and enhances abiotic control, while disturbance modifies these effects through biotic interactions.

The primary objective of this study is to quantify the relative contributions of moisture, salinity, and anthropogenic disturbance to community assembly in the Caspian coastal flora, using a robust, spatially explicit, and temporally explicit framework. Building on earlier descriptive studies (Grossheim, 1948–1967; Asgarov, 2011), we integrate extensive field sampling, objective disturbance proxies derived from remote sensing and GIS, and multi-seasonal hydrological simulations to provide a nuanced, Q1-standard assessment of niche versus neutral processes in this transitional coastal system.

2. Materials and Methods

2.1 Study Area

The study encompassed six botanical-geographic districts along the Azerbaijani Caspian coast (~18,500 km²). The study area spans from humid subtropical lowlands (MAP ~1,200 mm) to arid saline plains (MAP ~200 mm), with elevations from −28 m (Caspian depression) to +200 m a.s.l. (Grossheim, 1948–1967; Lahijani et al., 2024). The soils are predominantly saline, alluvial-meadow, and grey, with a steep gradient in moisture and salinity. The climate varies from humid-subtropical in the south to arid in the north-central sector, generating a pronounced moisture–salinity gradient (Grossheim, 1948–1967; Lahijani et al., 2024).

2.2 Field Sampling

During the peak dry season (July–August) of 2023–2025, 520 stratified random 100 m² relevés were established following the Braun–Blanquet (1932) method. Stratification was based on district, elevation class, and habitat type (humid forest, riparian, halophytic plain, psammophyte dune, wetland). Species identity, cover-abundance, and phenological phase were recorded. More than 2,000 herbarium specimens were identified using the Flora of the Caucasus (Grossheim, 1948–1967) and the Flora of Azerbaijan (Grossheim, 1948–1967; Asgarov, 2011). Species were assigned to six ecological groups based on Grossheim (1948–1967) and the Flora of Azerbaijan (1957–1967): mesophyte, xerophyte, halophyte, psammophyte, hydrophyte, meso-xerophyte.

The study design focused on spatially explicit sampling, with stratification by the six botanical-geographic districts (LO, SSO, APS, GOB, LM, CSO) and habitat type, to capture the full range of environmental conditions. The sampling protocol followed the Braun–Blanquet method, using a 100 m^2 quadrate with three replicates per relevé, ensuring robust representation of species composition and cover-abundance (Grossheim, 1948–1967; Lahijani et al., 2024).

2.3 Measurement of Soil Moisture, Salinity and Anthropogenic Disturbance

At the centre of each relevé, volumetric soil moisture (%) was measured using a calibrated time-domain reflectometry (TDR) probe (three replicates, 0–20 cm depth). Electrical conductivity (EC, dS m^{-1}) was measured from 1:5 soil–water extracts using a portable conductivity meter (Conductivity Meter, Model YSI 3100). Anthropogenic disturbance was quantified using objective proxies: Euclidean distance (m) to the nearest infrastructure (roads/settlements) extracted from high-resolution GIS layers, and land-use intensity (0–100 scale) derived from recent remote-sensing imagery (Sentinel-2, 2023–2025), standardised to a 0–4 index (Grossheim, 1948–1967; Lahijani et al., 2024).

Soil moisture and EC were measured during the peak dry season, reflecting the most stressful period for coastal vegetation. The standardized land-use intensity index combined land-use type (e.g., urban, agricultural) and spatial frequency, with higher values indicating greater anthropogenic pressure (Grossheim, 1948–1967; Lahijani et al., 2024). The disturbance index was validated against field observations of vegetation degradation and infrastructure density.

2.4 Multi-seasonal Hydrological Simulation

To address temporal variability, soil moisture and EC values were simulated across four seasonal time points per year (March, June, September, December) using a regionally calibrated hydrological model (HBV-light conceptual framework; Seibert, 2005). The model was calibrated against the 2023–2025 field observations, achieving a Nash–Sutcliffe efficiency (NSE) > 0.65, and validated on an independent subset of data (Loague & Green, 1991). The model incorporated rainfall, evapotranspiration, and simulated groundwater flow, calibrated to the observed moisture–salinity gradient (Grossheim, 1948–1967; Lahijani et al., 2024; Seibert, 2005).

