Phytocoenological and Ecogeographical study of Salvia nutans in Romania

Simona Dumitrița Chirilă

simonachirilasc@yahoo.com

Danube Delta National Institute for Research and Development: Institutul National de Cercetare-Dezvoltare Delta Dunarii https://orcid.org/0000-0003-3397-1834

Alexandru Sabin Bădărău

UBB: Universitatea Babes-Bolyai

Mihai Doroftei

Danube Delta National Institute for Research and Development: Institutul National de Cercetare-Dezvoltare Delta Dunarii

Kiril Vassilev

Bulgarian Academy of Sciences: B'lgarska akademia na naukite

Iuliia Vasheniak

National Academy of Sciences of Ukraine: Nacional'na akademia nauk Ukraini

---

Research Article

Keywords: anthropogenic impact, biogeography, dry grasslands, habitat requirement, Romanian flora, Salvia nutans, steppe relict

Posted Date: May 12th, 2025

DOI: https://doi.org/10.21203/rs.3.rs-6556566/v1

Version of Record: A version of this preprint was published at Biologia on April 24th, 2026. See the published version at https://doi.org/10.1007/s11756-026-02192-7.

Abstract

Salvia nutans is a steppe relict species, characteristic of the West Palearctic steppe and forest-steppe. It is vulnerable to overgrazing and the conversion of grasslands into arable land. Due to these anthropogenic impacts, the species is endangered in some locations in Romania. In this context, the study aims to find the plant associations in which the species occurs and the environmental factors that explain the floristic composition.

For the vegetation analysis, 870 relevés were used, and the data were analyzed in JUICE programme, applying the modified TWINSPAN algorithm for clustering. The floristic composition data and environmental variables were used for the multivariate analyses.

Salvia nutans was recorded most frequently in the *Festuco-Brometea* class, the *Festucetalia valesiacae* order, the *Stipion lessingianae* alliance, and the *Jurineo transylvanicae-Stipetum pulcherrimae* and *Allio albidi-Stipetum lessingianae* associations. Canonical Correlation Analysis indicates that annual precipitation (BIO12) explained most of the variation in floristic composition. *S. nutans* occurs predominantly on steep slopes with southwest aspects and at an average elevation of 359 m. The species occurs in moderately acidic to slightly alkaline soils, with moderate phosphorus and high potassium concentrations.

Salvia nutans is related to topographic and edaphic conditions, showing its role as an indicator species for continental, xerophilic grasslands. Given its vulnerability to land-use changes, *S. nutans* should be included in long-term monitoring programs to assess population dynamics.

Highlights

is a steppe relict species vulnerable to land-use changes.

The species occurs mainly in grasslands on steep, sunny slopes.

Its abundance is influenced by annual precipitation and temperature.

Biogeographic patterns suggest distinct regional lineages in Transylvania.

Long-term monitoring is needed due to habitat degradation and hybridization risks.

Introduction

Biodiversity decline represents a significant ecological challenge, affecting ecosystem services and human well-being (Dirzo and Raven 2003; Ceballos, García, and Ehrlich 2010; Isbell et al. 2023). Current species extinction rates far exceed historical natural rates, reaching levels that suggest the sixth major extinction event on Earth is underway (Barnosky et al. 2011; Ceballos, García, and Ehrlich 2017). This alarming acceleration underscores a conservation crisis where identifying the mechanisms driving biodiversity decline is a key priority for conservation biology (Didham et al. 2007). The causes of this decline are multiple, involving direct human activities and indirect environmental changes (Adla et al. 2022). Habitat loss, overexploitation, climate change, pollution, and the introduction of invasive species are the primary factors contributing to biodiversity decline, alongside other secondary threats (Maxwell et al. 2016; Caro et al. 2022). In particular, invasive species are frequently classified as the second most significant source of threat to biodiversity (Dueñas et al. 2018).

One of the plant species with restricted habitats is *Salvia nutans* L., a steppe relict (Gusztáv 2005; Sramkó and Laczkó 2020) and postglacial in the Carpathian Basin (Németh 1990; Simon 1992; Đakić, Knežević, and Boža 2012). The species *S. nutans* belongs to the Lamiaceae Martinov family (Sârbu, Ștefan, and Oprea 2013) and grows in a restricted range of habitats. Its habitat includes steppe and forest-steppe grasslands, where it co-occurs with various plants, ranging from herbaceous species to dicotyledons. These areas are characterized by chernozem soils on loess and a climate with continental influences. In natural conditions, the habitat exhibits a rich diversity of species, whereas, in degraded conditions, this diversity decreases, with the predominance of monocotyledons and grasses (Soó 1968; Csurös 1973, 1974; Gusztáv 2005). The species is also found in rocky areas and rock outcrops (Golevich, 2012), as well as in grasslands and scrublands (Sârbu, Ștefan, and Oprea 2013). From its phytocoenotic perspective, *S. nutans* occupies subdominant positions or is a central component of rank 1–2 in plant communities (Ziman 1976). There are places where this species dominates the vegetation layer (Kondratyuk et al. 1985).

Salvia nutans is found in Central and Eastern Europe, from the Danube Plain in the west to the Pre-Caucasus in the east (Golevich 2012). Thus, *S. nutans* occurs in Ukraine's southern and central regions, extending from the Crimean Peninsula and the northern Caucasus to the Volga bend. It then continues along the Ural River and the Ural Mountains to the Kama River region (Golevich 2012). Its distribution also extends to the outer edges of the Carpathians, from Galicia to the Danube (Csapody 1982), with occurrences in the Transylvanian Basin, Vojvodina, and the Great Plain. The western limit of its distribution reaches Hungary (Sramkó and Laczkó 2020). The species is also widespread in eastern Romania, more significant in the Transylvanian Basin (Soó 1942; Beldie et al. 1961) and in Serbia. Historical data indicate its presence in specific locations in Hungary and Romania, suggesting a broader distribution in the past (Gusztáv 2005). A wider distribution of the species *S. nutans* has been recorded throughout the Pannonian Plain, including areas between the Danube and the Tisza, as well as Vojvodina (Soó 1942). In Serbia, the species is no longer found (Jovanović and Lakušić 2006; Đakić, Knežević, and Boža 2012). However, in the Transylvanian Basin, the species has been confirmed in some locations (Soó 1942; Ruprecht et al. 2009). *S. nutans* reaches eastwards to the southern limits of the Ural Mountains, although it is no longer part of the current flora of Kazakhstan (Sramkó and Laczkó 2020).

The main threat to the survival of *S. nutans* is the ongoing transformation of its natural habitat, especially grasslands. Also, the collection of this species for its ornamental value is a major contributor to the population decline. The decline in the number of individuals resulting from these combined pressures also poses additional risks, including genetic hazards, which may impact the long-term viability of the population (Gusztáv 2005).

Salvia nutans has not been extensively evaluated for its conservation status at the global and European levels. However, given its presence across various European regions, local assessments might provide insight into its vulnerability or stability within specific habitats. In Romania, for instance, the species may be categorized under specific conservation statuses based on local biodiversity studies, mirroring the approach used for other flora and fauna. For hypothetical context, let us consider that *S. nutans* is vulnerable in specific habitats due to environmental pressures or anthropogenic factors. In Central and Southeastern Europe, where *S. nutans* naturally occurs, agricultural expansion and changes in land management practices could influence its conservation status.

The study aims to investigate the habitat and phytocoenological preferences of the *S. nutans* in Romania. The objectives of the study include (i) identification of the habitats and plant associations in which *S. nutans* is found, (ii) identification of the environmental factors that explain the variation of the floristic composition, and (iii) recommending conservation measures for the protection of the species. The hypothesis of this study is as follows: Due to the transformation of grasslands into agricultural lands and overgrazing, the habitat area of the *S. nutans* species in Romania has been reduced. In this case, these factors have led to a decline in the population and number of individuals of this species, especially in Transylvania. We also consider that hybridization with *Salvia nemorosa* L. has an essential role in reducing this species.

The development of measures to protect this species is also important for a unique butterfly species, namely *Pseudophilotes bavius* subsp. *hungarica* (Diószeghy, 1913) is endemic to Transylvania and dependent on the host plant *S. nutans* (Crișan 2012). The degradation and loss of the *S. nutans* species threaten the habitat of this butterfly. The life cycle of the butterfly, which involves laying eggs on host plants and developing into larvae, is directly affected by the conservation status of the *S. nutans* species (Crișan 2012; Crișan, Vizauer, and Rákosy 2023). In this case, the lack of adequate measures for the populations in Romania affects both the plant and the butterfly.

Materials and methods

Study area

The study areas were represented by the historical regions of Bucovina, Crișana, Dobrogea, Moldova, Muntenia, and Transylvania (Fig. 1) from Romania. Bucovina and Moldova are located in the northeastern part of Romania and are characterized by a temperate continental climate with moderate summers, cold winters, and abundant precipitation. Dobrogea is characterized by a moderate continental climate with maritime influences and reduced precipitation compared to the other regions. Transylvania features a continental climate characterized by significant thermal variations and abundant precipitation. In contrast, Crișana and Muntenia are characterized by a temperate continental climate, fertile soils, and favourable annual mean temperatures. The lowest elevation was recorded in Dobrogea, and the highest elevation was recorded in Transylvania (Fick and Hijmans 2017).

Salvia nutans, a species associated with xeric and mesoxeric grasslands in the steppe and forest-steppe zones, is linked to the typical soils characteristic of these ecosystems. On plateaus and gently inclined slopes in the steppe area, this species colonizes Kastanozems, Calcic, and Haplic Chernozems. In the same situation in the forest-steppe, the species is found on Haplic and Luvic Chernozems, as well as on various types of Phaeozems. It is interesting that in forest-steppe areas and at the borders of vicinal nemoral forest areas, the species can be frequently encountered on steep, sunny slopes with shallow soils, such as Lithic, Skeletic, Calcic, Brunic, and Calcaric Leptosols, as well as on short-profiled Kastanozems. According to our observations, the species typically avoids colonizing barren rocks (IUSS Working Group WRB 2022).

Study species

Salvia nutans (Fig. 2) is a perennial species (Ciocârlan 2009) with a Pannonian-Pontic distribution (Golevich 2012). The plant height ranges from 20 cm to 100 cm (Gusztáv 2005) or 120 cm (Beldie et al. 1961). The stem is erect, almost leafless in the upper part (Sârbu, Ștefan, and Oprea 2013) or sometimes with 1 or 2 pairs of small, simple leaves (Beldie et al. 1961; Ciocârlan 2009). Usually, 1–2 stems originate from the same rhizome (Beldie et al. 1961). The basal leaves are cordate-ovate in shape (Ciocârlan 2009; Sârbu, Ștefan, and Oprea 2013), with lengths ranging from 3 cm to 16 cm and widths ranging from 2 cm to 12 cm (Beldie et al. 1961). The leaf tips are either slightly pointed or rounded, and the margins are crenate. The leaf surface is either glabrous or partially hairy along the central veins. On the underside, the leaves are densely tomentose, with short hairs and numerous sessile glandular hairs of yellow-orange color. The petioles are longer than the leaf blades, with broad bases, and are covered with long, multicellular, dispersed hairs. The stem leaves are small, either sessile or short-petiolate, and lanceolate or occasionally ovate. They have a length from 15 cm to 30 cm and a width from 6 cm to 10 cm. Bracteoles are equal in size or slightly longer than the floral pedicels (Beldie et al. 1961). Inflorescence is pendulous at the tip before flowering (Ciocârlan 2009). The flowering period extends from late May to early July (Kondratyuk et al. 1985). Although most individuals flower in the third year of growth, there are cases in which flowering occurs as early as the second year (Udvardy 2002; Gusztáv 2005).

