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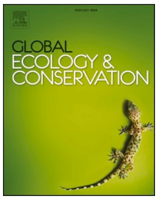

Vascular plant nano-hotspots in the central Balkan Peninsula – A novel GIS-based approach for identifying centres of species richness

Jovan Kovačević [a,*], Nevena Kuzmanović [b,*], Vladan Djordjević [b], Snežana Vukojičić [b], Ivana Stevanoski [b], Gordana Tomović [b], Marjan Niketić [c], Eva Kabaš [b], Predrag Lazarević [b], Sanja Đurović [d], Jelica Novaković [b], Uroš Buzurović [e], Miloš Zbiljić [f], Dmitar Lakušić [b]

[a] *Faculty of Civil Engineering, University of Belgrade, Bulevar kralja Aleksandra 73, Belgrade 11000, Serbia*
[b] *Faculty of Biology, University of Belgrade, Institute of Botany and Botanical Garden "Jevremovac", Takovska 43, Belgrade, Serbia*
[c] *Natural History Museum Belgrade, Njegoševa 51, Beograd, Serbia*
[d] *Faculty of Agriculture Kruševac, University of Niš, Kosančićeva 4, Kruševac 37000, Serbia*
[e] *Institute of Soil Science, Teodora Drajzera 7, Belgrade 11040, Serbia*
[f] *Faculty of Pharmacy, University of Belgrade, Vojvode Stepe 450, Beograd 11221, Serbia*

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ABSTRACT

Although the Balkan Peninsula is one of the most biodiverse regions in Europe, there is still a lack of knowledge about its plant diversity. This study aimed to fill this knowledge gap by studying the spatial patterns of plant diversity on three massifs that had previously been identified as hotspots for endemics, Arctic-alpine and Boreal relics. To achieve this objective, we employed data gap and GIS analysis techniques to identify species-rich areas and to assess the relationship between taxa richness and the components of environmental heterogeneity. Targeted field surveys were carried out over two seasons, and a total of 97 environmental factors were selected as elements of environmental heterogeneity. A considerable number of hotspots of plant richness were identified, comprising 18 actual and 57 potential nano-hotspots. Most of the identified potential nano-hotspots are situated in areas characterized by a pronounced canyon or ravine formation, while the lowest number was observed at the highest elevations of the mountains, especially in regions where silicate substrates predominate. Our findings confirm the importance of factors previously identified as pivotal, including terrain ruggedness, topoclimate, elevation, geological substrate, and vegetation types, and for the first time suggest that hydrographic factors exert a strong influence on patterns of species richness. Given the considerable taxa richness observed in the ravine habitats of the study area, which makes them of high conservation value, it is essential to implement robust protective mechanisms to mitigate the impending effects of global warming and carefully plan the construction of hydropower plants.

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* Corresponding authors.

E-mail addresses: jkovacevic@grf.bg.ac.rs (J. Kovačević), nkuzmanovic@bio.bg.ac.rs (N. Kuzmanović), vdjordjevic@bio.bg.ac.rs (V. Djordjević), sneza@bio.bg.ac.rs (S. Vukojičić), ijankovic@bio.bg.ac.rs (I. Stevanoski), gtomovic@bio.bg.ac.rs (G. Tomović), mniketic@nhmbeo.rs (M. Niketić), ekabas@bio.bg.ac.rs (E. Kabaš), predrag.lazarevic@bio.bg.ac.rs (P. Lazarević), djurovic.sanja@ni.ac.rs (S. Đurović), jelica@bio.bg.ac.rs (J. Novaković), soilsbuzurovic@gmail.com (U. Buzurović), milos.zbiljic@pharmacy.bg.ac.rs (M. Zbiljić), dlakusic@bio.bg.ac.rs (D. Lakušić).

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1. Introduction

Biodiversity, as an extraordinary feature of life, plays a pivotal role in the global functioning of ecosystems. These ecosystems provide essential resources such as drinking water, breathable air and fertile soils, underscoring the intrinsic link between human well-being and biodiversity (Cardinale et al., 2012; Hagen et al., 2012). It is now evident that the impact of biodiversity loss could be significant enough to compete with the effects of climate change, water and air pollution or desertification. Given the irreversible nature of biodiversity loss, there is a pressing need to intensify research on biodiversity, both as a natural phenomenon that remains surprisingly poorly understood, and as a phenomenon that meets a number of human needs in a variety of ways (Laurance and Edwards, 2011).

The identification of regions with high biodiversity is currently one of the most important challenges in the field of species conservation. The concept of a biodiversity hotspot, initially defined by Myers et al. (2000) and subsequently developed by Fenu et al. (2010) and Canadas et al. (2014), represents an effective tool for the conservation of most species at the lowest cost, the identification of priorities on a finer scale, and the maximization of the effectiveness of conservation investments (Murray-Smith et al., 2009).

The identification and monitoring of biodiversity hotspots has traditionally relied on extensive fieldwork (Melesse et al., 2007). Consequently, the implementation of such initiatives is inherently labor-intensive, costly, and in the case of challenging topographical conditions, even impracticable. The application of GIS technology coupled with remote sensing represents an effective tool to address these challenges (Melesse et al., 2007; Pimm et al., 2015). The increased availability of open and free-to-use databases, as well as open-source libraries and softwares, provides further impetus to this approach (Mose et al., 2018). Various successful examples and studies corroborate this, particularly in the context of regional and global studies, where the combination of such techniques, data and software is becoming the gold standard (Pocock et al., 2018; Kühl et al., 2020).

The process of identifying hotspots is contingent upon the selection of appropriate criteria and data types, as well as the establishment of clear thresholds for differentiating between hotspots and non-hotspots. These issues are thoroughly addressed by Canadas et al. (2014), who corroborate the assertion of Cayuela et al. (2011) that the criteria typically employed to identify hotspots are arbitrary, and that the selection of hotspots must be contextualized within the specific framework of each case study.

