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RESEARCH ARTICLE

Linking underground morphological adaptations with ecological niche differentiation in desert species of *Gagea* (Liliaceae): insights from section *Incrustatae*

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Abstract

This study investigates the relationship between underground morphological adaptations and ecological niche differentiation in desert species of the genus *Gagea* (Liliaceae), with particular focus on section Incrustatae. Three narrowly distributed geophytic species – *Gagea circumplexa*, *G. incrustata*, and *G. khassanovii* – were analyzed using an integrative approach combining detailed morphological observations and ecological niche modelling based on the MaxEnt algorithm. Occurrence records obtained from herbarium collections, online databases, and field surveys were used to model current and future habitat suitability under climatic and edaphic conditions. The models revealed spatially restricted areas of high suitability associated with arid and semi-arid habitats of Central Asia. Temperature

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seasonality (BIO4), precipitation variables, and soil properties were identified as the most important environmental predictors influencing species distributions. Morphological analyses demonstrated distinct adaptive features of underground organs, including sclerenchymatous root systems and velamen-like bulb tunics. These structures are interpreted as functional traits that enhance water retention, mechanical stability, and survival under extreme desert conditions. The close correspondence between morphological adaptations and ecological preferences suggests that underground structural traits play a significant role in shaping ecological niches and distribution limits of desert *Gagea* species. The results highlight the importance of integrating morphological, ecological, and distributional data to better understand evolutionary adaptation and diversification processes in arid environments.

Keywords
Arid environments, Central Asia, ecological specialization, geophytes, MaxEnt modeling, sclerenchymatous roots, velamen-like bulb tunics

Introduction

The genus *Gagea* Salisb. (Liliaceae) comprises more than 300 species of early-spring geophytes widely distributed across the temperate regions of Eurasia. The main centres of species diversity are associated with Central Asia and the Irano-Turanian floristic region, where numerous narrow-ranged and ecologically specialized species of the genus have evolved (Vvedensky 1971; Levichev 2005; Wang et al. 2023). Despite long-standing taxonomic attention, species delimitation within *Gagea* remains problematic. This difficulty is largely caused by high morphological variability of above-ground organs, the short vegetation period, and the widespread occurrence of homoplasy, i.e. the independent evolutionary emergence of similar characters in unrelated lineages (Qiu et al. 2023; Kubentayeva et al. 2026; Kurbaniyazova et al. 2026a, b).

In desert and semi-desert environments, geophytic plants rely predominantly on their underground organs for survival, as these structures play a crucial role in adaptation to water deficit, strong temperature fluctuations, and a short growing season. Bulbs, roots, and associated protective structures function as key adaptive organs responsible for water acquisition, storage, and protection against desiccation (Schimper 1888; Goebel 1921; Khodorova & Boitel-Conti 2013). These adaptations are especially important in early-spring ephemerals inhabiting arid regions, where climatic seasonality strongly constrains growth and reproductive phases (Carni et al. 2014).

One of the most intriguing yet insufficiently studied aspects of underground adaptation is the occurrence of velamen or velamen-like structures. In the classical sense, velamen is characteristic of aerial roots of epiphytic plants, particularly within Orchidaceae, where it facilitates rapid water uptake and reduces evaporative water loss (Zotz et al. 2017). Although velamen sensu stricto has not been documented in *Gagea*, several species adapted to arid and semi-arid environments exhibit struc-

tures that can be interpreted as functional analogues of velamen, representing convergent adaptations to water-limited conditions (Wang et al. 2026).

According to Levichev (1999) and earlier studies (Pascher 1942), several arid-adapted *Gagea* species, such as *G. circumplexa*, *G. afghanica*, *G. deserticola* and *G. villosula* possess well-developed sclerenchymatous roots composed of thick-walled, multilayered, and partially dead cells. These roots are thought to function as a soil velamen analogue, retaining capillary moisture, facilitating condensation, and maintaining a humid microenvironment within the root zone. In contrast, species from mesic habitats with deeply buried bulbs typically show weakly developed or entirely absent sclerenchymatous roots.

Gagea incrustata Vved. represents a distinct and highly specialized model of underground adaptation. In this species, a velamen-like system is not formed by the roots but by a multilayered, dead bulb tunic with a complex system of cavities. This structure is interpreted as a functional analogue of velamen, enabling temporary water storage and protecting the bulb from desiccation (Levichev 1999). Similar structural diversity in underground organs has been documented in other *Gagea* species, highlighting the importance of morphological plasticity in adaptation to heterogeneous environments (Qiu et al. 2023; Kubentayeva et al. 2026).

The morphological adaptations outlined above are particularly pronounced in species of *Gagea* sect. *Incrustatae* Levichev, a section comprising narrow-ranged, ecologically specialized species characterized by complex underground structures. However, the relationship between these structural adaptations and the ecological niches occupied by the species has not yet been comprehensively assessed.

In the present study, a detailed morphological analysis of underground and vegetative organs in species of *Gagea* sect. *Incrustatae* is integrated with an assessment of their ecological niche characteristics. By combining structural traits with species distribution modelling, we aim to clarify the role of underground adaptations in shaping the ecological strategies of desert-adapted geophytes and to provide deeper insights into morphological evolution within the genus *Gagea*. Despite increasing knowledge on both morphological adaptations and species distribution patterns in geophytes, the relationship between underground morphological traits and ecological niche differentiation remains poorly understood, particularly in desert-adapted taxa. Integrating morphological and ecological approaches can provide deeper insights into the functional mechanisms underlying species distribution and adaptation.

In this context, species of *Gagea* sect. *Incrustatae* represent an ideal model group due to their specialized underground structures and restricted distribution in arid environments of Central Asia. Species distribution modelling is widely used to assess potential habitat suitability and species–environment relationships (Booth et al. 2014).

The studied species represent different ecological strategies within desert environments. *Gagea circumplexa* is relatively widespread across arid lowlands and foothill regions, typically associated with calcareous and compact soils. In contrast,

G. incrustata exhibits a more restricted distribution linked to sandy and heterogeneous substrates, while *G. khassanovii* is a narrowly distributed species confined to specific desert microhabitats. This ecological contrast makes them an ideal model for investigating the relationship between morphological adaptation and niche differentiation.