Vegetation data

A total of 870 relevés, comprising 1,421 taxa, were used for the vegetation analysis. Of these, 492 relevés were sourced from the Romanian Grassland Database (RGD; Vassilev et al. 2018), while the remaining 378 relevés were collected between May 2017 and June 2024 (personal data). The size of each individual plot was 100 m², while the relevés from the Romanian Grassland Database ranged from 4 m² to 200 m².

Environmental variables

In the multivariate analysis, abiotic variables (elevation – m a.s.l., aspect – °, slope – °, mean annual temperature – °C, and annual precipitation – mm) and edaphic variables (P – mg kg^{-1}, K – mg kg^{-1}, and pH) were included.

Soil analyses

The values for the chemical elements P, K, and soil pH (Ballabio et al. 2019) were extracted from the European Soil Database & soil properties – ESDAC (European Soil Data Centre 2019).

Climatic data

The climatic data (mean annual temperature and annual precipitation) were obtained from the WorldClim database (Fick and Hijmans 2017) at a resolution of 30 arc. sec. Elevation, aspect, and slope data were collected in the field.

Data preparation for classification analyses

Before numerical data analysis, the dataset was standardized according to the following criteria: (i) unification of taxonomy and taxon nomenclature; (ii) species identified only at genus level were eliminated; (iii) unrecognized subspecies were combined into species; (iv) exclusion of bryophyte and lichen species, as they were recorded in only 20 relevés.

The classification of plant associations within the alliance and the nomenclature of these associations follow Chifu, Irimia, and Zamfirescu (2014) and Chifu and Irimia (2014a, 2014b). The nomenclature and taxonomy of plant species follow Euro + Med (2025), and the nomenclature of higher syntax units follows Mucina et al. (2016). Additionally EUNIS habitats were determined (Chytrý et al. 2020). The final data set included 870 relevés and 904 taxa.

Numerical classification and expert system development

We used the modified TWINSPAN algorithm (Roleček et al. 2009) with three pseudospecies cut levels of 0%, 5%, and 25% cover, minimum group size for division of five relevés, and Whittaker's beta coefficient as a measure of internal cluster heterogeneity. We assessed the optimal number of clusters using OptimClass 1 (Tichý et al. 2010). Diagnostic species for individual clusters were determined based on the *phi*-coefficient of association applied to virtually standardized cluster sizes (Chytrý et al. 2002, Tichý and Chytrý 2006). We used a fidelity threshold of *phi* = 0.25 combined with Fisher's exact test ($p < 0.05$). We used 25% and 50% constancy as thresholds for determining constant and highly constant species, respectively.

The data were represented as mean percentage cover values, according to the scale developed by the Braun-Blanquet (1964). The mean abundance-dominant interval corresponding to the notes was defined as follows (Cristea, Gafta, and Pedrotti 2004): r (0.05%); + (0.5%); 1 (5%); 2 (17.5%); 3 (37.5%); 4 (62.5%); and 5 (87.5%).

Vegetation–environment relationship

The correlation between floristic composition and environmental variables was analyzed with Detrended Correspondence Analysis (DCA) in the CANOCO v5.1 software (ter Braak & Šmilauer, 2018). In this context, DCA analysis was performed to detect floristic gradients, and CCA (Canonical Correspondence Analysis) was applied to quantify the effect of each environmental variable on floristic composition, using the Monte Carlo permutation test (9999 iterations). The average percentage coverage values represented the floristic composition, and the environmental variables were represented by variables with a VIF value of less than 5 (Table 1). We used the Variance Inflation Factor (VIF) in SPSS version 23 to assess collinearity between independent variables. Variables with a VIF value greater than 5 were considered multicollinear and were excluded from the model. The relevés distribution map was made in QGIS version 3.34.3 (QGIS Development Team 2025).

Analyses of differences between syntaxa

To determine whether there are statistically significant differences between plant communities regarding environmental variables, the ANOVA test was applied, using R Statistical Software (v4.1.4; R Core Team 2025) via the 'tidyverse' v.2.0.0 (Wickham et al. 2019), 'car' v.3.1.3 (Fox and Weisberg 2019), and 'stats' v.4.5.0 (R Core Team 2025). Since significant differences were found ($p < 0.05$), the post-hoc Tukey test was applied. In this context, communities that did not exhibit significant differences were denoted by the same letter, while communities that did exhibit significant differences were highlighted by different letters.

Results

Syntaxonomic overview of relevés

Salvia nutans populations were found to inhabit eight main phytocoenological classes:

Crataego-Prunetea, *Digitario sanguinalis-Eragrostietea minoris*, *Festuco-Brometea*, *Festuco-Puccinellietea*, *Molinio-Arrhenatheretea*, *Quercetea pubescentis*, *Sisymbrietea*, and *Trifolio-Geranietea sanguinei*.
Class: *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947

Order: *Festucetalia valesiacae* Soó 1947

All.: *Stipion lessingianae* Soó 1947

Ass.: *Allio albidi-Stipetum lessingianae* (Soó 1947) Coldea et Sârbu in Coldea 2012

Ass.: *Jurineo transylvanicae-Stipetum pulcherrimae* (Soó 1942) Coldea et Sârbu in Coldea 2012

Ass.: *Jurineo arachnoidea-Stipetum lessingianae* (Dobrescu 1974) Chifu, Mânzu et Zamfirescu 2006

Ass.: *Festucetum rupicolae* Burduja et al. 1956

Ass.: *Artemisietum ponticae* (Soó 1942) Păun 1969

Ass.: *Stipo ucrainicae-Festucetum valesiacae* (Dihoru 1969) Dihoru et Doniță 1970

Ass.: *Convolvulo cantabrici-Stipetum capillatae* (Horeanu 1976)

Ass.: *Agropyro pectinati-Stipetum capillatae* (Burduja et al. 1956) Chifu, Manzu et Zamfirescu 2006

Ass.: *Taraxaco serotinae-Festucetum valesiacae* (Burduja et al. 1956, Răvăruț et al. 1956) Sârbu, Coldea et Chifu 1999

Ass.: *Agropyro pectinati-Tanacetinetum millefolii* (Șerbănescu 1970) Chifu et Țupu 2009

Ass.: *Elytrigietum hispidi* (Dihoru 1970) Dihoru et Doniță 1970

Ass.: *Astero oleifolius-Ephedretum distachyae* Horeanu et Vițalariu 1992

Ass.: *Cynodonto-Poëtum angustifoliae* (Rapaics 1927) Soó 1957

Ass.: *Bombycilaeno erecti-Bothriochloetum ischaemi* (Dihoru 1970) Dihoru et Doniță 1970

Ass.: *Agropyretum pectiniformae* (Dihoru 1970) Dihoru et Doniță 1970

All.: *Festucion valesiacae* Klika 1931

Ass.: *Bothriochloetum ischaemi* (Kristiansen 1937) I. Pop 1977

Ass.: *Salvio-Festucetum rupicolae* Zolyomi 1958 corr. Soó 1964

Sub-ass.: *paeonietosum tenuifoliae* (Mititelu et al. 1990)

Ass.: *Festucetum valesiacae-rupicolae* Csürös et Kovács 1962

Ass.: *Stipetum capillatae* (Hueck 1963) Krausch 1961

Ass.: *Agrostio-Festucetum valesiacae* Borisavljevič et al. 1955

Ass.: *Agropyro pectinati-Kochietum prostratae* Zolyomi 1958

Ass.: *Taraxaco serotinae-Bothriochloetum ischaemi* (Burduja et al. 1956) Sârbu, Coldea et Chifu 1999

Sub-ass.: *koelerietosum macranthae* (Răvăruț et al. 1956) Chifu, Mânzu et Zamfirescu 2006

Ass.: *Medicagini minimae-Festucetum valesiacae* Wagner 1941

Ass.: *Festuceto rupicolae-Caricetum humilis* Polgár 1933

Sub-ass.: *thymio-salvietosum nutantis*

Order: *Brachypodietalia pinnati* Korneck 1974

All.: *Cirsio-Brachypodion pinnati* Hadač et Klika in Klika et Hadač 1944

Ass.: *Cariceto humilis-Brachypodietum pinnati* Soó 1947

Sub-ass.: *dichathietosum ischaemi* Chifu et al.. 2014

Ass.: *Helianthemo cani-Seslerietum heuflerianae* (Borza 1959) Popescu et Sanda 1992

Ass.: *Festuco rupicolae-Brachypodietum pinnati* Mahn 1965

Ass.: *Jurineo transsilvanicae-Chrysopogonetum grylli* (Csürös et Niedermaier 1966) Coldea et Sârbu in Coldea 2012

Ass.: *Danthonio alpinae-Stipetum stenophyllae* Ghișa 1941

Ass.: *Carici humilis-Stipetum joannis* Pop et Hodișan 1985

Ass.: *Convolvulo cantabrici-Chrysopogonetum grylli* (Dihoru 1970) in Chifu et al. 2014

Ass.: *Valerianello lasiocarpae-Chrysopogonetum grylli* (Dihoru 1970) Coldea et Sârbu in Coldea 2012

Ass.: *Ferrulago campestris-Caricetum humilis* (Ciocârlan 1969) Coldea et al. 2010

Ass.: *Galio octonarii-Stipetum tirsae* (Ciocârlan 1969) Popescu et Sanda 1992

Ass.: *Rhinantho rumelici-Brometum erecti* Sanda et Popescu 1999

Ass.: *Thymo comosi-Caricetum humilis* Morariu et Danciu 1977

Order: *Stipo pulcherrimae-Festucetalia pallentis* Pop 1968

All.: *Pimpinello-Thymion zygoidis* Dihoru et Doniţa 1970

Ass.: *Saturejetum caeruleae* Cristurean et Ionescu-Țeculescu 1970

Ass.: *Koelerio lobatae-Artemisietum lerchianae* (Dihoru 1970) Dihoru et Doniță 1970

Ass.: *Agropyro pontici-Thymetum zygioidis* (Dihoru 1970) Dihoru et Doniță 1970

Ass.: *Festucetum callierii* (Şerbănescu 1965) Dihoru et Doniță 1970

Class: *Crataego-Prunetea* Tx. 1962

Order: *Prunetalia spinosae* Tx. 1952

All.: *Prunion fruticosae* Tx. 1952

Ass.: *Prunetum tenellae* Soó 1951

All.: *Berberidion vulgaris* Br.-Bl. ex Tx. 1952

Ass.: *Pruno spinosae-Crataegetum* Hueck 1931

Class: *Trifolio-Geranietea sanguinei* T. Müller 1962

Order: *Antherico ramosi-Geranietalia sanguinei* Julve ex Dengler in Dengler et al. 2003

All.: *Geranion sanguinei* Tx. in T. Müller 1962

Ass.: *Inulo ensifoliae-Peucedanetum cervariae Kozlowska* 1925 em. Van Gils et Kovács 1977

Ass.: *Geranio-Dictamnetum* Wendelberger ex T. Müller 1962

Ass.: *Clematido rectae-Laserpitietum latifolii* Schneider-Binder 1984

Class: *Molinio-Arrhenatheretea* Tx. 1937

Order: *Arrhenatheretalia elatioris* Tx. 1931

All.: *Cynosurion cristati* Tx. 1947

Ass.: *Anthoxantho-Agrostetum capillaris* Sillinger 1933

All.: *Arrhenatherion elatioris* Koch 1926

Ass.: *Arrhenatheretum elatioris* Br.-Bl. ex Scherrer 1925

Order: *Potentillo-Polygonetalia avicularis* Tx. 1947

All.: *Potentillion anserinae* Tx. 1947

Ass.: *Rorippo austriacae-Agropyretum repentis* (Timar 1947) R. Tx. 1950

Class: *Festuco-Puccinellietea* Soó ex Vicherek 1973

Order: *Puccinellietalia* Soó 1947

All.: *Festucion pseudovinae* Soó 1933

Ass.: *Artemisio-Festucetum pseudovinae* Soó (1927) 1945

Class: *Sisymbrietea* Gutte et Hilbig 1975

Order: *Sisymbrietalia sophiae* J. Tx. ex Görs 1966

All.: *Sisymbrion officinalis* Tx. et al. ex von Rochow 1951

Ass.: *Bromo squarrosi-Xeranthemetum annui* Coroi 2001

Ass.: *Hordeo murini-Cynodontetum dactyloni* Felföldy ex Borhidi 1949

Class: *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959

Order: *Quercetalia pubescenti-petraeae* Klika 1933

All.: *Quercion petraeae* Issler 1931

Ass.: *Corno-Quercetum pubescentis* Mathé et Kovács 1962

Ass.: *Paeonio peregrinae-Quercetum pubescentis* (Sârbu 1982) Sanda et Popescu 1999