In most regions, the lack of comprehensive data sets on species occurrence hinders the accurate localization of hotspots. It is therefore of particular importance to gain an understanding of the factors that lead to high species diversity. In recent years, numerous studies have addressed these questions and demonstrated that environmental heterogeneity, which is influenced by both broad-scale factors (such as energy and water-related climatic variables), and fine-grained factors (such as topographic heterogeneity, bedrock chemistry, land cover, habitat diversity, hydrography, etc.), plays a significant role in determining species richness gradients (Stein et al., 2014; Canadas et al., 2014; Djordjević et al., 2016; Večeřa et al., 2019, and references therein). Moreover, several predictive models have been developed with the objective of mapping the expected number of vascular plant species that may co-occur and identifying the drivers that may determine the observed spatial patterns in species richness (Večeřa et al., 2019; Glasnović et al., 2023).

The Balkan Peninsula, situated within the Mediterranean region of Europe, is a region of exceptional biodiversity, making it a high conservation value area (HCVA). This is evidenced by its recognition as a global biodiversity hotspot and a global center of plant

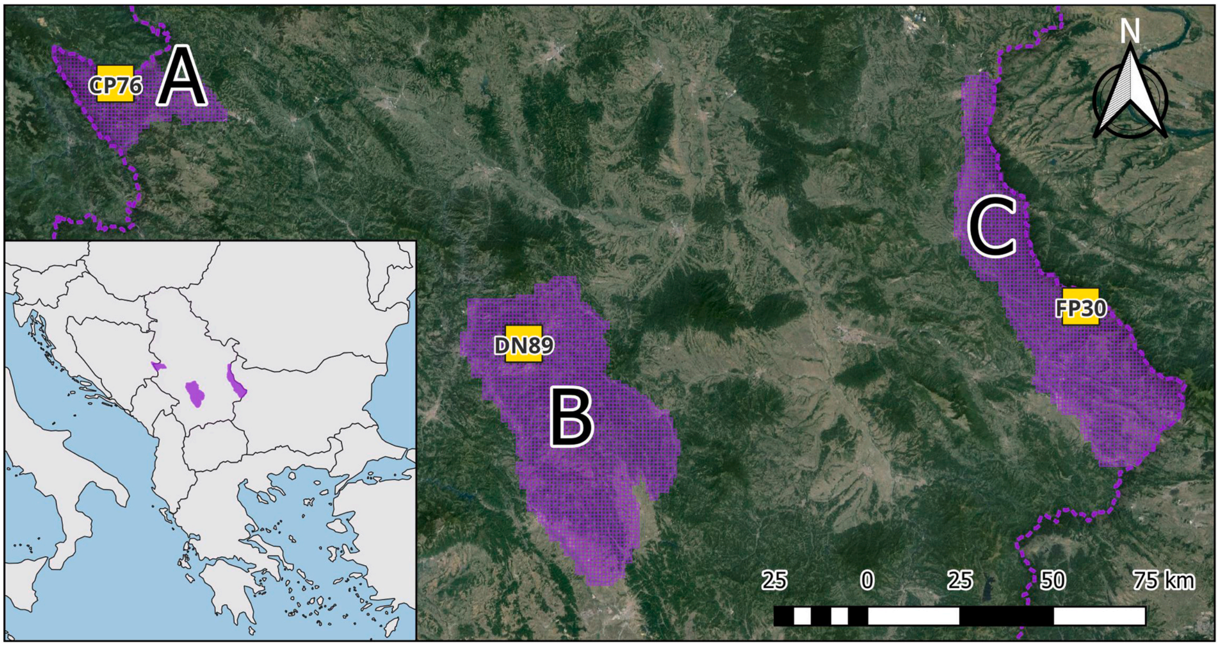

Fig. 1. Three study areas (massifs): A) Tara, B) Kopaonik, C) Stara. Highlighted in yellow are three representative MGRS 10 km grid cells for each mountain massif.

diversity (Barthlott et al., 2005; Brooks et al., 2006). Main hotspots for species richness are confined to the mountainous areas of the Balkan Peninsula (Stevanović, 1996; Ilić et al., 2022, 2023) and the region's heterogeneity of environmental factors, geological and historical changes, and human influences are considered to be the primary drivers of the extraordinary floristic diversity observed in this region (Horvat et al., 1974; Rahbek et al., 2019; Ilić et al., 2022). Despite the fact that the Balkan Peninsula represents one of the most biodiverse regions in Europe, knowledge about its plant diversity remains limited and incomplete. This paper aims to address this gap in knowledge by studying the spatial patterns of plant diversity in the Central Balkans. To achieve this, a variety of models will be employed to identify species-rich areas and employ a range of methods to assess the relationship between taxa richness and components of ecological heterogeneity. We focused our strategies on small areas that represent maximum diversity. In fact, we adopted the concept of nano-hotspots, as developed by Fenu et al. (2010) and Canadas et al. (2014) for endemic plants and applied it to the total flora of three major mountain massifs in the central Balkans.

By employing data gap and GIS analysis techniques, as well as different models for identifying and delimiting areas where species accumulate, and various methods for assessing the relationship between taxa richness and components of environmental heterogeneity, we aim to: (i) determine the complex interplay of spatial patterns associated with the variation of plant diversity in the central Balkan Peninsula; (ii) detect nano-hotspots – areas of exceptional concentration of species and (iii) demonstrate the usability of a new GIS-based approach for future nature conservation efforts, particularly those targeting not only endemic, but also endangered and rare plant species in the central Balkans.

2. Methods

2.1. Study area

The present study was conducted on a sample comprising three massifs: mt. Tara including mts. Zvijezda and Mokra Gora, mt. Kopaonik and mt. Stara planina including mt. Vidlič (Fig. 1). These massifs have previously been identified as hotspots for endemics (Tomović et al., 2014), Artic-alpine (Stevanović et al., 2009) and Boreal relics (Vukojičić et al., 2014). In order to facilitate the interpretation of the results and discussion, the individual massifs were assigned short names: Tara, Kopaonik and Stara.