Materials and methods

Study material and occurrence data

Occurrence data for *G. incrustata* (Fig. 4; Suppl. material 2: Fig. S2 (TASH064475)), *Gagea circumplexa* and *G. khassanovii* (Suppl. material 2: Fig. S2) were compiled from herbarium specimens, online biodiversity databases, and original field investigations. Herbarium materials were examined from TASH (Central Herbarium of Uzbekistan), LE (Komarov Botanical Institute, St. Petersburg), as well as major herbaria of Kyrgyzstan (FRU) and Tajikistan (TAD). Additional georeferenced records were obtained from GBIF (https://www.gbif.org/species/5300087), Plantarium (https://www.plantarium.ru/), and historical taxonomic sources, including Historia Gagearum (https://www.binran.ru/resources/archive/gagearum/nameslist-rus.html).

Field surveys were conducted across arid and semi-arid regions of Central Asia. All newly collected specimens were georeferenced using handheld GPS devices. After data cleaning, removal of duplicate records, and exclusion of spatially imprecise localities, the final datasets used for ecological niche modeling included 36 records for *G. circumplexa*, 20 records for *G. incrustata*, and 15 records for *G. khassanovii*. Sampling localities used for morphological analysis are indicated in Suppl. material 1: Fig. S1.

Environmental variables

Ecological niche modeling was based on a combined set of climatic and edaphic predictors to capture both macroclimatic and substrate-related constraints. Nineteen bioclimatic variables (BIO1–BIO19), representing temperature and precipitation regimes, were obtained from the WorldClim v2.1 database at a spatial resolution of approximately 1 km (Fick & Hijmans 2017). The environmental predictors considered in the climatic–topographic and soil-based models are listed in Suppl. material 6: Table S1.

To account for habitat-specific constraints typical of desert environments, edaphic variables were included, such as soil texture, pH, bulk density, organic carbon content, and sand and clay fractions, derived from global soil databases (Hengl et al. 2017). Elevation data were obtained from the SRTM digital elevation model (Farr et al. 2007).

To account for substrate-related environmental conditions, selected soil properties, including soil texture, pH, bulk density, cation exchange capacity, and coarse fragment content, were considered using global soil datasets (Hengl et al. 2017).

Climatic–topographic and soil-based suitability models were developed separately using MaxEnt version 3.4.4. The resulting species-specific models differed in their environmental predictor composition and relative variable contributions. The importance of individual predictors was assessed using percent contribution, permutation importance, and jackknife analyses, where available. Given the possibility of correlations among environmental variables, the relative contributions of individual predictors were interpreted cautiously. The environmental predictors included in the resulting models are summarized in Suppl. material 6: Table S1.

Future climatic suitability was explored using projections from the MIROC6 global climate model under the SSP2-4.5 scenario for the mid-century (2041–2060) and late-century (2061–2080) periods. These projections were used to examine potential changes in environmentally suitable areas under a selected climate-change scenario.

To explore possible ecological differentiation among the studied species, environmental conditions at occurrence localities were considered alongside the observed differences in underground morphological traits. These comparisons were treated as exploratory and were not interpreted as direct evidence of a causal relationship between environmental conditions and morphological differentiation.

Soil-based suitability modelling

Soil-based habitat suitability was modelled separately for each species using MaxEnt version 3.4.4. The edaphic predictors included cation exchange capacity (CECSOL), coarse fragment content (CRFVOL), clay content (CLYPPT), soil bulk density (BDRLOG), and soil pH (PHIHOX). The predictor sets varied among species: four variables were used for *G. circumplexa* and *G. khassanovii*, while five variables were used for *G. incrustata*. Variable importance was examined using percent contribution, permutation importance, and jackknife analyses. Model performance was assessed using receiver operating characteristic (ROC) curves and the area under the curve (AUC). The complete species-specific predictor sets are provided in Suppl. material 6: Table S1.

Ecological niche modeling

Species distribution models were generated using the Maximum Entropy algorithm implemented in MaxEnt v.3.4.4 (Phillips et al. 2006; Phillips & Dudík 2008), which performs well with presence-only data and limited sample sizes. For each species, 75% of occurrence records were randomly assigned for model training and 25% for model testing.

Models were run using automatic feature selection (linear, quadratic, and hinge features) and default regularization parameters. Ten replicate runs were performed using the bootstrap method, as recommended for small datasets (Elith et al. 2011). Model outputs were generated in cloglog format, providing continuous estimates of habitat suitability ranging from 0 (unsuitable) to 1 (highly suitable).

Model evaluation and mapping

Model performance was evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC) (Fielding & Bell 1997). AUC values above 0.7 were considered indicative of acceptable model performance, while values exceeding 0.8 indicated high predictive accuracy. The relative importance of environmental variables was assessed using jackknife tests and permutation importance implemented in MaxEnt (Phillips et al. 2006). Species-specific ecological preferences were further evaluated based on response curves. Species distribution maps were produced in ArcGIS, and final figure layouts were prepared using Adobe Photoshop CS6 (x64).

Morphological analysis

Morphological analyses of underground and vegetative organs were conducted using herbarium specimens and freshly collected material. A total of 58 specimens were examined, including 35 specimens of *Gagea circumplexa*, 12 specimens of *G. incrustata*, and 11 specimens of *G. khassanovii*. Macromorphological characters of bulbs, bulb tunics, and roots were examined using stereomicroscopes and light microscopes. Morphological illustrations were prepared based on stereomicroscopic observations and digitally processed using Adobe Photoshop CS6 (x64).