Class: *Digitario sanguinalis-Eragrostietea minoris* Mucina, Lososová et Šilc in Mucina et al. 2016

Order: *Eragrostietalia* J. Tx. ex Poli 1966

All.: *Salsolion ruthenicae* Philippi ex Oberd. 1983

Community: *Cynodon dactylon*

EUNIS habitats

The identified plant associations were assigned to eight major EUNIS habitat types, namely (at level 2 of the EUNIS hierarchy): R1 – **Dry grasslands (**R1A Semi-dry perennial calcareous grassland - meadow steppe, R1B Continental dry grassland - true steppe, R16 Perennial rocky grassland of Central and South-Eastern Europe); R2 – **Mesic grasslands** (R21 Mesic permanent pasture of lowlands and mountains, and

R22 Low and medium altitude hay meadow); R3 – **Seasonally wet and wet grasslands** (R36 Moist or wet mesotrophic to eutrophic pasture); R5 –**Woodland fringes and clearings and tall forb stands** (R51 Thermophilous forest fringe of base-rich soils); R6 – **Inland salt steppes** (R62 Continental inland salt steppe); S3 – **Temperate and Mediterranean montane scrub** (S35 Temperate and submediterranean thorn scrub); T1 –**Broadleaved deciduous forests** (T19 Temperate and submediterranean thermophilous deciduous forest); and V1 – **Arable land and market gardens** (V15 Bare tilled, fallow or recently abandoned arable land).

Cluster analysis

The cluster analysis results were presented as a dendrogram (Fig. 3), which illustrated the hierarchical relationships between the vegetation units, and a synoptic table (Supplementary Material 1). The analyzed vegetation was classified into six clusters, which were correlated with different syntax groups recognized in the specialized literature.

Cluster 1: Cl. Festuco-Brometea, **Ord. Festucetalia valesiacae**, **Al. Stipion lessingianae**, **Ass. Stipo ucrainicae-Festucetum valesiacae (17 relevés)**

Structure and composition of plant community

Phlomis herba-venti had a fidelity of 58% and was the species most strongly associated with this community. Other important species for this community that had relatively significant contributions were *Centaurea orientalis* (53.2%) and *Cytisus austriacus* (52.6%). The number of species per 100 m^2 ranged from 13 to 44, and vegetation cover varied between 48% and 83%. *Salvia nutans* had a cover ranging from 0.5–5%.

Ecology and distribution

The communities analysed were recorded at elevations varied between 22 to 122 m a.s.l. (above sea level). The climate is moderate, with annual mean temperatures ranging from 10.9 to 11.9°C. Annual precipitation was also moderate, ranging from 432 to 470 mm. The temperatures in May and June varied between 15.6 and 16.1°C. They ranged from 20.2 to 20.7°C in June, while precipitation was lower in May (37–45 mm) compared to June (48–55 mm), suggesting a gradual increase in humidity during the warm season. Soils ranged from neutral to slightly alkaline, with moderate phosphorus and potassium concentrations. The communities were recorded on gentle slopes with a northeastern aspect in the grasslands of Constanța County.

Cluster 2: Cl. Festuco-Brometea, **Ord. Festucetalia valesiacae**, **Al. Stipion lessingianae**, **Ass. Taraxaco serotinae-Festucetum valesiacae and Jurineo arachnoidea-Stipetum lessingianae (**36 relevés**)**

Structure and composition of plant community

Galium glaucum had a fidelity of 63.2%, the species most strongly associated with this community. Similarly, *Festuca stricta* subsp. *sulcata* (60.6%) and *Carex humilis* (60.1%) contributed significantly to the structure and functioning of the community. Another species contributing to the community structure was *Astragalus monspessulanus*, which had a fidelity of 56.6%, similar to *Thymus odoratissimus*, which had a fidelity of 54%. Similarly, *Peucedanum ruthenicum* is a representative species for this community, although it had a lower fidelity (51%). The number of plant species per 100 m^2 ranged from 13 to 95, while vegetation cover varied between 51% and 100%. *Salvia nutans* had a cover between 0.05% and 5%.

Ecology and distribution

The annual mean temperatures range from 6.9 to 11.6°C, indicating a moderate to cold climate. The annual precipitation ranges from 428 to 590 mm, indicating moderate humidity conditions. The mean monthly temperatures in May and June range from 12.6 to 16.1°C in May and 16 to 20.7°C in June. The monthly precipitation ranges from 41 to 72 mm in May and from 50 to 95 mm in June. The soils had a pH ranging from weakly alkaline to neutral, characterized by moderate phosphorus and rich in potassium concentrations. The communities in this cluster were recorded at elevations ranging from 31 to 630 m a.s.l., on slopes that varied from gentle to very steep, predominantly with a northeastern aspect across the grasslands of Alba, Brașov, Constanța, Iași, Suceava, and Vaslui counties.

Cluster 3: Cl. Festuco-Brometea, Ord. Festucetalia valesiacae, All. Stipion lessingianae, Pimpinello-Thymion zygoidis, Ass. Taraxaco serotinae-Festucetum valesiacae and Agropyro pontici-Thymetum zygioidis (57 relevés)

Structure and composition of plant community

Convolvulus cantabrica was the species most strongly associated with this community, with a fidelity of 61.3%. *Erysimum diffusum* (59%) and *Koeleria lobata* (58.6%) had an essential role in these communities, contributing significantly to the community structure. Also, other species with relatively significant fidelity were *Euphorbia seguierana* (55.9%), *Satureja coerulea* (54.2%) and *Achillea coarctata* (54.2%). *Agropyron cristatum* recorded a fidelity of 50.7%. The number of plant species per 100 m^2 ranged from 15 to 85, and vegetation cover ranged from 45–100%. *Salvia nutans* had a cover ranging from 0.05–5%.

Ecology and distribution

The climate was characterized by moderate temperatures and precipitation. Mean monthly temperatures ranged from 14.8 to 16.8°C in May and from 19.1 to 20.7°C in June. Monthly precipitation was moderate, from 38 to 55 mm in May and from 47 to 67 mm in June. The soils associated with these communities had a pH ranging from slightly acidic to neutral and were characterized by moderate phosphorus and potassium concentrations. Communities in this cluster were recorded at elevations ranging from 10 to

286 m a.s.l., on slopes ranging from gentle to very steep, with a predominantly northeastern aspect in the grasslands of Constanța and Tulcea counties.

Cluster 4: Cl. Festuco-Brometea, **Ord. Festucetalia valesiacae**, **All. Stipion lessingianae**, **Ass. Jurineo transylvanicae-Stipetum pulcherrimae**, **Allio albidi-Stipetum lessingianae**, **and Prunetum tenellae** (562 relevés)

Structure and composition of plant community

Crataegus monogyna (66.9%) and *Potentilla taurica* (66.3%) had the highest fidelity values, characteristic species for this community. *Valeriana coronata* (65.2%) and *Rosa canina* (62.2%) were other important species, significantly contributing to the community structure. Also, the species *Marrubium vulgare* (61%) and *Salvia revelata* (55.9%) recorded a relatively high fidelity. Species such as *Thalictrum aquilegiifolium* (54.4%), *Achillea ochroleuca* (51.6%), *Potentilla reptans* (50.8%), and *Euphrasia stricta* (50%) recorded a moderate to high fidelity. The number of species per 100 m^2 ranged from 9 to 99, and the vegetation cover ranged from 29–100%. *Salvia nutans* had a cover ranging from 0.05–37.5%.

Ecology and distribution

The communities included in this cluster were recorded at elevations from 95 to 610 m a.s.l., on very steep slopes with a southwest aspect. Annual precipitation ranged from 575 to 731 mm, and annual mean temperatures ranged from 6.2 to 10 °C. The soils had a pH ranging from slightly acidic to weakly alkaline, characterized by moderate phosphorus and rich potassium concentrations in the grasslands of Alba, Bistrita-Năsăud, Brașov, Cluj, Mureș, Sălaj, Sibiu, and Suceava counties.

°

Cluster 5: Cl. Festuco-Brometea, **Ord. Brachypodietalia pinnati**, **All. Cirsio-Brachypodion pinnati**, **Ass. Cariceto humilis-Brachypodietum pinnati (**157 relevés**)**

Structure and composition of plant community

Brachypodium pinnatum recorded a fidelity of 62.2%, the species most strongly associated with this community. The number of species per 100 m^2 ranged from 45 to 58, and the vegetation cover ranged from 30–100%. Within this community, *Salvia nutans* recorded a relatively variable cover, ranging from 0.05–37.5%.

Ecology and distribution

The communities analysed were recorded at elevations ranging from 90 to 1553 m a.s.l., located on slopes ranging from moderate to very steep with a predominantly southern and western aspect. The soils presented a pH ranging from slightly acidic to neutral, characterised by moderate phosphorus and potassium concentrations. Annual precipitation ranged from 449 to 990 mm, and annual mean temperatures ranged from 2.4 to 10.5 °C in the grasslands of Alba, Bacău, Bihor, Brașov, Cluj, Covasna, Harghita, Mureș, Sălaj, Sibiu, and Suceava counties.

Cluster 6: Cl. Festuco-Brometea, **Ord. Festucetalia valesiacae**, **All. Stipion lessingianae**, **Ass. Taraxaco serotinae-Bothriochloetum ischaemi and Astero oleifolius-Ephedretum distachyae (**41 relevés**)**

Structure and composition of plant community

Galium humifusum was the species most strongly associated with this community, with a fidelity of 59.9%. The other species, such as *Astragalus onobrychis* (39.5%), *Ephedra distachya* (39.3%), and *Diplotaxis muralis* (39.3%), had lower fidelity. The number of species per 100 m^2 ranged from 7 to 61, and the vegetation cover ranged from 47–98%. *Salvia nutans* presented a cover range of 0.5–5%.

Ecology and distribution

The communities included in this cluster were recorded at elevations ranging from 5 to 387 m a.s.l., on moderate slopes with a northeastern aspect. Climatic conditions were characterized by annual precipitation ranging from 429 to 609 mm and annual mean temperatures ranging from 8.6 to 12 °C in the grasslands of Constanța, Iași, Sibiu, Suceava, Tulcea, and Vaslui counties.

Table 1
Measured values of bioclimatic, soil chemical, and topographic variables were analysed. Values are means ± standard deviations (SD). VEGC = vegetation cover; BIO12 = annual precipitation; BIO1 = annual mean temperature; Aspect: S – south, SSW – south-southwest, SE – southeast, SSE – south-southeast, SW – southwest, W – west; P = phosphorus, K = potassium.