The area under study encompasses the central part of the Balkan Peninsula – a mountainous region that is part of the Dinaric Alps in the west (Tara and Kopaonik), and part of the Balkan mountain systems in the east (Stara). In the context of physical geography, Tara is situated within the region of Western Serbia, Kopaonik within the region of Central Serbia, and Stara within the region of Eastern Serbia (Marković, 1970; Tomović et al., 2014). The highest peaks are Veliki Stolac (1675 m a.s.l.) on Tara, Pančićev vrh (2017 m a.s.l.) on Kopaonik and Midžor (2169 m a.s.l.) on Stara.

The Dinaric Alps in the west and the Balkan mountain systems in the east are distinguished by different climatic characteristics. The former region is characterized by humid temperate climate, whereas the latter displays semi-arid temperate-continental or subcontinental conditions, with a notable sub-Mediterranean influence (Stevanović and Šinžar-Sekulić, 2009).

The investigated area is characterized by three main groups of geological substrata. The first group comprises silicate rocks with an acidic to neutral pH (igneous, metamorphic, sedimentary). The second group encompasses silicate rocks with a basic to ultra-basic reaction (serpentinites and peridotites, ophiolitic belt). The third group consists of carbonate rocks with a neutral to basic reaction (clastic, sedimentary). All three types of geological substrata are represented on Kopaonik, whereas acidic silicate rocks (igneous and metamorphic) are absent on Tara, and ultra-basic silicate rocks (serpentinites and peridotites) are present only in traces on the Stara (OGK 1:300.000, (Geological Institute of Serbia, 2025)).

The investigated areas are characterized by the following main types of vegetation formations and vegetation classes (the nomenclature follows Mucina et al., 2016): (1) vegetation of rock crevices and screes (*Asplenietea trichomanis*, *Thlaspietea rotundifolii*); (2) freshwater aquatic (*Lemnetea*, *Potamogetonetea*) and vegetation of freshwater algae (*Charetea intermediae*); (3) vegetation of freshwater springs, shorelines and swamps (*Montio-Cardaminetea*, *Isoëto-Nanojuncetea*, *Phragmito-Magnocaricetea*); (4) vegetation of bogs and fens (*Scheuchzerio palustris-Caricetea fuscae*); (5) intrazonal boreo-temperate grasslands and heath (*Molinio-Arrhenatheretea*, *Calluno-Ulicetea*), and zonal steppe grasslands (*Festuco-Brometea*); (6) vegetation of the nemoral orosystems (montane tall-herb, and calcicolous and acidophilous grasslands) (*Mulgedio-Aconitetea*, *Elyno-Seslerietea*, *Juncetea trifidi*), and arctic and alpine-subnival snow-bed vegetation (*Salicetea herbaceae*); (7) temperate broadleaved forests and scrub (*Salicetea purpureae*, *Alno glutinosae-Populetea albae*, *Franguletea*, *Crataego-Prunetea*, *Carpino-Fagetea sylvaticae*, *Quercetea pubescentis*, *Quercetea robori-petraeae*); (8) primary dwarf heaths (tundra and European mountain tundra) (*Loiseleurio procumbentis-Vaccinietea*), and coniferous forests (*Erico-Pinetea*, *Vaccinio-Piceetea*); (9) anthropogenic vegetation (*Papaveretea rhoeadis*, *Polygono-Poetea annuae*, *Artemisietea vulgaris*, *Epilobietea angustifolii*, *Bidentetea*) (Kojić et al., 1998; Lakušić, 2005a). With the exception of formation (6), which is absent from Tara due to insufficient elevation, all other main types of vegetation formations are present in all three investigated areas (Zupančić, 1986; Kojić et al., 1998; Lakušić, 2005a).

2.2. Data on species richness

To eliminate the potential impact of disparate area sizes and varying study levels, the total number of vascular plants (TNVP) was quantified through targeted field research within a 1 km grid cell based on the Military Grid Reference System (MGRS) and Universal Transverse Mercator (UTM) projection (Lampinen, 2001).

The total number of vascular plants (TNVP) in this paper corresponds to the number of species and subspecies registered in each grid cell. To avoid confusion regarding the use of the term "species", this paper employs the term "taxa" which refers to species and subspecies.

Targeted field surveys were carried out over two seasons. Based on data indicating a high concentration of endemics, Artic-alpine and Boreal relics, we selected representative MGRS 10 km grid cells for each mountain massif for targeted field research in each mountain massif during the first field season (CP76 for Tara, DN89 for Kopaonik, and FP30 for Stara, all in 34 T UTM zone – Fig. 1). In the initial season, comprehensive floristic research was conducted within 56 MGRS 1 km grid cells, with the aim to establish the total number of vascular plants (TNVP) for a representative sample. This will allow for the identification of grid cells with different levels of biodiversity (rich, moderate and poor grid cells), the analysis of environmental factors and the prediction of biodiversity hotspots. TNVP was calculated based on the species recording per transect, which included all habitat types in a MGRS 1 km grid cell that were identified from orthophotos prior to fieldwork. The transect scheme utilized to compile a comprehensive list of all recorded taxa within a MGRS 1 km grid cell is illustrated in Fig. 2.

A preliminary analysis of environmental factors was conducted based on data collected during the first season of targeted field research. This analysis allowed for the initial identification of potential nano-hotspots. In the second season of targeted field research, an additional detailed floristic survey was conducted in new 37 MGRS 1 km grid cells. The selection of these new MGRS 1 km grid cells was based on the preliminary prediction of potential nano-hotspots, thus allowing the second field season to be dedicated to the verification of this preliminary prediction and the improvement of the model applied in the final prediction.

The cumulative data on floristic richness of 93 MGRS 1 km grid cells, collected during the first and the second years of fieldwork, constituted an integral data set for the analysis of environmental factors for all investigated squares, the selection of key environmental predictors, and the final modeling of floristic richness in MGRS 1 km grid cells for all three studied areas.

In order to collect input data on the floristic richness of 93 MGRS 1 km grid cells, 28 field days were conducted, in which 17 researchers participated, with a total of 220 researcher/days.

The collection of field data was conducted using the mobile application Fulcrum. A customized electronic field data form was developed for the purpose of data collection, wherein basic information regarding the registered plants was entered directly in the field. The application enabled researchers to accurately determine their location on a topographic map or orthophoto in real time, facilitating the tracking of optimal transects covering all identified macrohabitat types.