Results

Present and future potential distribution patterns

Under historical climate (1970–2000), the three studied species exhibit markedly different patterns of habitat suitability, reflecting their distinct ecological strategies. *Gagea circumplexa* shows a relatively broad and continuous distribution across arid and semi-arid regions of Central Asia, particularly in lowland deserts and adjacent foothill plains (Table 1, Fig. 1A). In contrast, *G. incrustata* is characterized by a more fragmented and spatially restricted distribution, largely associated with specific edaphic conditions, particularly sandy and loamy desert substrates (Table 1, Fig. 2A). *G. khassanovii* occupies the narrowest ecological niche, with suitable habitats confined to highly specific desert microhabitats (Table 1, Fig. 3A). Previous taxonomic investigations documented that *G. khassanovii* is endemic to the eastern Fergana Valley, particularly the Chatkal and Alay mountain ranges, where it pre-

dominantly inhabits gravelly soils and rocky outcrops of mountain spurs (Turginov et al. 2025). These documented habitat characteristics provide an ecological context for interpreting the species potential distribution and its association with specific edaphic conditions. Model performance varied among the three studied species. The climatic–topographic models yielded mean test AUC values of 0.866 ± 0.143 for *Gagea circumplexa*, 0.959 ± 0.034 for *G. incrustata*, and 0.971 ± 0.003 for *G. khassanovii*. Temperature seasonality (BIO4) was the dominant climatic predictor in all three models, although its relative contribution differed among species (Table 1). Separate soil-based models indicated species-specific variation in the relative importance of edaphic predictors. Detailed model diagnostics, including jackknife tests, ROC curves, and omission-rate analyses, are provided in the Suppl. materials 3–5: Figs S3–S5.

Future climate projections reveal consistent trends of habitat contraction and spatial restructuring across all species, although the magnitude of change differs among taxa. By 2050, *G. circumplexa* is predicted to undergo a partial northward and altitudinal shift of suitable habitats, accompanied by a reduction in southern desert areas (Fig. 1B). These changes become more pronounced by 2070, with increasing fragmentation of highly suitable zones (Fig. 1C).

Table 1. Model performance and key environmental predictors for the studied *Gagea* species, including the number of occurrence records, AUC values for training and test datasets, and the most influential bioclimatic and soil variables

Species	Number of records	Climatic test AUC (mean ± SD)	Key climatic predictors (% contribution)	Key soil predictors (% contribution)
Gagea circumplexa	36	0.866 ± 0.143	BIO4 (81.1), elevation (7.0), BIO10 (5.1)	CECSOL (45.5), CRFVOL (29.1), CLYPPT (15.9)
G. incrustata	20	0.959 ± 0.034	BIO4 (40.8), BIO6 (22.0), BIO9 (11.0)	CECSOL (63.6), BDRLOG (17.9), PHIHOX (9.6)
G. khassanovii	15	0.971 ± 0.003	BIO4 (80.0), BIO15 (16.9), BIO1 (3.1)	CRFVOL (97.7), CLYPPT (1.8), CECSOL (0.6)

Note: BIO4, temperature seasonality; BIO6, minimum temperature of the coldest month; BIO9, mean temperature of the driest quarter; BIO10, mean temperature of the warmest quarter; BIO15, precipitation seasonality; BIO1, annual mean temperature; CECSOL, cation exchange capacity; CRFVOL, coarse fragment content; CLYPPT, clay content; BDRLOG, soil bulk density; PHIHOX, soil pH. Climatic and soil models were developed separately.

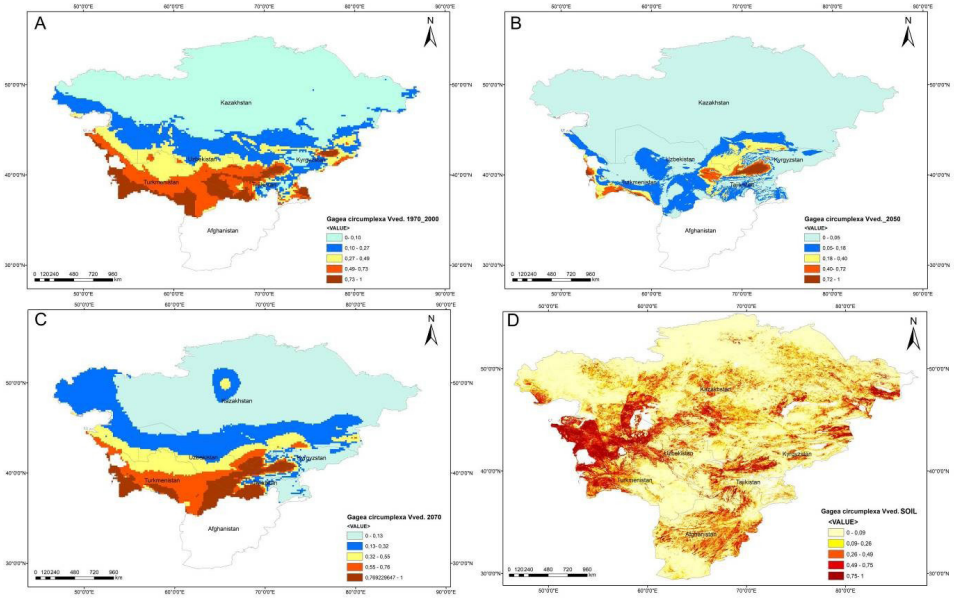


Figure 1. Potential distribution of *Gagea circumplexa* under (**A**) historical climate (1970–2000), (**B**) future climate scenario 2050, (**C**) future climate scenario 2070, and (**D**) soil-based suitability model.