Cluster	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6
No. of species/relevés	28 ± 8.5	43 ± 20	48 ± 14.5	40 ± 16.8	38 ± 16.6	35 ± 15.3
Vegetation cover (%)	61 ± 9.1	87 ± 12.1	83 ± 13.4	83 ± 12.9	82 ± 14.7	77 ± 14.9
Aspect	W	SSE	SE	SW	SW	SSW
Slope (°)	5.6 ± 3.1	14.5 ± 15.3	8.1 ± 6	30.6 ± 14.5	22.1 ± 14.4	12.4 ± 10
Elevation (m a.s.l.)	76.6 ± 25.8	204 ± 142.7	91.5 ± 85	392.6 ± 67.3	450.6 ± 138.8	178.3 ± 99.4
pH	7.1 ± 0.2	6.3 ± 0.4	7 ± 0.3	6 ± 0.6	5.7 ± 1.2	6.4 ± 1.1
P (mg kg^{-1})	27.2 ± 7.5	28.2 ± 6	27 ± 7.3	26.0 ± 6.5	24.5 ± 8.8	28.4 ± 7.3
K (mg kg^{-1})	263.3 ± 71.9	342.1 ± 99.4	278.5 ± 76.7	297.4 ± 56.4	281.2 ± 73	331.4 ± 132
BO1 (°C)	11.5 ± 0.3	9.4 ± 0.9	11.1 ± 0.7	8.5 ± 0.4	8.2 ± 0.8	9.8 ± 0.9
BIO12 (mm)	453.7 ± 16.7	549.7 ± 34.8	443.9 ± 15.6	608.3 ± 19.1	608.5 ± 43.5	524.2 ± 53.1
Mean temperature – May	15.7 ± 0.1	15.4 ± 0.9	15.8 ± 0.4	14.5 ± 0.4	14 ± 1	15.4 ± 0.4
Mean temperature – June	20.3 ± 0.1	18.9 ± 1	20.3 ± 0.5	17.3 ± 0.4	16.9 ± 1	19.2 ± 0.9
Mean precipitation – May	41.5 ± 2.2	62.8 ± 7.2	43.5 ± 3.8	72.7 ± 1.7	73.5 ± 4.6	58.5 ± 10
Mean precipitation – June	52.1 ± 2.1	85.2 ± 10.5	53.8 ± 4.4	93.5 ± 2	93.7 ± 5.9	76.6 ± 14.9

Salvia nutans occurs predominantly on steep slopes (from 21° to 35°; 31%), followed by very steep slopes (> 35°), with 26%. The species also occurs on gentle slopes (3–10°; 23%), moderate slopes (11–20°; 15%), and very gentle slopes (0–3°; 5%). The dominant aspect in which *S. nutans* occurs is southwest (39%), followed by southern (23%), and western (13%). The species also occurs on secondary aspects, such as southeast (8%) and northeast (7%). In contrast, on the northwest (5%), eastern (3%), and northern (3%) aspects, the species recorded a reduced presence. In terms of elevation, *S. nutans* prefers low elevations. The average elevation was 359 m, ranging from 5 to 850 m a.s.l. (Fig. 4).

The soils were predominantly moderately acidic (pH range of 5.81 to 6.80, 59%). The species was also identified on slightly acidic soils (pH 5.01–5.80, 27%), neutral soils (pH 6.81–7.20, 11%), slightly alkaline soils (pH 7.21–8.40, 2%), and moderately strongly acidic soils (pH 4.31–5.00, 1%). Based on the soil phosphorus concentration, the species distribution indicates a preference for soils with low phosphorus concentrations (ranging from 18.1 to 36 mg kg^{-1}, or 81%). The presence of the species in soils with moderate phosphorus concentrations (ranging from 8.1 to 18 mg kg^{-1}, 13%) and high phosphorus levels (ranging from 36.1 to 72 mg kg^{-1}, 6%) was reduced. Regarding potassium concentration, a preference for soils very rich in potassium (from 265.1 to 400 mg kg^{-1}; 69%) was observed among the species. The presence of the species in soils rich in potassium (ranging from 200.1 to 265 mg kg^{-1}, 25%) was moderate. In soils with moderate (ranging from 132.1 to 200 mg kg^{-1}; 3.8%), excessive (> 400 mg kg^{-1}; 2.1%), and poor potassium levels (ranging from 66.1 to 132 mg kg^{-1}; 0.2%), the species exhibited a reduced presence (Fig. 5).

The annual mean temperature (BIO1) ranged from 2.5 to 11.9°C, with an average of 8.78°C. The average annual precipitation was moderate, ranging from 426 to 748 mm, with an average of 588 mm.

The relationship between floristic composition and environmental variables

The DCA data showed that Axis 1 was the most important. It explained the most variation and had the most extended gradient length (Table 2; Fig. 6). The other axes made a minor contribution.

Table 2
Summary of the DCA analysis.

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.6026	0.4672	0.3416	0.2854
Explained variation (cumulative)	2.57	4.57	6.02	7.24
Gradient length	4.43	3.07	4.36	3.99
Pseudo-canonical correlation (suppl.)	0.8254	0.2208	0.4329	0.3782

CCA data showed that annual precipitation (BIO12) explained most of the variation in the floristic composition of *S. nutans* communities, followed by slope (Table 3).

Table 3
Results of the CCA ordination.

Variable	Explains %	Contribution %	pseudo-F	P	P(adj)
Annual Precipitation (BIO12)	1.86	53.09	16.3	0.002	0.014
Slope (°)	0.34	9.57	3	0.002	0.014
Elevation (m a.s.l.)	0.31	8.93	2.8	0.002	0.014
Aspect	0.3	8.66	2.7	0.002	0.014
Potassium (K)	0.24	6.71	2.1	0.002	0.014
pH	0.24	6.88	2.1	0.008	0.056
Phosphorus (P)	0.22	6.15	1.9	0.002	0.014

In locations (50 locations in Tulcea and Constanța counties) with precipitation ranging from 400 to 450 mm/year, *S. nutans* has a low cover, ranging from 0.5–5%. In these locations, the species occurs at low elevations (54 m a.s.l.) on gentle slopes (9°). The soils are neutral, with an average phosphorus and high potassium. The dominant associations were *Agropyro pontici-Thymetum zygioidis* and *Taraxaco serotinae-Bothriochloetum ischaemi*. In contrast, the temperature is higher (11.3 ℃) compared to the other precipitation intervals (Fig. 7).

In the range of 451 and 500 mm/year, *S. nutans* had a similar cover, from 0.5–5%, but was identified in fewer locations (38 locations in Tulcea, Constanța and Galați counties). Within these locations, *S. nutans* was recorded at moderate elevations (127 m a.s.l.), on gentle slopes (5°) and at lower temperatures of 11.03 ℃. Competition with other species may be one reason why the cover with *S. nutans* was lower. The soils are neutral, with medium phosphorus concentrations and very high potassium. The dominant association was *Stipo ucrainicae-Festucetum valesiacae* (Fig. 7).

In the interval from 501 to 550 mm/year, *S. nutans* had the same cover, from 0.5–5%. In these locations (19 locations in Vaslui, Iași, and Bacău counties), *S. nutans* was observed at elevations higher than 158 m a.s.l., on moderate slopes (12.7°). The mean annual temperature was lower (9.7℃). The soils are moderately acidic, with a medium phosphorus concentration and very high potassium levels. The dominant associations were *Astero oleifolius-Ephedretum distachyae* and *Taraxaco serotinae-Festucetum valesiacae* (Fig. 7).

In 325 locations across Vaslui, Iași, Suceava, Covasna, and Alba counties, with annual precipitation ranging from 551 to 600 mm/year, *S. nutans* had a cover ranging from 0.05–62.5%. The elevations were higher (362 m a.s.l.), and steep slopes (24°). The temperatures were lower (8.7°C). The soils were moderately acidic, with medium phosphorus and very high potassium concentrations. The dominant associations were *Allio albidi-Stipetum lessingianae*, *Danthonio alpinae-Stipetum stenophyllae, Festuceto rupicolae-Caricetum humilis*, and *Festucetum rupicolae* (Fig. 7).

Most observations of the species were recorded in locations with annual precipitation from 601 to 650 mm/year. In these locations (412 locations in Sălaj, Bistrița, Cluj, and Mureș counties), *S. nutans* had a cover from 0.05–37.5%. Elevations were high (416 m a.s.l.), steep slopes (32°) and much lower temperatures (8.3°C). The soils were moderately acidic, with medium phosphorus and very high potassium concentrations (Fig. 7).

In locations (20 locations in Cluj and Bistrița-Năsăud counties) with precipitation higher than 650 mm/year, *S. nutans* had a cover ranging from 0.05–17.5%. In these locations, the highest elevations (604 m) and the lowest average annual temperatures (7.52°C) were recorded on steep slopes (21°). The soils are weakly acidic, with medium to high phosphorus concentrations (Fig. 7).

Discussion

General aspects

Salvia nutans is widely distributed in steppe grasslands across Ukraine, Russia, and other Eastern European regions (Budak 1999; Gusztáv 2005; Đakić, Knežević, and Boža 2012). The results indicate a high presence of the species in Transylvania and the plains of Eastern Romania, confirming its presence in the marginal areas of its European distribution (Soó 1968; Csapody 1982). In Romania (Oprea 2005) and Hungary (Gusztáv 2005), the species was much more widespread in the past. Due to overgrazing and the transformation of grasslands into agricultural land, the habitat of the species is threatened in Hungary (Gusztáv 2005) and Romania.

Syntaxonomical scheme and EUNIS habitats

This study confirms that *S. nutans* occurs predominantly in dry grasslands of the *Festuco-Brometea* class (827 relevés, representing 95% of the total), which is in agreement with the data in the literature (Soó 1968; Sârbu, Ștefan, and Oprea 2013), where the species is described as a xerophytic species characteristic of open habitats. The high percentage of 95% compared to the presence of the species in other habitats shows a clear preference for this type of grassland, where the soils are well-drained.

In the vegetation classes *Crataego-Prunetea* (19 relevés, representing 2% of the total) and *Trifolio-Geranietea* (13 relevés, representing 2% of the total), the presence of the species was reduced, indicating that *S. nutans* also colonizes less typical habitats. In contrast, the presence of the species in the classes *Digitario sanguinalis-Eragrostietea minoris* (one relevé, representing 0.1% of the total), *Festuco-Puccinellietea* (one relevé, representing 0.1% of the total), *Molinio-Arrhenatheretea* (four relevés, representing 0.5% of the total), *Quercetea pubescentis* (two relevés, representing 0.2% of the total), and *Sisymbrietea* (three relevés, representing 0.3% of the total) was significantly reduced, indicating a marginal presence, not being characteristic for these communities. Some of these data are also confirmed by specialized literature (Horeanu 1974; Kovács 2003; Germany 2013), which shows that *S. nutans* has been recorded in other vegetation classes as well.

At the order level, the results indicated that *S. nutans* was associated with *Festucetalia valesiacae* (659 relevés, representing 77% of the total). The second most frequent order was *Brachypodietalia pinnati* (127 relevés, representing 15% of the total). In the orders *Stipo pulcherrimae-Festucetalia pallentis* (24 relevés, representing 3% of the total), *Prunetalia spinosae* (19 relevés, representing 2% of the total), *Antherico ramosi-Geranietalia sanguinei* (13 relevés, representing 2% of the total), *S. nutans* had a reduced presence. In the remaining orders (*Arrhenatheretalia elatioris*, *Eragrostietalia*, *Potentillo-Polygonetalia avicularis*, *Puccinellietalia*, *Quercetalia pubescenti-petraeae*, and *Sisymbrietalia sophiae*), *S. nutans* had a significantly reduced presence.

At the alliance level, *S. nutans* was recorded most frequently in *Stipion lessingianae* (468 relevés, representing 54% of the total), *Festucion valesiacae* (191 relevés, representing 22% of the total), and *Cirsio-Brachypodion pinnati* (144 relevés, representing 17% of the total). In the alliances *Pimpinello-Thymion zygoidis* (24 relevés, representing 3% of the total) and *Geranion sanguinei* (13 relevés, representing 2% of the total), *S. nutans* had a low presence. In the remaining alliances (*Arrhenatherion elatioris*, *Berberidion vulgaris*, *Cynosurion cristati*, *Festucion pseudovinae*, *Potentillion anserinae*, *Quercion petraeae*, *Salsolion ruthenicae*, and *Sisymbrion officinalis*), *S. nutans* had a very low presence. According to the literature, *S. nutans* is characteristic of *Stipion lessingianae* (Ruprecht et al. 2009; Sârbu, Ștefan, and Oprea 2013) and *Festucion valesiacae* alliances (Kovács 2011).