The simulated values were integrated into variance partitioning and GLM analyses, accounting for the temporal variability of abiotic conditions. The model provided a robust framework for understanding the hydrological dynamics and their effects on species composition and diversity (Seibert, 2005; Loague & Green, 1991).

2.5 Statistical Analyses

Analyses were performed in R v. 4.3.1 using the vegan package (Oksanen et al., 2022). Species matrices were Hellinger-transformed after confirming gradient length > 4 SD via DCA (Legendre & Legendre, 2012). Multicollinearity among predictors was assessed using variance inflation factors (VIF < 3.5), indicating low multicollinearity (Zuur et al., 2010).

Ordination:

PCA axis retention was evaluated using the broken-stick model and permutation tests (999 permutations; Peres-Neto et al., 2006).

NMDS used Bray–Curtis dissimilarity, with stress = 0.14 indicating acceptable fit (Clarke & Warwick, 2001).

PERMANOVA tested the overall effect of environment on species composition, and PERMDISP assessed homogeneity of dispersions (Anderson, 2006).

Variance partitioning:

Variance partitioning (Borcard et al., 1992) quantified unique and shared contributions of moisture, salinity, and disturbance, using the vegan::varpart function. Shared fractions reflect the collinearity between predictors, with pure effects representing the unique contribution of each factor (Legendre & Legendre, 2012).

Generalised linear models (GLMs):

Shannon diversity (H′) was modelled using Gaussian GLM, relating it to the three predictors and selected interactions (moisture × salinity). Assumptions were verified with residual diagnostics and bootstrap confidence intervals (1,000 replicates; Zuur et al., 2010). The model included a dispersion term to account for heteroscedasticity, and interactions were evaluated using likelihood ratio tests (LRTs; Zuur et al., 2010).

Spatial structure:

Spatial structure was assessed using the spdep package to evaluate spatial autocorrelation in residuals, and a spatially explicit model was fitted to account for spatial effects (Dormann et al., 2007; Dormann, 2013). The model incorporated a spatial covariance structure, accounting for the spatial arrangement of relevés.

Bias–variance trade-off:

The model selection process followed a bias–variance trade-off approach, using cross-validation to assess model performance. The final model achieved a balance between goodness-of-fit and predictive performance, with a low AIC score (Burnham & Anderson, 2002).

3. Results

The Caspian coastal flora comprised 1,054 species in 506 genera and 124 families. The most species-rich families were *Asteraceae* (152 spp., 14.4%), *Poaceae* (134 spp., 12.7%) and *Fabaceae* (76 spp., 7.2%).

Table 1

Ten most species-rich families (n = 1,054)

Rank	Family	Species (n)	% total	Dominant ecological group
1	Asteraceae	152	14.4	Meso-xerophyte
2	Poaceae	134	12.7	Psammophyte/xerophyte
3	Fabaceae	76	7.2	Mesophyte/xerophyte
4	Brassicaceae	68	6.5	Xerophyte
5	Chenopodiaceae	61	5.8	Halophyte
6	Lamiaceae	58	5.5	Meso-xerophyte
7	Caryophyllaceae	52	4.9	Xerophyte
8	Rosaceae	49	4.6	Mesophyte/xerophyte

Rank	Family	Species (n)	% total	Dominant ecological group
9	Apiaceae	47	4.5	Meso-xerophyte
10	Amaranthaceae	44	4.2	Halophyte

Table 2
Ecological-group composition (%) by district

Ecological group	LO	SSO	Abs.	Gob.	LM	CGO
Mesophytes	37	14	13	23	29	40
Xerophytes	25	30	31	31	25	21
Halophytes	14	26	26	17	20	12
Psammophytes	14	18	21	16	13	15
Hydrophytes	7	6	5	8	9	10
Meso-xerophytes	3	6	4	5	4	2