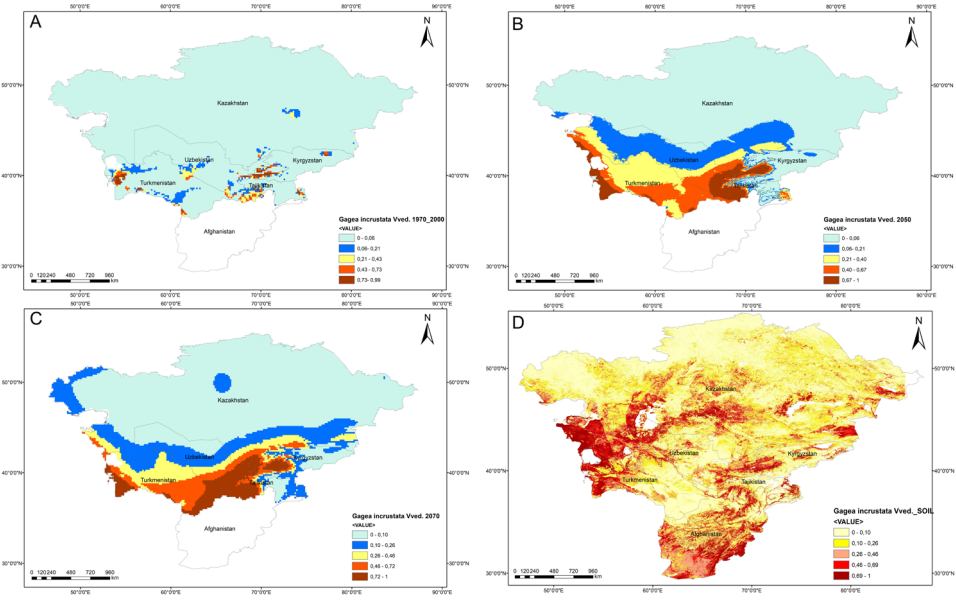


Figure 2. Potential distribution of *Gagea incrustata* under (**A**) historical climate (1970–2000), (**B**) future climate scenario 2050, (**C**) future climate scenario 2070, and (**D**) soil-based suitability model.

Gagea incrustata demonstrates stronger sensitivity to climate change, with future projections indicating substantial habitat fragmentation and a marked reduction of highly suitable areas, particularly under the 2070 scenario (Fig. 2B–C). The most pronounced response is observed in *G. khassanovii*, which shows a drastic decline in suitable habitats across all future scenarios, suggesting limited ecological tolerance and reduced capacity to track shifting climatic conditions (Fig. 3B–C).

Separate soil-based suitability models revealed differences in the relative importance of edaphic predictors among the three *Gagea* species (Figs 1D, 2D, 3D). Cation exchange capacity (CECSOL) was the dominant soil predictor for *G. circumplexa* (45.5%) and *G. incrustata* (63.6%), whereas coarse fragment content (CRFVOL) contributed most strongly to the model for *G. khassanovii* (97.7%). These results suggest that different soil properties may be associated with the environmental suitability of the studied species. The soil-based predictions provide complementary information to the climatic projections, although the independent modelling approaches do not allow direct assessment of whether edaphic conditions mitigate the effects of future climate change.

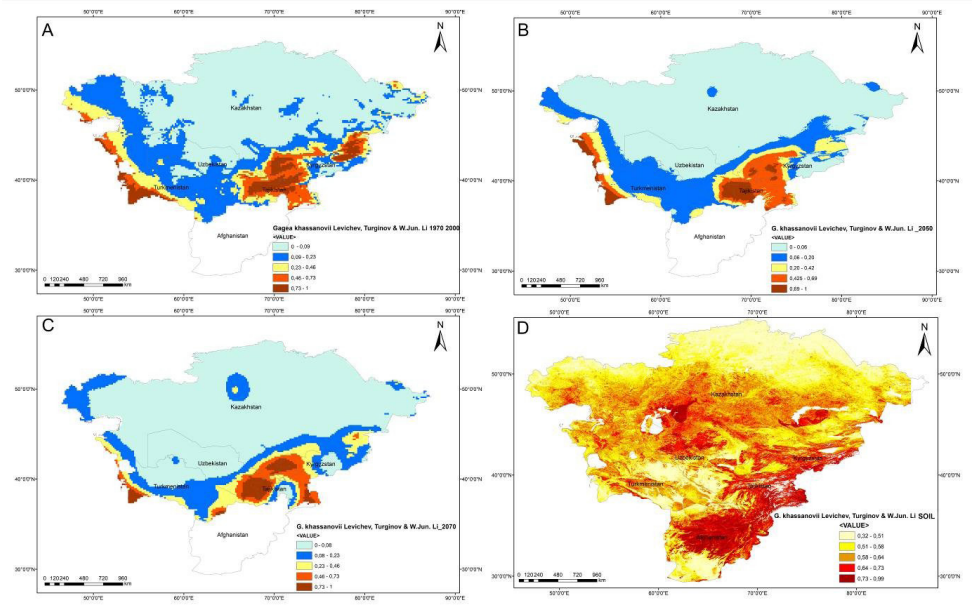


Figure 3. Potential distribution of *Gagea khassanovii* under (**A**) historical climate (1970–2000), (**B**) future climate scenario 2050, (**C**) future climate scenario 2070, and (**D**) soil-based suitability model.

Environmental characteristics of occurrence localities

Quantitative comparison of environmental conditions among the three studied species revealed significant ecological differentiation (Table 2). Significant interspecific differences were detected for BIO10, BIO12, BIO15, BIO17, and elevation (Kruskal–Wallis test, $P < 0.05$), whereas BIO4 did not differ significantly among species ($P = 0.199$). *Gagea khassanovii* occurred at higher elevations and under wetter climatic conditions characterized by higher BIO12 and BIO17 values, whereas *G. incrustata* occupied comparatively warmer habitats with the highest BIO10 values.

Table 2. Environmental characteristics of occurrence localities of the three studied *Gagea* species

Variable	*G. circumplexa* (n = 28)	*G. incrustata* (n = 12)	*G. khassanovii* (n = 11)	Kruskal–Wallis (P)
BIO4	1019.3 ± 43.4 (924.9–1190.1)	1016.8 ± 20.9 (977.9–1034.9)	995.8 ± 33.6 (960.4–1045.8)	0.199
BIO10	24.0 ± 4.8 (12.4–29.8)	26.8 ± 0.7 (25.4–27.7)	21.9 ± 2.4 (19.1–25.4)	<0.001
BIO12	236.2 ± 139.8 (117–816)	255.8 ± 49.9 (216–351)	383.2 ± 50.4 (305–432)	<0.001
BIO15	58.3 ± 18.5 (44.1–94.2)	61.2 ± 1.4 (58.0–62.5)	45.1 ± 2.8 (39.4–48.0)	<0.001
BIO17	13.1 ± 9.1 (1–45)	11.8 ± 3.8 (9–19)	37.9 ± 6.8 (25–46)	<0.001
Elevation (m)	1038.2 ± 937.9 (232–3169)	547.7 ± 215.0 (330–906)	1119.5 ± 199.4 (672–1277)	0.001

Contribution of environmental variables

Temperature seasonality (BIO4) was the leading climatic predictor in the MaxEnt models of all three *Gagea* species, although its relative contribution varied among taxa. BIO4 accounted for 81.1% of the model contribution in *G. circumplexa*, 40.8% in *G. incrustata*, and 80.0% in *G. khassanovii*. Other influential climatic and topographic predictors included elevation (7.0%) and mean temperature of the warmest quarter (BIO10; 5.1%) for *G. circumplexa*, minimum temperature of the coldest month (BIO6; 22.0%) and mean temperature of the driest quarter (BIO9; 11.0%) for *G. incrustata*, and precipitation seasonality (BIO15; 16.9%) for *G. khassanovii* (Table 1).