Regarding plant associations, *S. nutans* occurs most frequently in the associations *Jurineo transylvanicae-Stipetum pulcherrimae* (159 relevés, representing 18% of the total) and *Allio albidi-Stipetum lessingianae* (123 relevés, representing 18% of the total). Also, other associations in which *S. nutans* occurs were *Festucetum rupicolae* (81 relevés, representing 9% of the total), *Salvio-Festucetum rupicolae* (54 relevés, 6%), *Festuceto rupicolae-Caricetum humilis* (49 relevés, 6%), *Taraxaco serotinae-Festucetum valesiacae* relevés (49 relevés, 6%), *Cariceto humilis-Brachypodietum pinnati* (45 relevés, 5%). The presence of *S. nutans* species in *Salvio-Festucetum rupicolae* Zolyomi 1958 corr. Soó 1964, *Jurineo transylvanicae-Stipetum pulcherrimae* and *Festuceto rupicolae-Caricetum humilis* in Transylvania was reported by Soó (1942, 1968), Cśurös (1973, 1974) and Gusztáv (2005). Also, Irimia and Mânzu (2013) mention the presence of the species in *Taraxaco serotinae-Festucetum valesiacae*. At the same time, the presence of the species in *Crataego monogynae-Cerasetum mahaleb* (Pînzaru, 2021) shows the adaptability of the species in transitional areas between grasslands and shrub vegetation.

Moreover, *S. nutans* has also been reported in associations such as *Elytrigietum hispidi*, *Jurineo arachnoideae-Stipetum lessingianae*, *Stipo ucrainicae-Festucetum valesiacae*, and *Thymio pannonici-Chrysopogonetum grylli* (Popescu et al., 2008). In addition, C*ariceto humulis-Festucetum rupicolae* and *Bothriochloetum ischaemi* (Kovács 2011) indicate a consistent presence in the *Festucion valesiacae* alliance. The species is also found in *Medicagini minimae-Festucetum* (Aniței and Mititelu 1997), an association specific to xerophilous mesophilous grasslands. Habitat degradation in the loess grasslands of the Crișana region is described in the literature (Gusztáv 2005) as leading to a simplification of diversity and the dominance of grasses, e.g. *Festuca valesiaca* subsp. *parviflora* (Hack.) Tracey.

The relationship between floristic composition and environmental variables

The most influential environmental factor explaining the variation in the floristic composition of *S. nutans* phytocenoses was annual precipitation (BIO12). This finding is consistent with previous research demonstrating the influence of edaphic and climatic factors on the formation of grassland communities (Klimeš and Doležal 2010rök et al. 2018; Bai et al. 2021). The abundance and distribution of *S. nutans* may be affected by changes in climate patterns, such as increased precipitation and prolonged droughts.

Topographic variables had a significant role in explaining the variation in floristic composition. Similar findings have been recorded in other grassland communities, where competition between species, environmental conditions, and soil water retention are influenced by topographic diversity (Moeslund et al. 2013). The species' preference for very steep slopes in locations with precipitation from 551 to 650 mm/year may be related to the reduced competition with mesophytic species (Grime 2001).

Soil chemical variables had a secondary role in explaining the variation in floristic composition. In general, soil pH and phosphorus availability varied slightly, while potassium concentrations were very high. This means that *S. nutans* can tolerate a broader range of soil conditions, which is a characteristic of species adapted to semi-arid grasslands (Janišová et al. 2014). Additionally, in locations with high precipitation, soil pH is typically lower, suggesting an interaction between soil acidity and plant communities (Chytrý et al. 2015).

Bioclimatic variables, primarily precipitation and topographic factors, played a significant role in the formation of *S. nutans* communities. Considering the species' vulnerability to water availability, future climate variations may lead to changes in its abundance and distribution. In this context, in locations where the species is threatened by anthropogenic impact, it is important to develop conservation and monitoring measures.

The biogeographic, ecological, and evolutionary context of the species

Salvia nutans is a member of the section *Plethiosphace* Benth. in the subgenus *Sclarea* (Moench). Benth. The section has a Palearctic range and was considered monophyletic in a single molecular analysis addressing it (Will and Classen-Bockhoff 2017), which, however, involved only a few species, none of which were *Salvia nutans*. According to the authors, the evolutionary relationships among the species in this section remain unknown. In Transylvania, Romania, the hybrid *S. nutans × nemorosa* is very frequently encountered wherever the two species come into contact. At the same time, *S. nemorosa* seems to actively displace *S. nutans* in many locations, including well-preserved steppe grasslands (personal observations). This is a serious problem for *S. nutans* conservation, at least in Romania, but it also implies that the two species are closely related evolutionarily and ecologically. The other hybrid, known as *S. nutans*, is *S.* × *simonkaiana* Borb. (*nutans* × *pratensis*) it is far rarer. No other hybrids are known between *S. nutans* and any other species in the section *Plethiosphace* that occur within its range.

Salvia nutans is a West Palearctic steppe and forest-steppe element (Pobedinova 1954; Ozenda 1994; Sramkó et al. 2020) with a wide range extending continuously from the Lower Danube forest-steppe areas to the steppe and forest-steppe of the Ufa-Samara-Orenburg region immediately west of the Ural Mountains. Isolated populations are found in the insular forest-steppes of Thrace, the Pannonian Basin, and the Transylvanian Basin. While in the Transylvanian Basin the species is frequent in the mesoxeric and xeric grasslands (as it is presented here) from the forest-steppe and the nemoral adjacent area (here only on steep sunny slopes) in the Pannonian Basin it is scarce – two locations only in Hungary (Sramkó et al. 2020) while in Vojvodina, all the previously known five populations are extinct nowadays (Đakić, Knežević, and Boža 2012). Interestingly, two distinct sampled populations from the Transylvanian Basin exhibit different genetic affinities; one is more closely related to Hungarian populations west of the region, while the other is more closely related to populations north of the Black Sea (Sramkó et al. 2020). This implies a biogeographically interesting heterogeneity for *Salvia nutans* from Transylvania, with one possible explanation being that the species migrated into this region from two directions: from the west (Pannonia) and the east (Moldova), presumably in different and distant periods.

Conclusions

Salvia nutans was found in eight main phytocoenological classes, showing its versatility in various habitats. This species was most frequently recorded in dry grasslands, with the highest abundance reported in the associations *Jurineo transylvanicae-Stipetum pulcherrimae* and *Allio albidi-Stipetum lessingianae*. The species was recorded in areas with moderate elevation, on gentle to very steep slopes, being affected by overgrazing and the transformation of grasslands into arable land.

The abundance of the species varies significantly in the six clusters, highlighting different environmental conditions that influence its distribution. Thus, the highest average cover of the species *S. nutans* was recorded in cluster 4 (75%). A moderate abundance of the species was reported in cluster 5 (19%). In contrast, low abundance was recorded in clusters 1 and 2 (2%), 3, and 6 (1%).

Canonical Correspondence Analysis (CCA) revealed that the mean annual temperature (BIO1) accounted for the majority of the variation in floristic composition.

In locations with precipitation ranging from 400 to 550 mm/year, *S. nutans* had a low cover, ranging from 0.05–0.5%. Thus, once the precipitation increases to 650 mm/year, the cover increases to 62.5%. At intervals higher than 650 mm/year, cover decreased. This suggests that the abundance of the species may be limited by excess moisture and lower temperatures.

From a biogeographical perspective, *S. nutans* is characteristic of the West-Palaearctic steppe and forest-steppe. The species has a continuous range from the forest-steppe areas of the Lower Danube to the steppe and forest-steppe areas of the Ufa-Samara-Orenburg region. In the Transylvanian region, *S. nutans* is frequent, while in the Pannonian Basin, it is very rare.

Declarations

ORCID iDs

Simona Dumitrița Chirilă https://orcid.org/0000-0003-3397-1834

Alexandru Sabin Bădărău https://orcid.org/0000-0001-5113-2802

Mihai Doroftei https://orcid.org/0000-0002-8388-087X

Kiril Vassilev https://orcid.org/0000-0003-4376-5575

Iuliia Vasheniak https://orcid.org/0000-0003-1020-3007

Author contributions

Simona Dumitrița Chirilă: Conceptualization, Methodology, Investigation, Software, Data curation, Writing- Original draft preparation. **Alexandru Sabin Bădărău**: Data curation, Visualization, Investigation, Writing- Original draft preparation, Supervision. **Mihai Doroftei**: Data curation, Visualization, Investigation, Writing - review and editing, Supervision. **Kiril Vassilev**: Data curation, Visualization, Writing - review and editing, Supervision; **Iuliia Vasheniak**: Visualization, Software, Data curation, Writing- Original draft preparation, Supervision.

Conflicts of Interest

The authors declare no conflicts of interest.

Funding

No funding was received for conducting this study.

Data availability

The data that support the findings of this study are included within this paper and its supplementary information. Any other data are available from the corresponding author upon request.

References

1. Adla K, Dejan K, Neira D, Šiljić D (2022) Degradation of ecosystems and loss of ecosystem services. In: One Heal*th*. Academic Press: 281–327. https://doi.org/10.1016/B978-0-12-822794-7.00008-3

2. Aniţei A, Mititelu D (1997) Vegetaţia pajiştilor din bazinul Bahluieţului. Buletinul Grădinii Botanice Iaşi 6(2):359–370
3. Bai X, Zhao W, Wang J, Ferreira CSS (2021) Precipitation drives the floristic composition and diversity of temperate grasslands in China. Global Ecol Conserv 32:e01933. https://doi.org/10.1016/j.gecco.2021.e01933
4. Ballabio C, Lugato E, Fernández-Ugalde O, Orgiazzi A, Jones A, Borrelli P, Montanarella L, Panagos P (2019) Mapping LUCAS topsoil chemical properties at European scale using Gaussian process regression. Geoderma 355:113912. https://doi.org/10.1016/j.geoderma.2019.113912
5. Bai X, Zhao W, Wang J, Ferreira CSS (2021) Precipitation drives the floristic composition and diversity of temperate grasslands in China. Global Ecol Conserv 32:e01933
6. Barnosky AD, Matzke N, Tomiya S, Wogan GO, Swartz B, Quental TB, Ferrer EA (2011) Has the Earth's sixth mass extinction already arrived? Nature 471(7336):51–57. https://doi.org/10.1038/nature09678
7. Beldie A, Buia A, Grințescu G, Grințescu I, Gușuleasc M, Morariu I, Nyárády A, Nyárády EI, Paucă A, Prodan I, Răvăruț M, Țopa E (1961) *Salvia nutans* L., 260 pp. In: Săvulescu T (ed) Flora Republicii Populare Române, vol VIII. Editura Academiei Republicii Populare Romîne, București, p 704
8. Braun-Blanquet J (1964) Pflanzensoziologie. Grundzüge der Vegetationskunde. Springer, Wien
9. Budak V (1999) *Blackstonia acuminata* (Koch et Ziz) Domin. In: Stevanović V (ed.) *Crvena knjiga flore Srbije*, Vol. 1. Ministarstvo za životnu sredinu Republike Srbije, Biološki fakultet Univerziteta u Beogradu, Zavod za zaštitu prirode Republike Srbije, Beograd: 274–276
10. Caro T, Rowe Z, Berger J, Wholey P, Dobson A (2022) An inconvenient misconception: Climate change is not the principal driver of biodiversity loss. Conserv Lett 15(3):e12868. https://doi.org/10.1111/conl.12868
11. Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences 114(30): E6089–E6096. https://doi.org/10.1073/pnas.1704949114
12. Ceballos G, García A, Ehrlich PR (2010) The sixth extinction crisis: Loss of animal populations and species. J Cosmol 8(1821):31
13. Chifu T, Irimia I (2014a) Diversitatea fitosociologică a vegetației României. II. Vegetația erbacee antropizată. Tom. 2. Vegetația pioneră și a buruienișurilor. Institutul European, Iași 1119 pp
14. Chifu T, Irimia I (2014b) Diversitatea fitosociologică a vegetației României. III. Vegetația pădurilor și tufișurilor [The phytosociological diversity of Romania's vegetation. III. Vegetation of forests and bushes]. Institutul European, Iași 551 pp
15. Chifu T, Irimia I, Zamfirescu O (2014) Diversitatea fitosociologică a vegetației României. II. Vegetația erbacee antropizată. Vegetația pajiștilor [The phytosociological diversity of Romania's vegetation. II. Anthropogenic herbaceous vegetation. A. Grassland vegetation]. Institutul European, Iași 659 pp
16. Chytrý M, Dražil T, Hájek M, Kalníková V, Preislerová Z, Šibík J (2015) The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). Preslia 87(3):217–278.