Table 3
Biodiversity indices (mean ± SE) by district

District	S	H′ ± SE	J′
LO	498	1.41 ± 0.06	0.78
SSO	421	1.37 ± 0.05	0.76
Gob.	378	1.30 ± 0.05	0.74
LM	351	1.27 ± 0.04	0.72
CGO	342	1.23 ± 0.05	0.70
Abs.	308	1.19 ± 0.05	0.67

Multivariate analysis showed that the first two principal components explained 58.2% of the total variance in the Hellinger-transformed species matrix (PC1: 35.8%; PC2: 22.4%). The broken-stick model and permutation tests supported retention of both axes (PC1, $p < 0.001$; PC2, $p = 0.002$). Soil moisture was strongly correlated with PC1 ($r = 0.81$), confirming its role as the dominant gradient, whereas salinity (EC; $r = 0.69$) and disturbance ($r = 0.62$) loaded primarily on PC2.

Non-metric multidimensional scaling (Bray–Curtis dissimilarities, stress = 0.14) revealed a clear separation of mesophytic, xerophytic and halophytic communities. PERMANOVA showed that the measured environmental variables explained 42% of compositional variation (pseudo-$R^2 = 0.42$, $p < 0.001$). PERMDISP indicated homogeneous dispersions ($p = 0.12$), confirming that differences were mainly in community composition, not in dispersion.

Variance partitioning attributed 28% of the total variation in species composition to pure environmental effects (14% to moisture, 9% to salinity, and 5% to disturbance), with 12% explained by shared fractions. Approximately 58% of the variation remained unexplained by the measured variables. Multi-seasonal hydrological simulations reduced residual variance by ~2%, indicating that including temporal variability marginally improved model fit.

Generalised linear models confirmed that salinity had a significant negative effect on Shannon diversity ($\beta = -0.20$, 95% CI [−0.27, −0.13]), as did anthropogenic disturbance ($\beta = -0.14$, 95% CI (−0.21, −0.07). The interaction between moisture and salinity was significant ($\beta = -0.09$, $p = 0.003$), indicating that the negative effect of salinity on diversity was stronger under lower moisture availability. Residual diagnostics and VIF values (< 3.5) supported the validity of the models.

4. Discussion

The observed decline in diversity and evenness with increasing salinity and aridity is consistent with the stress-gradient hypothesis, which predicts that species richness and evenness decrease under stronger abiotic stress (Maestre et al., 2009; Bertness & Callaway, 1994). The Caspian coastal gradient from humid mesophytic communities to salt-tolerant halophytic assemblages illustrates a classic transition from resource-driven to stress-dominated community regulation, with moisture availability as the primary niche axis and salinity as a secondary filter (Chase & Myers, 2011; Chase, 2007).

However, the fact that the measured environmental variables explain only 42% of compositional variation implies that additional processes play a substantial role in community assembly. The 58% unexplained variation likely reflects the combined effects of dispersal limitation, microsite-scale heterogeneity, spatial structure and temporal dynamics. The strong interaction between moisture and salinity on H' ($\beta = -0.09$, $p = 0.003$) indicates that the negative effect of salinity on diversity is amplified under low-moisture conditions, consistent with the osmotic stress reducing the pool of physiologically feasible species when both water and salt are limiting (Flowers & Colmer, 2008; Rozema & Schat, 2013).

The modest effect of multi-seasonal hydrological simulations (~2% reduction in residual variance) suggests that, over the 2023–2025 sampling window, short-term temporal variability in soil moisture and EC has limited leverage on community structure compared with spatial heterogeneity. This pattern aligns with the idea that spatially explicit, fine-scale gradients (microtopography, soil texture, patchy disturbance) often dominate community organisation in heterogeneous coastal systems (Legendre & De Cáceres, 2013; De Cáceres et al., 2012). The 12% shared variance between moisture and disturbance indicates that human-driven land-use changes do not create entirely new compositional patterns but rather reshape the realised niche space along the existing moisture–salinity gradient.

The role of neutral processes is harder to quantify without trait data or explicit spatial null models, but the large unexplained variation is consistent with the partial contribution of stochastic dispersal and demographic drift (Vellend, 2016; Hubbell, 2001). The observed structure—clear separation of mesophytic, xerophytic and halophytic communities, yet strong β-diversity within districts—suggests a mixture of deterministic filtering and neutral assembly. The modest impact of multi-seasonal simulations further implies that current methods would benefit from combining spatially explicit null models (e.g., db-MEM or PCNM) and trait-based filtering analyses to disentangle niche and neutral contributions.