In cases where taxonomically critical groups and taxa could not be identified with certainty in the field, herbarium specimens were collected and deposited in BEOU and BEO (acronyms follow Thiers, 2024).

Following the identification of the disputed taxa and the validation of the accuracy and consistency of the data entered into the application during the fieldwork phase, a central database comprising 23,668 records was created to represent the distribution of species within 93 MGRS 1 km grid cells in three study areas (massifs). This database formed the basis for subsequent analyses and predictions.

2.3. Environmental data

In order to gain insight into the factors that contributed to high species diversity at the fine scale, a total of 97 environmental factors (EFs) were selected as elements of environmental heterogeneity (EH). Each factor is classified into one of the following seven classes of

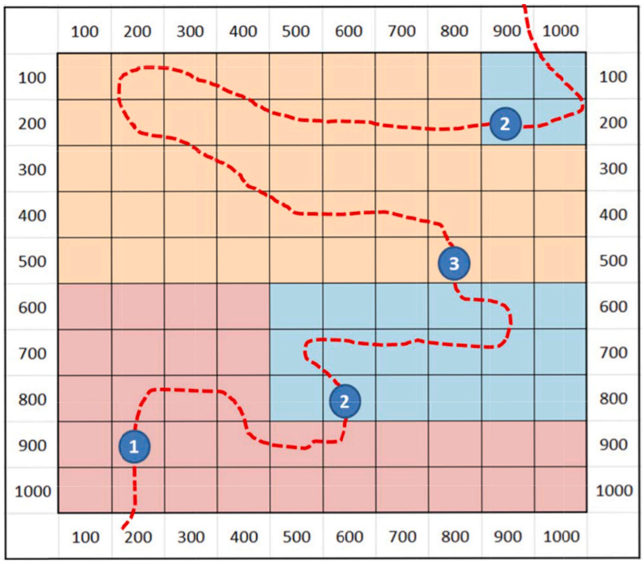

Fig. 2. Transect scheme used to compile a comprehensive list of all recorded taxa per 1 km^2 square. **Red dashed line with arrow** - line transect along which a census of species was recorded in a given square. **Blue points** - representative points by habitat types, to which the list of species in the field application is linked. The coloration of 100 × 100 m squares indicates the predominant habitat type observed in the 1 × 1 km base grid cell, as identified through the analysis of orthophotos.

environmental factors: (1) Topography, (2) Topoclimate, (3) Substrate, (4) Hydrography, (5) Land cover, (6) Vegetation types and (7) Vegetation diversity. Detailed classification of the environmental factors with their respective sources is presented in Table 1. The selection of environmental factors and the principles of their classification into seven classes are based on the concepts proposed by Stein et al. (2014), Buttrick et al. (2015) and Večeřa et al. (2019). The Digital Elevation Model (EU-DEM v.1.1 - https://land.copernicus.eu/), the Generalized habitat map of Serbia (Lakušić et al., 2021, 2022), the Basic geological maps of Serbia 1:100.000 (Geological Institute of Serbia, 2025), and the data on water courses and water surfaces (https://land.copernicus.eu/imagery-in-situ/eu-hydroEU) were employed as the basic sources of data for the purpose of quantifying the influence of individual environmental factors.

The cumulative plant species richness per vegetation type (veg_types) was recalculated based on the percentage of basic vegetation types in each square and the floristic richness class for each vegetation type. For the purposes of this work, 14 floristic richness classes were defined, which correspond to the data on the established floristic richness of different vegetation types in Serbia according to Lakušić (2005a). The affiliation of individual vegetation types to corresponding classes of floristic richness is shown in Table 2.

2.4. *Modeling environmental drivers and identification of potential nano-hotspots*

The methodology employed for modeling environmental drivers and potential nano-hotspots identification consists of five interconnected steps: 1) data preparation, 2) modeling environmental drivers, 3) prediction of the total number of vascular plants (TNVP), 4) validation and ranking, and 5) identification of potential nano-hotspots. All processing was conducted within the R environment (R Core Team, 2024) employing various R packages. A detailed explanation of the methodology employed will be provided in the following sections.

2.4.1. *Data preparation*

The initial stage of the process, data preparation, was designed to create a database in a format suitable to be used for all subsequent steps. This includes reprojecting all spatial data to the same coordinate reference system (UTM zone 34 T), as well as vector to raster conversion and raster alignment when necessary. The preprocessed spatial data were used as the input for calculating and extracting all 97 environmental factors (EF) previously discussed, for each of the MGRS 1 km grid cells. This was achieved through coupling R statistical functions with terra (Hijmans, 2024), vegan (Oksanen et al., 2022), landscapemetrics (Hesselbarth et al., 2019), spatialEco (Evans and Murphy, 2023) and whitebox (Lindsay, 2016; Wu and Brown, 2022) R packages. The resulting dataset comprises 5363 MGRS 1 km grid cells with EFs, 626 for Tara, 2656 for Kopaonik and 2081 for Stara. Of the aforementioned cells, 93 also had data regarding TNVP. These cells were used as a main input for the following steps.

2.4.2. *Modeling environmental drivers*

Not all EF are equally relevant for the prediction of potential nano-hotspots. Therefore, removing redundant and non-informative EFs is a prerequisite to achieve accurate and robust predictions (Cai et al., 2018). Filtering out non-informative and redundant predictors is a standard procedure in machine learning, with a variety of feature selection techniques available for this purpose (Tang et al., 2014; Cai et al., 2018). This research is focused on the application of filter-methods for feature selection, using various statistical metrics and methods to define the set of key environmental drivers for modeling TNVP.