https://www.preslia.cz/P153Chytry.pdf

17. Chytrý M, Tichý L, Hennekens SM, Schaminée JHJ (2020) EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. Appl Veg Sci 23:648–675. https://doi.org/10.1111/avsc.12519
18. Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. J Veg Sci 13:79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x
19. Ciocârlan V (2009) Flora Ilustrată a României: Pteridophyta et Spermatophyta, 3rd edn. Editura Ceres, București
20. Cristea V, Gafta D, Pedrotti F (2004) Fitosociologie. Presa Universitară Clujeană, Cluj-Napoca
21. Crişan A (2012) Evaluarea vulnerabilităţii nişei ecologice la *Pseudophilotes bavius hungarica* în raport cu utilizarea terenurilor şi a schimbărilor climatice folosind tehnici GIS. Doctoral dissertation, Babeș-Bolyai University, Cluj-Napoca
22. Crişan A, Vizauer TC, Rákosy L (2023) The protected species *Pseudophilotes bavius hungarica* (Diószeghy, 1913): oviposition strategy, new records and conservation (Lepidoptera: Lycaenidae). SHILAP Revista de lepidopterología 51(204):709–719
23. Csapody I (1982) Védett növényeink. Gondolat Könyvkiadó, Budapest, 346 pp
24. Csűrös I (1973) Az Erdélyi-mezőség élővilágáról. Tudományos Könyvkiadó, București, p 173
25. Csűrös I (1974) Az Erdélyi-medence növényvilágáról. Dácia Könyvkiadó, Kolozsvár, p 119
26. Đakić ŽS, Knežević AS, Boža PP (2012) Some extinct plant taxa on the territory of Novi Sad and their vulnerability status in Vojvodina and Serbia. Zbornik Matice srpske za prirodne nauke 122:45–61
27. Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22(9):489–496. https://doi.org/10.1016/j.tree.2007.07.001
28. Dirzo R, Raven PH (2003) Global state of biodiversity and loss. Annu Rev Environ Resour 28(1):137–167. https://doi.org/10.1146/annurev.energy.28.050302.105532
29. Duenas MA, Ruffhead HJ, Wakefield NH, Roberts PD, Hemming DJ, Diaz-Soltero H (2018) The role played by invasive species in interactions with endangered and threatened species in the United States: a systematic review. Biodivers Conserv 27:3171–3183. https://doi.org/10.1007/s10531-018-1595-x
30. Euro + Med (2025) Euro + Med PlantBase – the information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed. Accessed on 20 February 2025
31. European Soil Data Centre (2019) European Soil Database & Soil Properties. European Commission, Joint Research Centre. https://esdac.jrc.ec.europa.eu/resource-type/european-soil-database-soil-properties. Accessed on 2 January 2025
32. Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315. https://doi.org/10.1002/joc.5086

33. Fox J, Weisberg S (2019) An R Companion to Applied Regression, 3rd edn. Sage, Thousand Oaks, CA. https://www.john-fox.ca/Companion/
34. Germany M (2013) Island biogeography of steppe grasslands on sloping hills in the Târnava Mare Region in Transylvania (Romania). Diploma thesis, Mainz University
35. Golevich OV (2012) Ontogenetic structure of cenopopulations of *Salvia nutans* L. Industrial Botany
36. Grime JP (2001) Plant Strategies, Vegetation Processes, and Ecosystem Properties. Wiley
37. Gusztáv J (2005) Bókoló zsálya (*Salvia nutans*). https://termeszetvedelem.hu/wp-content/uploads/2024/09/Fajmegorzesi-terv-Bokolo-zsalya-2005.pdf
38. Horeanu C (1974) Studiul florei și vegetației din Podișul Casimcei. PhD Thesis, Universitatea „Al. I. Cuza, Iași
39. Irimia I, Mânzu C (2013) *Iris pontica* Zapal. in Moldova's flora (Romania). Analele Ştiinţifice ale Universităţii „Al. I. Cuza din Iaşi. Secţiunea II a. Biol Vegetală 59(1)
40. Isbell F, Balvanera P, Mori AS, He JS, Bullock JM, Regmi GR, Palmer MS (2023) Expert perspectives on global biodiversity loss and its drivers and impacts on people. Front Ecol Environ 21(2):94–103. https://doi.org/10.1002/fee.2536
41. IUSS Working Group WRB (2022) World Reference Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps. Fourth Edition. International Union of Soil Sciences (IUSS), Vienna, 236 pp
42. Janišová M, Michalcová D, Bacaro G, Ghisla A (2014) Landscape effects on diversity of semi-natural grasslands. Agric Ecosyst Environ 182:47–58. https://doi.org/10.1016/j.agee.2013.06.012
43. Jovanović S, Lakušić D (eds) (2006) Ugrožene biljke Srbije [Szerbia veszélyeztetett növényei]. Antić Jovan SZGR, Beograd, p 95
44. Klimeš L, Doležal J (2010) An experimental assessment of the upper elevational limit of flowering plants in the western Himalayas. Ecography 33(3):590–596. https://doi.org/10.1111/j.1600-0587.2009.05995.x
45. Kondratyuk EN, Burda RI, Ostapko VM (1985) Abstract of the flora of the south-east of Ukraine. Naukova Dumka, Kyiv, p 275
46. Kovács JA (2003) Meso-xerophilous grassland and fringe communities in the eastern part of the Transylvanian Basin. Kanitzia 11:97–126
47. Kovács JA (2011) Coenological differentiation of *Peucedanum* species (Sect. *Peucedanum*) stands in the Carpathian Basin. Annali di Bot 1:19–28
48. Maxwell SL, Fuller RA, Brooks TM, Watson JE (2016) Biodiversity: The ravages of guns, nets and bulldozers. Nature 536(7615):143–145. https://doi.org/10.1038/536143a
49. Moeslund JE, Arge L, Bøcher PK, Dalgaard T, Odgaard MV, Nygaard B, Svenning JC (2013) Topographically controlled soil moisture is the primary driver of local vegetation patterns across a lowland region. Ecosphere 4(7):1–26. https://doi.org/10.1890/ES13-00102.1

50. Mucina L, Bültmann H, Dierßen K, Tichý L et al (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen and algal communities. Appl Veg Sci 19:3–264. https://doi.org/10.1111/avsc.12257
51. Németh F (1990) Száras növények. In: Rakonczay Z (ed.) Vörös Könyv. Akadémiai Kiadó, Budapest: 265–321
52. Oprea A (2005) Lista critică a plantelor vasculare din România. Editura Universității Alexandru Ioan Cuza, Iași
53. Ozenda P (1994) Végétation du continent européen. Delachaux et Niestlé
54. Pînzaru P (2021) *Crataego monogynae-Cerasetum mahaleb* Pînzaru (*Berberidion vulgaris* Br.-Bl. ex Tx. 1952) – asociație nouă în vegetația de stâncării din Republica Moldova. Revista Botanică 23(2):32–43
55. Pobedinova EG (1954) Genus *Salvia* L. In: Shishkin BK (ed) Flora of the USSR, vol 21. Akademii Nauk USSR, Moscow
56. Popescu A, Doniță N, Roșca V, Băjenaru B (2008) Vegetația Parcului Național „Munții Măcinului. Editura Silvică, București, 240 pp. https://editurasilvica.ro/wp-content/uploads/2023/05/Vegetatia-Parcului-National-Muntii-Macinului-integral.pdf. Accessed on 23 March 2025
57. QGIS Development Team (2025) QGIS Geographic Information System. Version 3.34.3. Open Source Geospatial Foundation Project. https://qgis.org/ Accessed on 4 August 2025
58. R Core Team (2025) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
59. Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. J Veg Sci 20:596–602. https://doi.org/10.1111/j.1654-1103.2009.01062.x
60. Ruprecht E, Szabó A, Enyedi MZ, Dengler J (2009) Steppe-like grasslands in Transylvania (Romania): characterisation and influence of management on species diversity and composition. Tuexenia 29:353–368
61. Sârbu I, Ștefan N, Oprea A (2013) Plante vasculare din România – Determinator ilustrat de teren. Editura Victor B Victor, București, 1320 pp
62. Simon T (1992) *A* magyarországi edényes flóra határozója, Harasztok – Virágos növények. Tankönyvkiadó, Budapest, p 891
63. Soó R (1942) Az Erdélyi-medence endemikus és reliktum növényfajai. Acta Geobotanica Hungarica 5(1):141–183
64. Soó R (1968) A magyar flóra és vegetáció rendszertani-növényföldrajzi kézikönyve. Vol. III. Akadémiai Kiadó, Budapest, p 506
65. Sramkó G, Laczkó L (2020) A hazai bókoló zsálya (*Salvia nutans* L.) populációk konzervációgenetikai összehasonlítása erdélyi és oroszországi populációkkal = Conservation genetic analysis of

Transylvanian and Russian *Salvia nutans* L. populations in comparison with the relict Hungarian populations. Crisicum: Körös-Maros Nemzeti Park Igazgatóság Időszaki Kiadványa 11:111–125

66. ter Braak CJF, Šmilauer P (2018) Canoco reference manual and user's guide: Software for ordination (version 5.10). Biometris. Wageningen University & Research
67. Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. J Veg Sci 17:809–818. https://doi.org/10.1111/j.1654-1103.2006.tb02504.x
68. Tichý L, Chytrý M, Hájek M et al (2010) OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. J Veg Sci 21(2):287–299
69. Török P, Janišová M, Kuzemko A, Rūsiņa S, Stevanović ZD (2018) Grasslands, their threats and management in Eastern Europe. In: Squires VR, Dengler J, Feng H, Hua L (eds) Grasslands of the World. CRC, pp 78–102. https://doi.org/10.1201/9781315156125-11
70. Udvardy L (2002) Szaporodásbiológiai megfigyelések a *Salvia nutans* veszélyeztetettségének megítéléséhez. In: Az I. Magyar Természetvédelmi Biológiai Konferencia Program és Absztrakt kötete: 216
71. Vassilev K, Ruprecht E, Alexiu V, Dengler J et al (2018) The Romanian Grassland Database (RGD): historical background, current status and future perspectives. Phytocoenologia 48:91–100. https://doi.org/10.1127/phyto/2017/0229
72. Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. J Open Source Softw 4(43):1686. https://doi.org/10.21105/joss.01686
73. Will M, Classen-Bockhoff R (2017) Time to split *Salvia* s.l. (Lamiaceae) – New insights from Old World *Salvia* phylogeny. Mol Phylogenet Evol 109:33–58. https://doi.org/10.1016/j.ympev.2016.12.041
74. Ziman SN (1976) Life forms and biology of steppe plants of Donbass. Naukova Dumka, Kyiv, p 191