Under ongoing Caspian Sea-level decline (Court et al., 2025; Lahijani et al., 2024), the salinity-moisture gradient is expected to intensify, with potential shifts from mesophytic to halophytic dominance in many coastal sectors. This trend, combined with the strong negative effect of disturbance, underscores the vulnerability of high-diversity humid districts to both hydrological and land-use changes. Conservation strategies should therefore prioritise the protection of mesic refugia, the enforcement of buffer zones around saline-arid habitats and the restoration of degraded halophytic communities under the predicted trajectory of increasing aridity and salinity.

5. Limitations

Several methodological and conceptual limitations should be acknowledged. First, floristic sampling was spatially stratified but temporally limited to 2023–2025, providing a robust snapshot of community structure yet capturing only short-term temporal variability. Direct assessment of temporal turnover (α/β-diversity through time) would strengthen the evaluation of neutral versus niche processes (Chase & Myers, 2011; Legendre & De Cáceres, 2013).

Second, the study did not incorporate functional trait data, which would allow a more explicit test of environmental filtering versus clustering relative to dispersal limitation (Kraft et al., 2015; Vellend, 2016). Without trait information, inferences about the role of neutral theory remain largely indirect. Third, anthropogenic disturbance was quantified using distance-to-infrastructure and remote-sensing-derived land-use intensity, which are objective but still crude proxies for the true complexity of disturbance regimes (e.g., grazing intensity, fire frequency, urbanisation pressure). These metrics integrate some aspects of disturbance but likely miss fine-scale heterogeneity in disturbance intensity and type.

Fourth, the decision to use unconstrained PCA on the Hellinger-transformed species matrix, rather than a constrained RDA with explicit environmental predictors, is appropriate for exploratory gradient detection but limits the ability to partition variance directly within the constrained ordination framework. The subsequent use of variance partitioning on separate GLM/PERMANOVA outputs is statistically sound but introduces analytical separation between ordination and partitioning steps that could be streamlined under a unified constrained ordination + redundancy-based partition framework (Legendre & De Cáceres, 2013; De Cáceres et al., 2012).

Finally, the 58% unexplained variation, while consistent with expectations in open, heterogeneous coastal systems, must be interpreted cautiously. It likely reflects the combined effects of dispersal limitation, fine-scale microsite heterogeneity, spatial autocorrelation, and temporal dynamics not captured by the measured variables or the multi-seasonal simulation. However, the current design does not allow a mechanistic separation of these processes; explicit tests of spatial structure (e.g., Mantel tests, db-MEM or PCNM decomposition) and future trait-based analyses are required for stronger causal inference.

6. Conclusion

Environmental filtering associated with soil moisture and salinity plays a significant role in structuring the Caspian coastal flora, yet a large proportion of compositional variation (~58%) remains unexplained by the measured variables. The modest contribution of multi-seasonal hydrological simulations (~2% reduction in residual variance) suggests that fine-scale spatial structure and microsite heterogeneity, rather than temporal variability, are the primary drivers of the remaining variance. The observed decline in diversity and evenness under increasing stress, combined with the significant moisture × salinity interaction, is consistent with the stress-gradient hypothesis and niche-based environmental filtering, but the magnitude of unexplained variation implies that neutral and stochastic processes are also important (Vellend, 2016; Chase & Myers, 2011).

These results provide a quantitative baseline for conservation planning along the Caspian coast under ongoing sea-level decline and intensifying anthropogenic pressures. The strong negative effect of disturbance and the concentration of high-diversity communities in the most humid districts indicate that conservation efforts should prioritise the protection of mesic habitats and the reduction of land-use intensity in vulnerable saline-arid zones. Future research should combine long-term, multi-seasonal monitoring, functional trait measurements, and explicit spatial modelling to disentangle the relative contributions of niche and neutral processes in this ecologically and socially important coastal region.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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