The six sets of environmental drivers were determined. The first two sets were determined by employing simple regression analysis, the approach initially proposed by Canadas et al. (2014). Simple regression was calculated between each environmental factor (EF) and TNVP and the statistical significance p of each EF was then determined. The first set (**SR $p < 0.05$**) consisted of all moderately statistically significant EFs ($p < 0.05$), while the second (**SR $p < 0.01$**) comprised those EFs with strong statistical significance ($p < 0.01$). The approach employed in Glasnović et al. (2023) was replicated in order to determine the third set of environmental drivers (**VIFSTEP**). This included filtering out EFs by calculating variance inflation factor (VIF ≥ 5) using usdm R package (Naimi et al., 2014), and the subsequent removal of EFs which were statistically unsignificant. The fourth set of environmental drivers (CFS) was determined by employing the Correlation Feature Selection method (Hall, 2000) implemented in FSelector R package (Romanski et al., 2023). Additionally, two more EF sets were determined non-statistically. These included empirically selected important EFs based on practical experience gained through observation of biogeographical and ecological rules affecting the distribution of flora and vegetation on the Balkan Peninsula (**ES EFs**), as well as the complete set of EFs (**All EFs**).

2.4.3. *Prediction of the total number of vascular plants (TNVP) by MGRS 1 km grid cells*

Random Forest (RF) is a widely used machine learning method, successfully applied for solving a variety of problems in a range of fields. The core concept of the Random Forest (RF) method is the construction of an ensemble of decision trees during the training phase. This is achieved through the use of bootstrap sampling to create each tree, and the remaining data is used to evaluate the tree's performance and refine the tree-building process. Once the forest of decision trees is complete, predictions are made by averaging the outputs of all the trees (Breiman, 2001). The RF method was selected over other ML techniques due to its demonstrated applicability in similar hotspot identification studies (Divíšek and Chytrý, 2018; Večeřa et al., 2019), as well as its simplicity, robustness and capacity to provide high accuracy even with smaller training datasets. In this study, the RF implementation in the ranger R package was employed (Wright and Ziegler, 2017).

Separate RF model was trained for each of the previously defined sets of EFs. The predicted value was TNVP, while the EFs are used as predictor variables. Each forest consisted of 1000 trees, while all other ranger parameters were left at the default values.

Table 1
Classification of environmental factors (EF) analyzed in this study.

Environmental factors (EF) - acronym	Environmental factors (EF) - full name	Source
Topography		
dem_elevation_min	Elevation minimum	EU-DEM v.1.1
dem_elevation_max	Elevation maximum	
dem_elevation_sd	Elevation standard deviation	
dem_curvature_sd	Profile curvature standard deviation	
dem_slope_min	Slope minimum	
dem_slope_max	Slope maximum	
dem_slope_sd	Slope standard deviation	
dem_elevation_range	Elevation range	
dem_slope_range	Slope range	
dem_tri_min	Terrain Ruggedness Index (TRI) maximum	
dem_tri_max	Terrain Ruggedness Index (TRI) minimum	
dem_tri_range	Terrain Ruggedness Index (TRI) range	
dem_tri_sd	Terrain Ruggedness Index (TRI) standard deviation	
Topoclimate		
dem_hli_max	Heat Load Index (HLI) maximum	EU-DEM v.1.1
dem_hli_min	Heat Load Index (HLI) minimum	
dem_hli_range	Heat Load Index (HLI) range	
dem_hli_sd	Heat Load Index (HLI) standard deviation	
dem_tci_max	Topoclimatic Diversity Index (TDI) maximum	
dem_tci_min	Topoclimatic Diversity Index (TDI) minimum	
dem_tci_range	Topoclimatic Diversity Index (TDI) range	
dem_tci_sd	Topoclimatic Diversity Index (or TDI) standard deviation	
dem_twi_max	Compound Topographic Index (CTI) maximum	
dem_twi_min	Compound Topographic Index (CTI) minimum	
dem_twi_range	Compound Topographic Index (CTI) range	
dem_twi_sd	Compound Topographic Index (CTI) standard deviation	
Substrate		
Sgeol	No. of geology types	OGK 1:100.000
Ca	% cover of carbonate bedrock	
MgFe	% cover of ultramafic bedrock	
Mix	% cover of mixture bedrock	
Si	% cover of silicate bedrock	
Ca_1	% cover of carbonate bedrock - type Ca_1	
Ca_2	% cover of carbonate bedrock - type Ca_2	
Ca_3	% cover of carbonate bedrock - type Ca_3	
MgFe_1	% cover of ultramafic bedrock - MgFe_1	
Mix_1	% cover of mixture bedrock - type Mix_1	
Mix_2	% cover of mixture bedrock - type Mix_2	
Mix_3	% cover of mixture bedrock - type Mix_3	
Si_1	% cover of silicate bedrock - type Si_1	
Si_2	% cover of silicate bedrock - type Si_2	
Si_3	% cover of silicate bedrock - type Si_3	
Si_4	% cover of silicate bedrock - type Si_4	
Shannon_H_Geol	Shannon index of geology types	
soil_types	No. of soil/geology types	OGK 1:300.000
soil_shannon	Shannon index of soil/geology types	
krecnjaci_perc	% cover of limestone bedrock	
ultramafiti_perc	% cover of ultramafic bedrock	
Hydrography		
sw_perc	% cover of standing water	eu-hydroEU
sw_edge_density	edge density of standing water	
sw_mean_patch_area_ha	mean patch_area of standing water	
sw_patch_count	patch count of standing water	
rw_perc	% cover of running water	
rw_edge_density	edge density of running water	
Land cover		
lc_edge_density	edge density of land cover types	Lakušić et al., (2021)
lc_mean_patch_area_ha	mean patch_area of land cover types	
lc_shannon	Shannon index of land cover types	
lc_summary_perc_1	% cover of forest habitat types (GkaSS 1–9)	
lc_summary_perc_2	% cover of scrub habitat type (GkaSS 10–13)	
lc_summary_perc_3	% cover of herbaceous habitat types (GkaSS 14–25)	
lc_summary_perc_4	% cover of freshwater habitat types (GkaSS 27–28)	
lc_summary_perc_5	% cover of anthropogenic habitat types (GkaSS 28–29)	
lc_types	No. of land cover types	
rocks_perc	% cover of rocks (% GkaSS 22)	
wetlands_perc	% cover of wetlands (% GkaSS 23–25)	

(*continued on next page*)

Table 1 (*continued*)