The separate soil-based models revealed differences in the relative importance of edaphic predictors among the studied species. Cation exchange capacity (CECSOL) contributed most strongly to the models of *G. circumplexa* (45.5%) and *G. ncrustata* (63.6%), followed by coarse fragment content (CRFVOL; 29.1%) and clay content (CLYPPT; 15.9%) in *G. circumplexa*, and soil bulk density (BDRLOG; 17.9%) and soil pH (PHIHOX; 9.6%) in *G. incrustata*. In contrast, coarse fragment content (CR-

FVOL) was the dominant soil predictor for *G. khassanovii* (97.7%). These findings indicate species-specific differences in the relative importance of soil properties and suggest that edaphic conditions may contribute to ecological niche differentiation among the studied taxa. However, the individual contributions of environmental predictors should be interpreted cautiously because of potential correlations among variables.

Quantitative relationships between morphological traits and environmental conditions

To explore potential associations between underground morphological characteristics and environmental conditions, selected environmental variables were examined at the occurrence localities of the three *Gagea* species. These comparisons were used to characterize species-specific environmental conditions rather than to establish direct functional relationships between morphological traits and individual environmental predictors. The three species exhibited differences in their modelled environmental associations. For *G. circumplexa*, the soil-based model identified cation exchange capacity (CECSOL; 45.5%), coarse fragment content (CRFVOL; 29.1%), and clay content (CLYPPT; 15.9%) as influential predictors. In *G. incrustata*, cation exchange capacity (63.6%) and soil bulk density (17.9%) contributed most strongly to the soil-based model. For *G. khassanovii*, coarse fragment content was the dominant edaphic predictor (97.7%). These species-specific patterns suggest that the studied taxa occupy environmentally differentiated habitats. Such differences may be relevant to the variation observed in their underground morphological structures, including sclerenchymatous roots and velamen-like bulb tunics. However, the present analyses do not directly test the functional relationship between individual morphological traits and environmental predictors. Therefore, these interpretations remain preliminary and require further investigation.

Morphological differentiation and velamen-associated root systems

Morphological analysis revealed pronounced interspecific differentiation in underground organs, particularly in root systems and bulb coverings, which closely correspond to the ecological patterns identified by niche models. These results demonstrate a clear functional link between structural adaptations and environmental constraints.

In *Gagea circumplexa*, bulbs are densely surrounded by thick, multilayered sclerenchymatous roots forming a compact protective envelope (Fig. 4). This structural configuration likely enhances mechanical stability and reduces water loss, representing an adaptation to compact, calcareous soils with high bulk density, as identified by the ecological models. The strong correspondence between this morphology and the dominance of carbonate-rich substrates supports the interpretation of sclerenchymatous roots as key adaptive traits for survival under physically restrictive soil conditions.



Figure 4. Morphological characteristics of *Gagea circumplexa*. **A** – Whole plant with bulb and sclerenchymatous root system; **B** – Bulb enclosed by a dense mass of thick, sclerenchymatous fibrous roots forming a compact protective sheath; **C** – Bulb after partial removal of the sclerenchymatous roots, showing the bulb scales and basal plate; **D** – Basal portion of the bulb with partially preserved sclerenchymatous root sheath; **E** – Dense sclerenchymatous root system surrounding the bulb, illustrating the compact protective envelope characteristic of the species.

In contrast, *Gagea incrustata* lacks well-developed sclerenchymatous roots and instead exhibits a highly specialized bulb structure, where multilayered, dead bulb tunics form a velamen-like protective system with internal cavities and ridges (Fig. 5). This morphology likely enhances water retention and thermal insulation while allowing limited root penetration into sandy substrates. The association of this species with soils characterized by variable texture and moderate stability suggests that this alternative structural strategy represents an adaptation to more heterogeneous and dynamic edaphic environments.

Gagea khassanovii, which occupies the narrowest ecological niche, is characterized by reduced or less specialized protective structures compared with *G. circumplexa* (Fig. 6). Morphological observations revealed a relatively simple fibrous root system and slender bulb, while root cross sections of the root showed no multilayered sclerenchymatous tissues comparable to those observed in *G. circumplexa*. These features are consistent with its restriction to specific desert microhabitats and its comparatively lower structural buffering capacity.

The morphology of *G. incrustata* further demonstrates bulb deepening and specialized bulb tunics, which likely facilitate vertical relocation of the bulb and improve protection under unstable sandy substrates (Fig. 5).