Figures

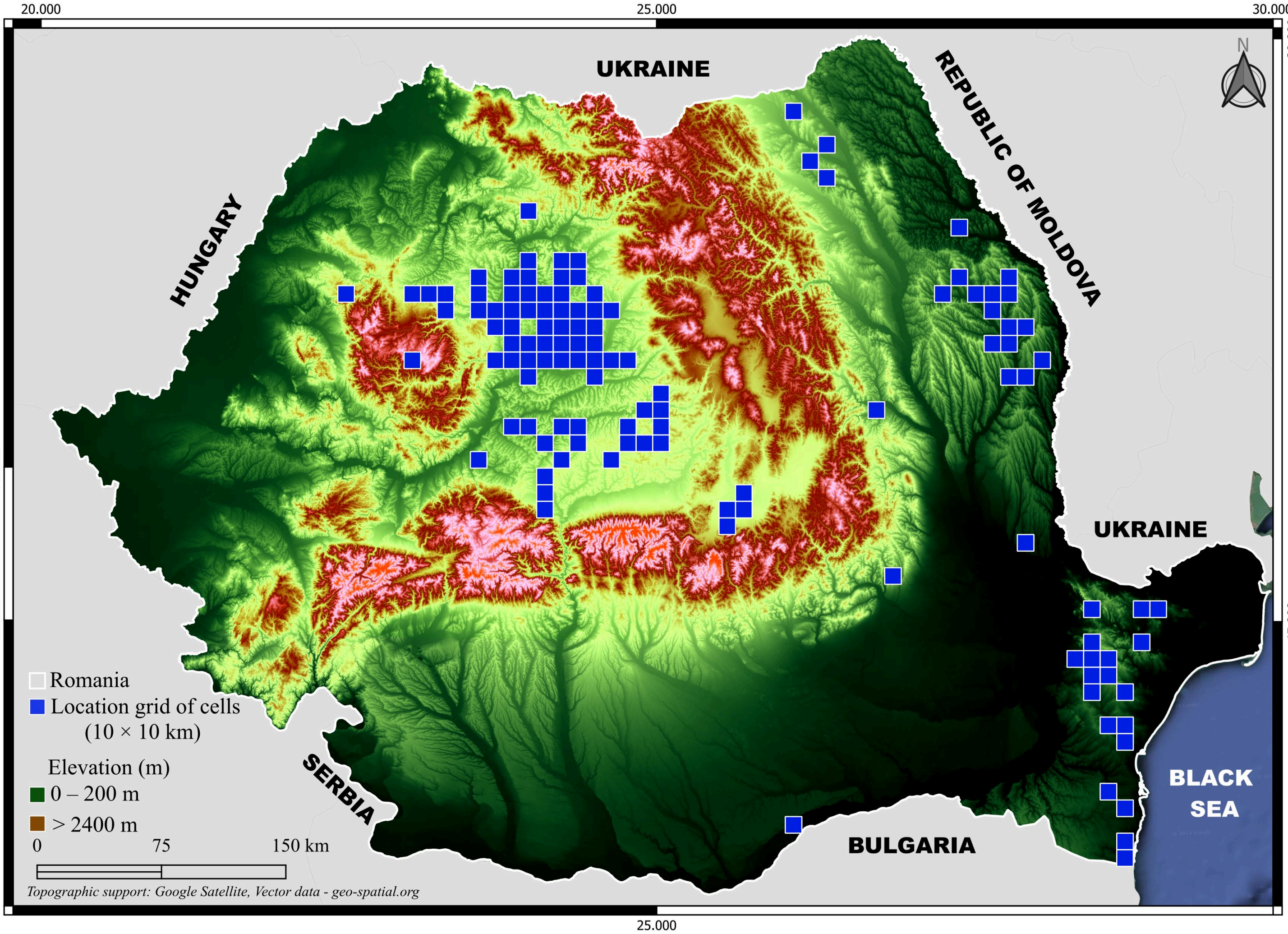

Figure 1

Map of the study area in Romania, showing the location of the grid cells (10 × 10 km) with markers from the literature and personal observations (Map: S. D. Chirilă).

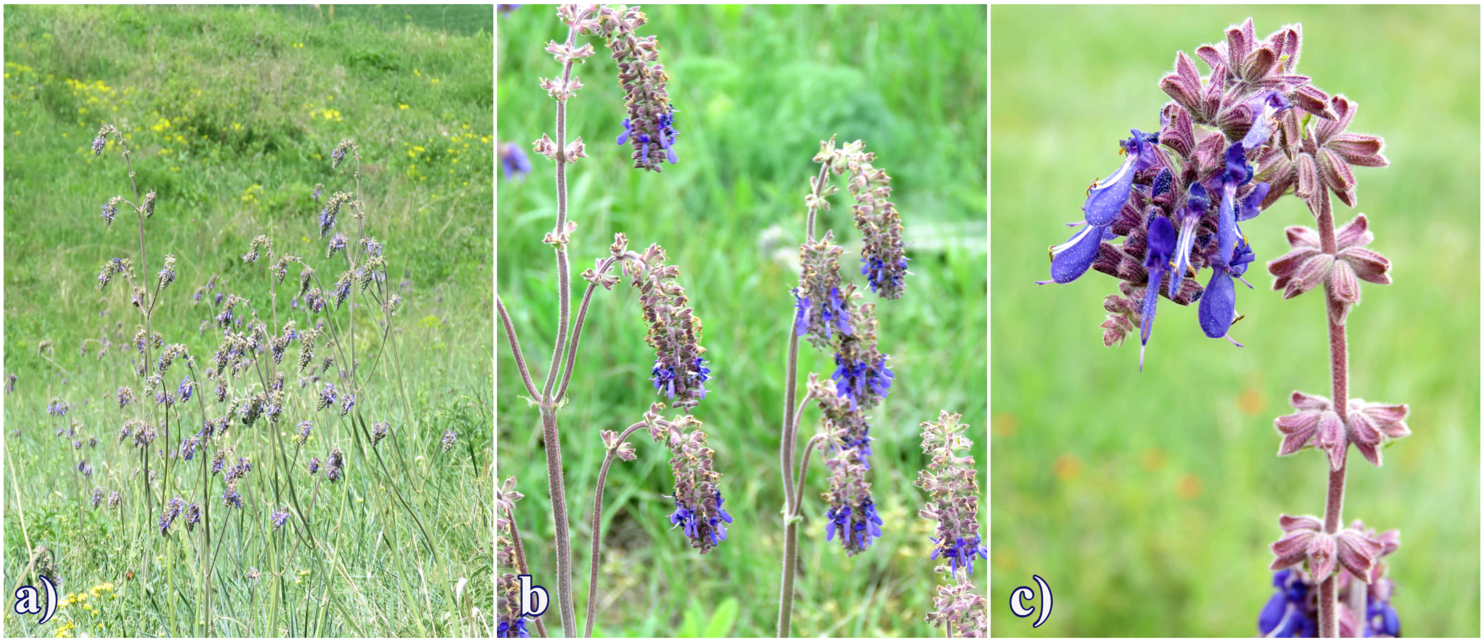

Figure 2

Salvia nutans L.: A, B, C – the flowering stage. (Photographs: S. Chirilă, May 2024).

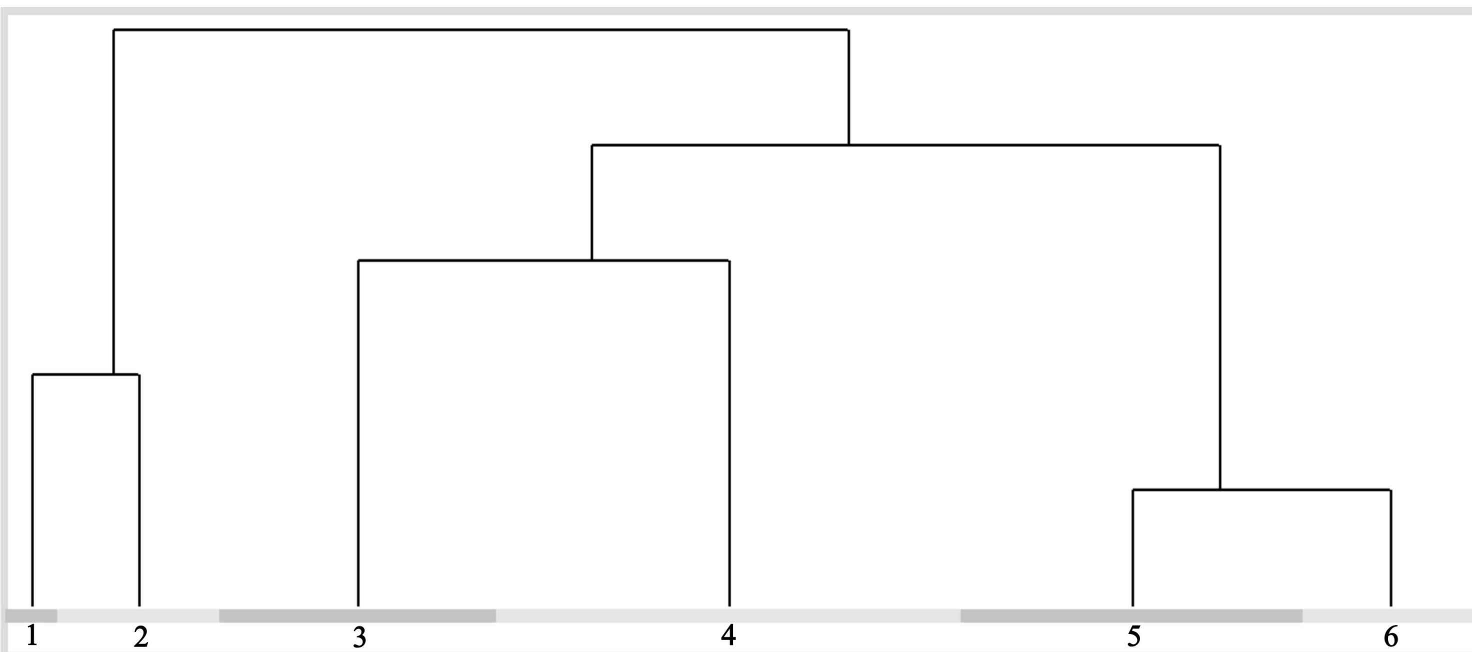

Figure 3

Dendrogram of relevés with *Salvia nutans* in Romania.

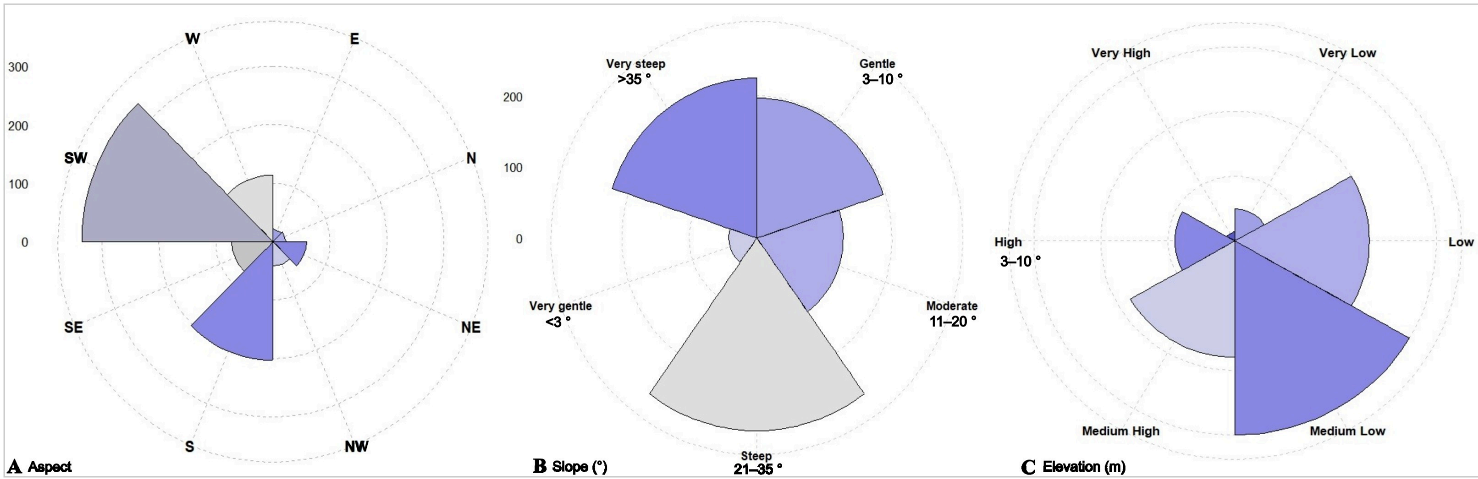

Figure 4

Topographic preferences of *Salvia nutans*.