Environmental factors (EF) - acronym	Environmental factors (EF) - full name	Source
Vegetation types		
gkass_summary_perc_1	% cover of "Salicion"	Lakušić et al., (2021)
gkass_summary_perc_2	% cover of "Quercion roboris"	
gkass_summary_perc_3	% cover of "Quercion frainetto"	
gkass_summary_perc_4	% cover of "Ostryo-Carpinion orientalis"	
gkass_summary_perc_5	% cover of "Fagion sylvaticae"	
gkass_summary_perc_6	% cover of "Pinion nigrae"	
gkass_summary_perc_7	% cover of "Vaccinio-Piceetea"	
gkass_summary_perc_8	% cover of "Abieti-Fagenion"	
gkass_summary_perc_9	% cover of "Pino-Quercion"	
gkass_summary_perc_10	% cover of "Salicetea purpureae" + "Crataego-Prunetea" + "Sambuco-Salicion"	
gkass_summary_perc_11	% cover of „Vaccinion myrtilli-uliginosi“	
gkass_summary_perc_12	% cover of „Pinion mugo“	
gkass_summary_perc_13	% cover of „Juniperion nanae“	
gkass_summary_perc_14	% cover of "Festucion vaginatae"	
gkass_summary_perc_15	% cover of "Festucion rupicolae"	
gkass_summary_perc_16	% cover of "Festuco-Brometea"	
gkass_summary_perc_17	% cover of "Molinio-Arrhenatheretea"	
gkass_summary_perc_18	% cover of „Festuco-Seslerietea“	
gkass_summary_perc_19	% cover of „Puccinelion“	
gkass_summary_perc_20	% cover of "Festucion pseudovinae"	
gkass_summary_perc_21	% cover of „Puccinelion“	
gkass_summary_perc_22	% cover of „Asplenietea trichomanis“	
gkass_summary_perc_23	% cover of "Scheuchzerio-Caricetea fuscae"	
gkass_summary_perc_24	% cover of "Phragmitetea"	
gkass_summary_perc_25	% cover of "Salicornietea"	
gkass_summary_perc_26	% cover of "standing water"	
gkass_summary_perc_27	% cover of "running water"	
gkass_summary_perc_28	% cover of "Agriculture"	
gkass_summary_perc_29	% cover of "Urban habitats"	
Vegetation diversity		
veg_types	# Cumulative plant species riches per vegetation types	Lakušić, (2005a)
veg_S_klasa	No. of vegetation types (1 to 29)	Lakušić et al., (2021)
veg_shannon	Shannon index of vegetation type	
veg_edge_density	Vegetation edge density	
veg_mean_patch_area_ha	Vegetation mean patch size	

2.4.4. *Validation and ranking*

All created models were validated in order to allow comparisons and to determine the optimal prediction model. For this purpose, Leave-One-Out Cross-Validation (LOOCV) was employed over the 93 MGRS 1 km grid cells with known TNVP. The observed and LOOCV predicted values of TNVP were used to calculate the following validation metrics: root mean square error (*RMSE*), coefficient of determination (R^2), and Akaike Information Criterion (*AICc*). Using these validation metrics, the ranking between models was performed, choosing the most optimal one.

2.4.5. *Identification of potential nano-hotspots*

The identification of nano-hotspots was based on the TNVP values predicted by the optimal prediction model. This was achieved through comparing the number of plants present in a MGRS 1 km grid cell with those in complete data set for all three massifs. The term „nano-hotspot“ was used in sense proposed by Fenu et al. (2010) and Canadas et al. (2014). Given that the selection of hotspots must be contextualized in relation to the specificities of each case study, which implies understanding local ecological, biogeographical and historical peculiarities of researched area (Cayuela et al., 2011; Canadas et al., 2014), we have identified a given MGRS 1 km grid cell as a nano-hotspot whenever it accounted for more than 300 taxa. Additionally, in relation to floristic richness, all MGRS 1 km grid cells were classified into four classes based on the predicted number of plants in each MGRS 1 km grid cells: a) very rich = nano-hotspot ($S > 300$), b) rich (S 250–300), c) moderately rich (S 200–250), and d) poor ($S < 200$).

3. Results

3.1. *Identifying nano-hotspots within massifs*

Following the identification of disputed taxa and the verification of data collected during the first and the second year of fieldwork, a central database comprising 23,668 records on the distribution of taxa in 93 individual MGRS 1 km grid cells was compiled.

In terms of floristic richness, 18 (19 %) MGRS 1 km grid cells were identified as very rich = nano-hotspots, 14 (15 %) MGRS 1 km grid cells as rich, 28 (30 %) MGRS 1 km grid cells as moderately rich and 33 (35 %) MGRS 1 km grid cells as floristically poor areas (Fig. 3). The largest number of grid cells identified as very rich = nano-hotspots was recorded on Tara 8 (9 %), the smallest on Stara 4 (4 %). Contrary, the largest number of grid cells identified as poor was registered on Kopaonik 17 (18 %) and the smallest on Tara 6

Table 2
The basic types of land cover and vegetation types (according to Generalized habitat map of Serbia (GkaSS) Lakušić et al., 2021) with species richness class (S class). The values pertaining to species richness class per vegetation type (S class) are employed in the analyses and predictions.