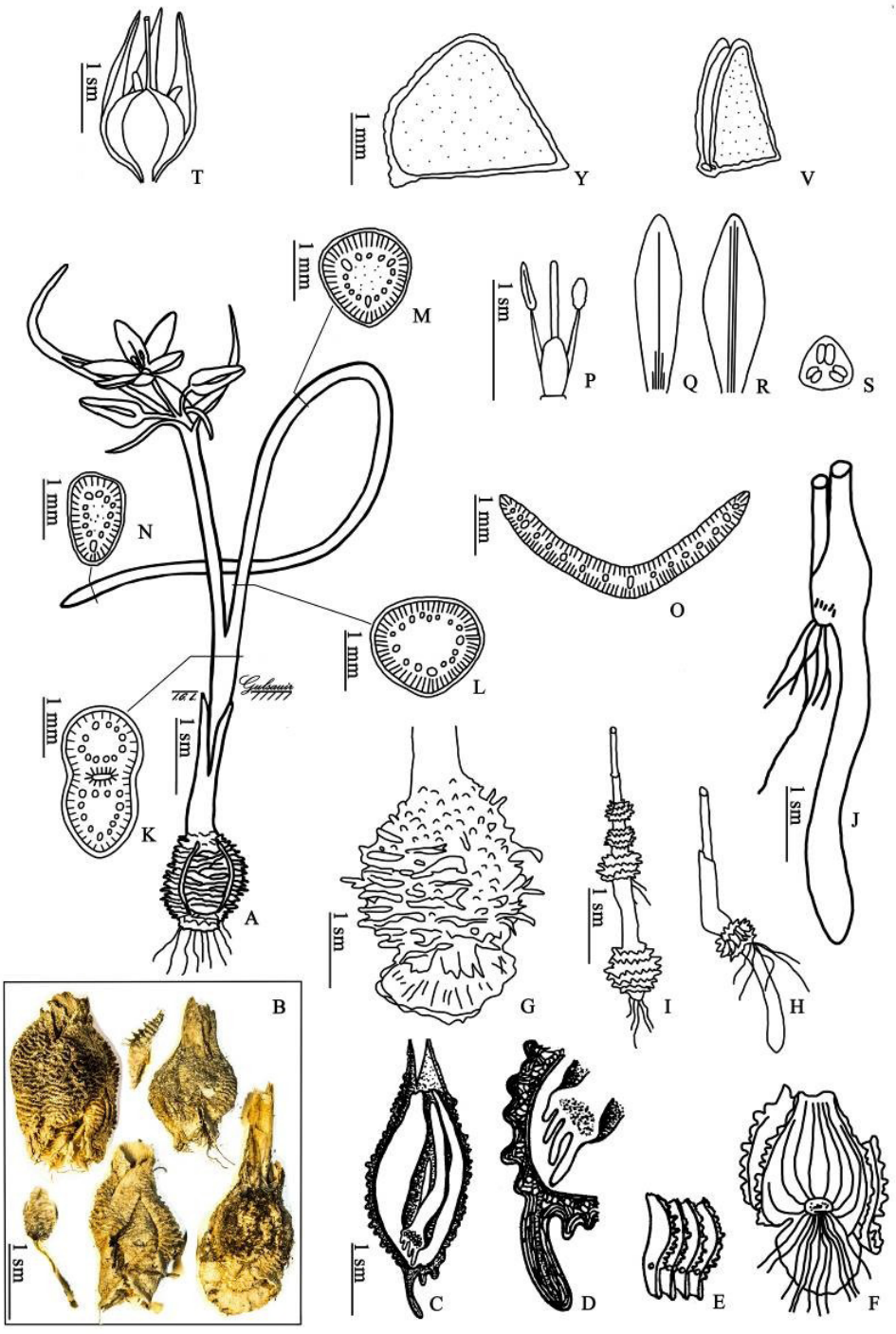


Figure 5. The description is on the next page.

Figure 5. *Gagea incrustata* Vved.; sclerified roots are not developed. **A** – General view of the generative shoot and bulb. **B** – Dead, dry protective bulb tunics performing a velamen-like function. **C** – Longitudinal section of the bulb during the autumn–winter period; in the central canal, the bud of the next growth cycle with primordia of thin roots emerging from the basal plate. **D** – Enlarged fragment of the previous section; the tunic, complicated by external ridges, is penetrated by a complex system of cavities and voids. **E** – Sections of dry tunic fragments originating from four successive shoots of previous years. **F** – Inner surface of the tunic with a ridge (directed downward), the basal plate with a bundle of roots oriented into the fissure of the ridge. **G** – External view of the bulb of a three-year-old plant. Bulb-deepening stolons: **H** – 2–3-year-old juvenile plant with a dry tunic from the previous year and a deepening stolon of the current growth cycle. **J** – 5–6-year-old plant with dead tunics representing four successive stages of bulb deepening from previous years. **I** – Immature plant (with a floral stalk primordium); all tunics removed. **K** – Transverse section showing the fusion of the basal leaf with the flowering stalk. **L**, **M**, **N** – Successive transverse sections of the basal leaf above the fusion zone. **O** – Transverse section of the bract subtending the inflorescence in its expanded part. **P** – Ovary, style, and anthers (left anther dehisced). Perianth segments: **Q** – inner tepal. **R** – outer tepal. **S** – Transverse section of the ovary. **T** – Mature capsule with dry perianth segments and anthers. **Y** – Seed, lateral view (micropyle and point of attachment on the right). **V** – Seed, view from the chalazal side.

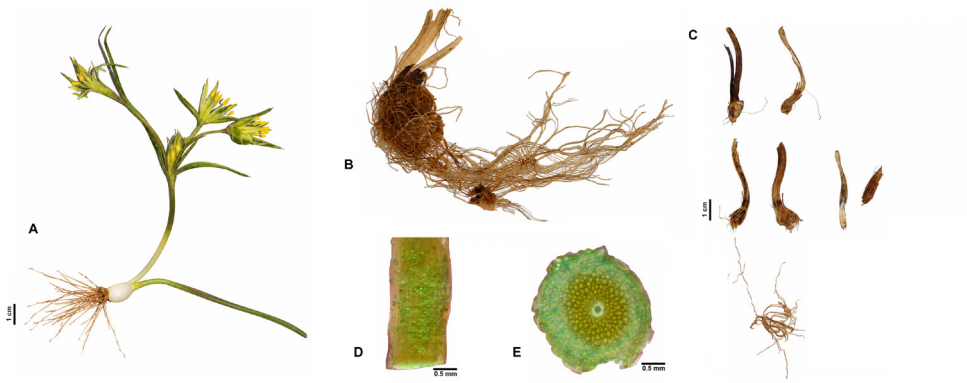


Figure 6. Morphological characteristics of *Gagea khassanovii*. **A** – Whole plant showing the bulb and fibrous root system. **B** – Bulb with fibrous root system. **C** – Variation in bulb morphology and root development among examined individuals. **D** – Longitudinal section of the root. **E** – Transverse section of the root.