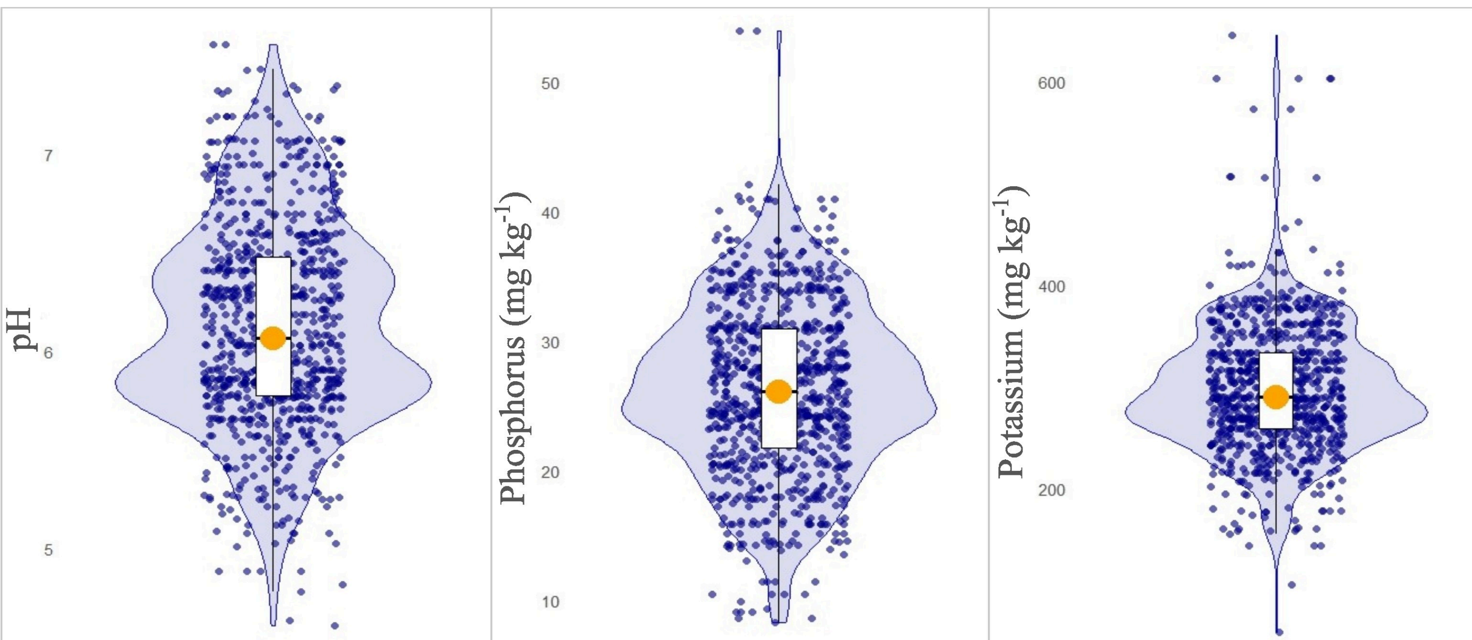

Figure 5

Soil chemical preferences of *Salvia nutans*.

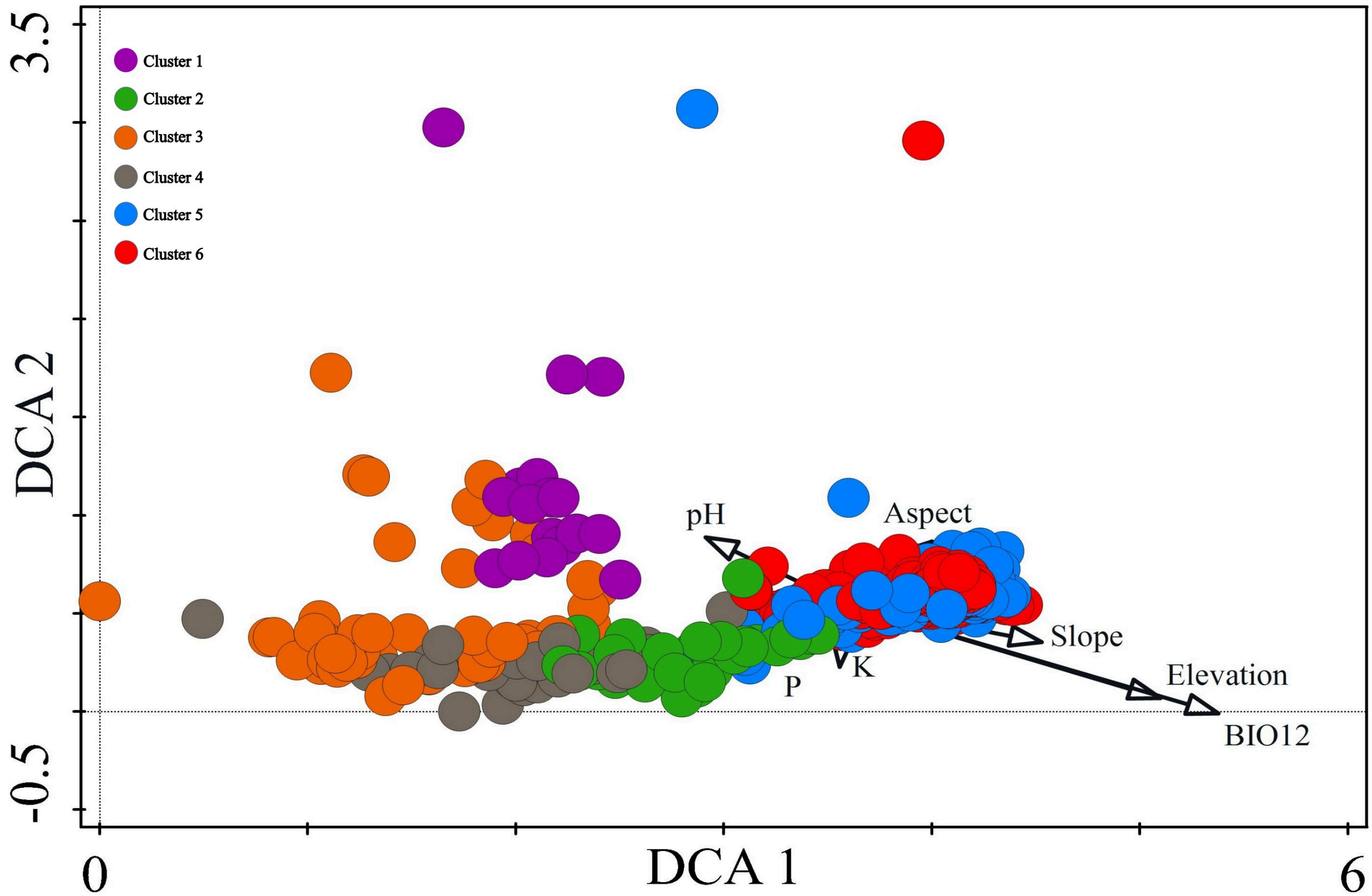

Figure 6

DCA ordination diagrams of the 870 vegetation plots

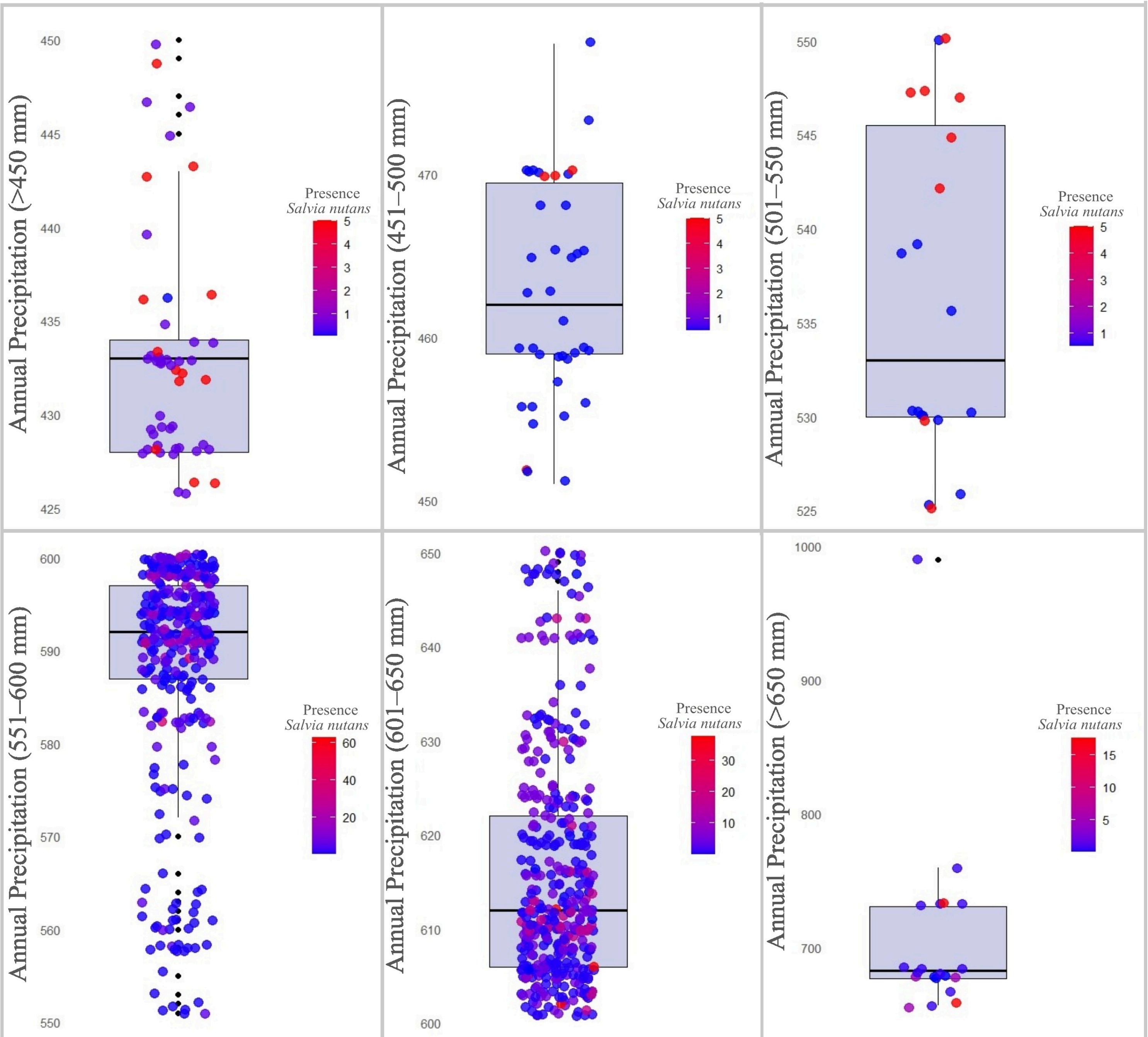

Figure 7

Distribution of *Salvia nutans* according to annual precipitation.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- TableSupplementary1.xlsx