GKaSS unit	GKaSS code	GKaSS - Land cover type	GkaSS - Vegetation type	S class
1	A1_a	Forest	"Salicion"	2
2	A1_b	Forest	"Quercion roboris"	2
3	A2_a	Forest	"Quercion frainetto"	14
4	A2_b	Forest	"Ostryo-Carpinion orientalis"	14
5	A3_a	Forest	"Fagion sylvaticae"	14
6	A5_a	Forest	"Pinion nigrae"	6
7	A6_a	Forest	"Vaccinio-Piceetea"	7
8	A8_a	Forest	"Abieti-Fagenion"	7
9	A8_b	Forest	"Pino-Quercion"	7
10	B1–2–3	Scrub	"Salicetea purpureae", "Crataego-Prunetea", "Sambuco-Salicion"	7
11	B4_a	Scrub	„Vaccinion myrtilli-uliginosi“	2
12	B6_a	Scrub	„Pinion mugo“	7
13	B6_b	Scrub	„Juniperion nanae“	7
14	C1_a	Grasslands	"Festucion vaginatae"	6
15	C1_b	Grasslands	"Festucion rupicolae"	11
16	C1_c	Grasslands	"Festuco-Brometea"	11
17	C2_a	Grasslands	"Molinio-Arrhenatheretea"	8
18	C4_a	Grasslands	„Festuco-Seslerietea“	6
19	C6_a	Grasslands	„Puccinellion“	2
20	C6_b	Grasslands	"Festucion pseudovinae"	2
21	C6_c	Grasslands	„Puccinelion“	2
22	D2_a	Grasslands	„Asplenietea trichomanis“	5
23	E2_a	Grasslands	"Scheuchzerio-Caricetea fuscae"	2
24	E4_a	Grasslands	"Phragmito-Magnocaricetea"	2
25	E5_a	Grasslands	"Beckmanion"	2
26	F1_a	Aquatic habitats	Standing water	1
27	F2_c	Aquatic habitats	Running water	1
28	G	Anthropogenic habitats	Agricultural habitats	6
29	H	Anthropogenic habitats	Urban and artificial habitats	6

(6 %) (Table 3). The MGRS cells CP7548 (Beli Rzav, Kaskade) on the Tara with 429 species and FN5681 (Garište) on the Stara with 415 taxa represent the richest polygons, i.e., the most significant nano-hotspots on all three mountain massifs (Table 4). On the contrary, MGRS cells with the poorest flora are FP3408 (Tupanar) with only 79 species, FP3605 (Midžor I) and FP3605 (Midžor II) with 81 species (Table 4).

3.2. Modeling key environmental factors (EFs)

Of the initial 97 EFs, a considerable number were ultimately deemed irrelevant for the purpose of predicting TNVP values. The employed feature selection method influenced the degree of informativeness of the EFs, with different EFs emerging as more or less informative than others. Consequently, the total number of EFs varied, ranging from 10 to a maximum of 52 (see Table A.1 for the complete list of selected EFs by each method). In the next step, each set of EFs was ranked using the previously described validation procedure. As shown in Table 5, the difference in validation metrics exists, but in many cases only by mark.

The results of the validation metrics showed that no set of EFs can be identified as a clear superior to all others. It is only evident that the VIFSTEP method produced the least favorable results and should therefore be excluded from further consideration. Using the *RMSE*, and R^2 validation metrics, the optimal set of EFs is that which was identified through SR $p < 0.01$ method. Nevertheless, the SR $p < 0.05$ method exhibited slightly inferior metrics, while the use of All EFs method provided results that are relatively similar. On the other hand, the *AICc* ranking yielded markedly different results, where the CFS method provided the most optimal results, followed by the ES EFs method. The use of All EFs method yielded the poorest results according to the *AICc* metric, while remaining methods (SR $p < 0.01$, SR $p < 0.05$ and VIFSTEP) exhibited highly similar *AICc* values.

The optimal set of EFs was determined by ranking of all tested methods. The ranking is primarily based on the *RMSE* and R^2, with *AICc* and the number of EFs used as a secondary criterion to differentiate between the methods with similar *RMSE* and R^2 values. This approach demonstrated that the optimal set of EFs is the one determined by SR $p < 0.01$ method. Its *RMSE* and R^2 are the highest of all tested methods while using smaller number of EFs and with better *AICc* value compared to other two methods with similar metrics. Therefore, this set of EFs was employed to create the prediction model of TNVP across the entire study area (Table 5).

3.3. Modeling of species richness and identifying potential nano-hotspots by massifs

The random forest model trained to predict TNVP values in the study area showed that TNVP exhibited a clear spatial pattern in all massifs. A larger number of taxa were mainly concentrated in the deep river valleys, especially in areas with a pronounced canyon or ravine character, and decreased towards the highest elevations of the mountain range, especially in regions where silicate substrate predominates (Fig. 4).