In addition to the specialized underground organs, *Gagea incrustata* exhibits characteristic vegetative and reproductive morphological features (Fig. 5K–V). Successive transverse sections of the basal leaf (Fig. 5K–N) demonstrate changes in leaf anatomy above the fusion zone with the flowering stalk. The bract shows a narrow expanded lamina (Fig. 5O). Floral morphology includes a typical ovary, style, and stamens (Fig. 5P), inner and outer tepals (Fig. 5Q–R), and a trilocular ovary in

transverse section (Fig. 5S). Mature capsules (Fig. 5T) contain triangular seeds with distinct lateral (Fig. 5Y) and chalazal (Fig. 5V) views, providing additional diagnostic characters for species identification. These characters are presented primarily for taxonomic documentation and species identification, whereas the ecological interpretation in the present study is based mainly on underground organs (bulbs, roots, and bulb tunics).

Overall, the strong correspondence between underground morphological traits and the dominant environmental predictors identified by ecological niche models provides robust evidence that root and bulb adaptations represent key functional traits shaping the ecological niches, distribution patterns, and environmental tolerance of desert *Gagea* species.

Discussion

Ecological differentiation and niche dynamics in desert *Gagea* species

The present study demonstrates pronounced ecological differentiation among desert-dwelling species of *Gagea*, as evidenced by both current and projected ecological niche models. Despite their close taxonomic relationships, *G. circumplexa*, *G. incrustata*, and *G. khassanovii* occupy clearly distinct environmental spaces, indicating limited niche conservatism and a high degree of ecological specialization. The model performance, as assessed by AUC values, indicates the ability of the selected environmental predictors to discriminate occurrence localities from background conditions, although it does not establish the relative roles of deterministic environmental constraints and stochastic processes in shaping species distributions (Wang et al. 2023). Previous studies on desert trees and shrubs have demonstrated that differ-ences in water-use strategies and root plasticity lead to clear ecological niche dif-ferentiation (Li et al. 2025). The observed differences in underground morphology may be associated with the contrasting environmental conditions occupied by the studied species.

Projected distribution shifts under future climate scenarios (2050 and 2070) further highlight the sensitivity of desert geophytes to climatic variability. While *G. circumplexa* retains comparatively broader areas of climatic suitability, *G. incrustata* and especially *G. khassanovii* show progressive habitat contraction and increasing fragmentation. Such patterns are consistent with general trends observed in arid and semi-arid ecosystems, where increasing temperature seasonality and aridification lead to range reduction and habitat isolation (Wang et al. 2023). The pronounced decline in suitability predicted for *G. khassanovii* suggests a limited capacity for climatic buffering and indicates high vulnerability to future environmental change.

The climatic–topographic models yielded mean test AUC values of 0.866 ± 0.143 for G. circumplexa, 0.959 ± 0.034 for *G. incrustata*, and 0.971 ± 0.003 for *G. khassanovii* (Table 1). These values indicate differences in model discrimination

performance, but should not be interpreted as direct measures of ecological niche breadth or environmental tolerance.

Another potential source of uncertainty is the spatial distribution of occurrence records, particularly for narrowly distributed species represented by relatively small datasets. Geographic sampling bias may influence the estimated environmental suitability patterns, and spatial filtering has been proposed as one approach to reduce its effects (Boria et al. 2014).

The observed differences in environmental suitability may be associated with variation in underground morphological structures. However, the present analyses do not directly establish whether these morphological traits determine ecological niche breadth or environmental tolerance. Further functional and comparative investigations are needed to evaluate these potential relationships.

The observed morphological variability is consistent with previous studies demonstrating that *Gagea* species exhibit significant structural plasticity in response to environmental heterogeneity (Kubentayeva et al. 2026; Qiu et al. 2023; Gargano & Peruzzi 2021).

Although ecological niche models provide useful insights into potential distribution patterns, their projections should be interpreted cautiously because correlative models do not fully account for species interactions, dispersal limitations, or adaptive responses to environmental change (Araújo and Peterson 2012). Furthermore, future habitat suitability projections may be sensitive to the selection of climate models and emission scenarios. As the present study considered only the MIROC6 global climate model under the SSP2-4.5 scenario, the projected distributional changes should be regarded as scenario-dependent estimates rather than definitive predictions of future species ranges (Araújo et al. 2005).

Role of climatic and edaphic factors in shaping niche structure

Among climatic predictors, temperature seasonality (BIO4) emerged as the dominant variable across all species, emphasizing the importance of extreme annual temperature fluctuations in shaping desert plant distributions. This result is ecologically consistent with the life-history strategy of early-spring geophytes, whose growth, flowering, and reproduction are restricted to short favorable climatic windows and tightly synchronized with seasonal temperature dynamics (Khodorova & Boitel-Conti 2013). Similar patterns have been documented in Mediterranean and Balkan early-spring geophytes, where temperature seasonality strongly determines species distribution and phenological timing (Carni et al. 2014). On the other hand, at global scale precipitation patterns where crucial in the evolution of geophytism, while temperature may be a driving force in rhizome evolution of rhizomatous and non-geophytic taxa (Howard et al. 2019) In addition to climatic factors, edaphic predictors contributed to the soil-based suitability models, although their relative importance differed among species. Cation exchange capacity (CECSOL) was the leading predictor for *G. circumplexa* and *G. incrustata*, whereas coarse fragment

content (CRFVOL) was most influential for *G. khassanovii*. These patterns suggest that soil properties may contribute to differences in habitat suitability among the studied taxa. However, because climatic and edaphic models were developed separately, their combined effects and potential interactions were not directly evaluated.

Morphological adaptations and velamen as an ecological trait

The studied *Gagea* species exhibit distinct underground morphological structures and differences in their modelled environmental suitability. These observations suggest a possible relationship between morphological differentiation and ecological conditions, although the functional significance of individual traits has not been directly tested.

In *Gagea circumplexa*, the dense, multilayered envelope of sclerenchymatous roots forms a rigid protective system that enhances mechanical stability, reduces water loss, and buffers temperature extremes. This structural configuration is consistent with its association with compact, carbonate-rich soils and supports the interpretation of sclerenchymatous roots as key adaptive traits for survival under physically restrictive conditions. In contrast, *G. incrustata* lacks true sclerenchymatous roots and instead exhibits a highly specialized bulb structure in which multilayered, dead tunics form a velamen-like system with internal cavities. This alternative strategy likely enhances water retention and thermal insulation while allowing flexible root penetration into sandy substrates.

The observed morphological variability is consistent with previous studies demonstrating that *Gagea* species exhibit significant structural plasticity in response to environmental heterogeneity (Kubentayeva et al. 2026; Qiu et al. 2023). Notably, while population-level variability has been reported, key underground structures such as bulb organization remain relatively stable, suggesting strong selective pressure on functional traits associated with survival in arid environments. For example, some desert geophytes have specific leaf traits which help them to absorb water from dew and fog (Vogel & Müller-Doblies 2011). Our findings support the interpretation of velamen-like structures not merely as morphological peculiarities but as functional ecological traits associated with adaptation to water-limited and edaphically complex environments. Similar adaptive strategies have been described in other plant groups inhabiting extreme environments, where structural traits evolve convergently in response to similar ecological constraints (Wang et al. 2026).

Integrating morphology and ecological niche modelling

The comparison of MaxEnt-derived environmental suitability patterns and underground morphological characteristics suggests possible associations between ecological differentiation and structural variation. However, these relationships remain exploratory because direct statistical tests linking individual morphological traits to environmental predictors were not performed.

This morphology–niche coupling highlights the importance of integrating morphological data into ecological niche modelling, particularly for geophytic plants in which underground organs play a decisive role in survival and persistence. From a systematic perspective, these results indicate that underground morphological traits – such as velamen development and sclerenchymatous root architecture – may carry greater evolutionary and taxonomic significance than previously assumed. Their occurrence across phylogenetically distinct taxa suggests that these features represent convergent adaptations rather than strictly inherited characters.

Implications for evolution and conservation

The observed ecological and morphological differences among desert *Gagea* species may reflect divergent responses to climatic seasonality and edaphic conditions, although the evolutionary mechanisms underlying these patterns remain to be investigated. This process likely contributed to the high ecological heterogeneity observed within the genus across Central Asia. The morphology of geophyte underground organs still requires further investigation to better understand the evolutionary mechanisms underlying their structural diversification (Howard et al. 2019).

From a conservation perspective, species such as *G. khassanovii*, characterized by narrow ecological niches and limited morphological buffering capacity, may be particularly vulnerable to ongoing and future climate change. Similar situation is observed for rare and endemic semi-desert tulip species of Central Asia which may lose all current habitats by 2050 (Wilson et al. 2021). The identification of soil-dependent refugia highlights the importance of substrate-specific conservation strategies for desert geophytes.

Conclusion

Desert species of *Gagea* exhibit clear ecological differentiation associated with underground morphological adaptations. Ecological niche modelling revealed that both climatic seasonality and edaphic factors jointly shape species distributions and habitat specialization. Velamen-like structures and sclerenchymatous roots function as important adaptive traits enhancing survival under arid conditions. Future climate projections indicate increasing vulnerability of narrowly distributed species, particularly *Gagea khassanovii*, to habitat contraction and fragmentation. Overall, the integration of ecological and morphological approaches provides important insights into adaptive evolution and conservation of desert geophytes.

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Supplementary material 1

Figure S1. Spatial distribution of studied species of *Gagea* sect. *Incrustatae* in Central Asia based on georeferenced occurrence data

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Data type: image

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Supplementary material 2

Figure S2. Gagea species in nature and herbarium

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Data type: image

Explanation note: A – *Gagea circumplexa* Vved. B – *Gagea khassanovii* Levichev, Turginov & W. Jun (Photographs by O. Sheraliev). C – Herbarium voucher of *Gagea incrustata* Vved.

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Supplementary material 3

Figure S3. MaxEnt model diagnostics for three desert species of the genus *Gagea*
Authors: Gulsauir T. Kurbaniyazova, Dilafruz N. Jamalova, Gulchehra S. Dadayeva, Sirojiddin Z. Jumayev, Venera B. Davletmuratova, Rukhsora O. Atoeva, Yulduz N. Fayzulloyeva, Farxod I. Karimov, Denis V. Sandanov
Data type: image
Explanation note: (A–C) *Gagea circumplexa*: (A) jackknife test of variable importance, (B) receiver operating characteristic (ROC) curve showing model performance for training and test data, and (C) omission and predicted area curves.
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Link: https://journal.asu.ru/biol/article/view/19461/17660

Supplementary material 4

Figure S4. MaxEnt model diagnostics for three desert species of the genus *Gagea*
Authors: Gulsauir T. Kurbaniyazova, Dilafruz N. Jamalova, Gulchehra S. Dadayeva, Sirojiddin Z. Jumayev, Venera B. Davletmuratova, Rukhsora O. Atoeva, Yulduz N. Fayzulloyeva, Farxod I. Karimov, Denis V. Sandanov
Data type: image
Explanation note: (D–F) *Gagea incrustata*: (D) jackknife test of variable importance, (E) ROC curve, and (F) omission and predicted area curves.
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Supplementary material 5

Figure S5. MaxEnt model diagnostics for three desert species of the genus *Gagea*
Authors: Gulsauir T. Kurbaniyazova, Dilafruz N. Jamalova, Gulchehra S. Dadayeva, Sirojiddin Z. Jumayev, Venera B. Davletmuratova, Rukhsora O. Atoeva, Yulduz N. Fayzulloyeva, Farxod I. Karimov, Denis V. Sandanov
Data type: image

Explanation note: (G–I) *Gagea khassanovii*: (G) jackknife test of variable importance, (H) ROC curve, and (I) omission and predicted area curves. These diagnostics demonstrate high model performance and highlight the relative contribution of climatic and edaphic variables shaping the ecological niches of desert-dwelling *Gagea* species.

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Supplementary material 6

Table S1. Environmental predictors used in climatic–topographic and soil-based MaxEnt models for three *Gagea* species

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Data type: table

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