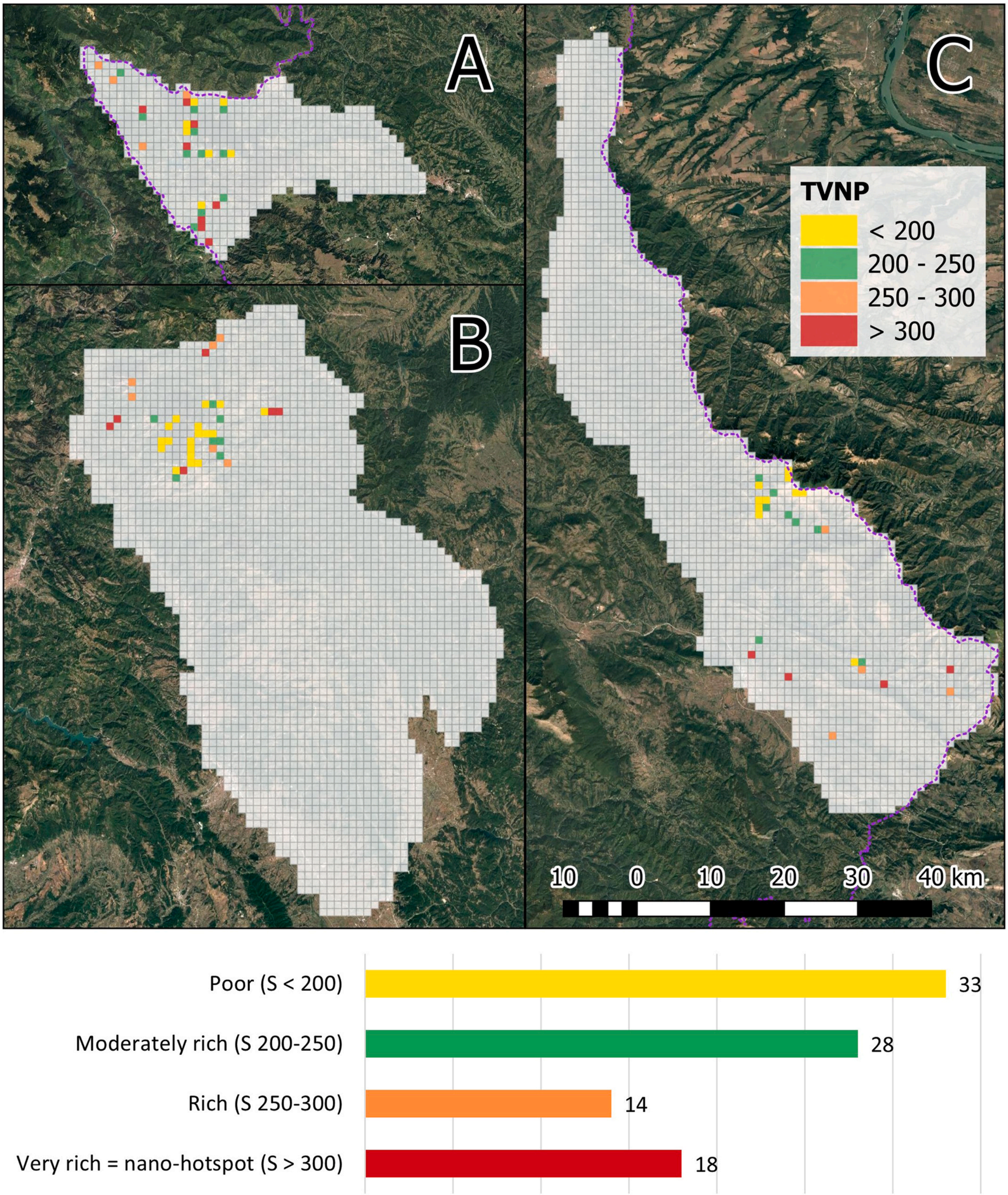

Fig. 3. The spatial distribution and number of MGRS 1 km grid cells belonging to different classes of floristic richness based on the established total number of vascular plants (TNVP) during the first and second years of fieldwork.

The number of MGRS 1 km grid cells belonging to different classes of floristic richness based on the predicted total number of vascular plants (TNVP_rf) is shown in Table 6. A total of 57 potential nano-hotspots were identified across all three massifs, representing 1 % of all analyzed cells. The greatest number of potential nano-hotspots was identified on Stara and Tara, 23 and 21 respectively. In contrast, only 13 grid cells on Kopaonik exhibited a higher level of floristic richness, with more than 300 taxa. The majority of grid cells were classified as moderately rich (3317 grid cells, i.e. 62 %), 1511 cells (28 %) were classified as rich, while the

Table 3
The number of Military Grid Reference System (MGRS) 1 km grid cells belonging to different classes of floristic richness by mountain massif, based on the established total number of vascular plants (TNVP) during the first and second years of fieldwork.

	Number of **MGRS 1 km** cells	% of **MGRS 1 km** cells
TARA		
a) very rich = nano-hotspot (S > 300)	8	9 %
b) rich (S 250–300)	4	4 %
c) moderately rich (S 200–250)	12	13 %
d) poor (S < 200)	6	6 %
KOPAONIK		
a) very rich = nano-hotspot (S > 300)	6	6 %
b) rich (S 250–300)	6	6 %
c) moderately rich (S 200–250)	8	9 %
d) poor (S < 200)	17	18 %
STARA		
a) very rich = nano-hotspot (S > 300)	4	4 %
b) rich (S 250–300)	4	4 %
c) moderately rich (S 200–250)	8	9 %
d) poor (S < 200)	10	11 %

remaining 471 (9 %) grid cells were classified as poor. The majority of poor grid cells were identified in Stara and Kopaonik (227 and 198, respectively), while the lowest number were identified in Tara (only 46).

3.4. Environmental factors affecting species richness by massifs

The analysis of the EFs shows strong correlations between TNVP and many of the predictor variables (Table A.1). SR $p < 0.01$ method, which had the best validation metrics, identified 44 EFs as optimal predictor variables (Table 7). In addition, significant correlations were identified between the TNVP and the predictor variables, which were positive for some EFs but negative for other EFs (Fig. 5).

4. Discussion

The Balkan Mountains, and in particular the Dinarides region, are characterized by an exceptionally high species richness at both the regional level and at the level of small standard squares (Jimenez-Alfaro et al., 2021; Ilić et al., 2022, 2023). Furthermore, the vascular flora of the central part of the Balkan Peninsula comprises a highly diverse assemblage of plants of diverse origins and ages (Stevanović et al., 2009; Tomović et al., 2014; Vukojičić et al., 2014). This is the reason why the Balkans is recognized as a global biodiversity hotspot and a global center of plant diversity, being at the same time a high conservation value area (Barthlott et al., 2005; Brooks et al., 2006).

Although many regional hotspots for species richness have been identified in the mountainous regions of the Balkan Peninsula, there is no data on smaller hotspots within larger hotspots, which could be an important tool for focusing conservation efforts. In this study focused on the central part of the Balkans, we used different methods to assess the relationship between taxa richness and components of the environment, as well as data gap and GIS analysis techniques and different models to delimit nano-hotspots as areas where species highly accumulate. In fact, we adopted the concept of "hotspots within hotspots", developed for endemic plants by Fenu et al. (2010) and Canadas et al. (2014), and applied it to the total flora of three major mountain massifs in the central Balkans. Although these massifs offer valuable insights for studying patterns of plant diversity in the central part of the Balkan Peninsula, we acknowledged that this selective approach may not fully capture the overall patterns of plant diversity across the entire Balkan Peninsula. Therefore, future studies encompassing a broader range of regions would undoubtedly enhance our understanding and provide a more comprehensive perspective.

The proposed methodology strongly relies on GIS and modeling, therefore the resulting accuracy hinges on the quality and completeness of input data and the assumptions behind the applied models. In such cases, both visual and statistical validation are essential to assess the quantitative and qualitative uncertainty of the results. To this end, the authors conducted a visual inspection and applied LOOCV. LOOCV is chosen as a well established and known method used for statistical validation and unbiased accuracy estimate. Given the extensive fieldwork required to determine TNVP for each MGRS 1 km grid cell, this approach can be considered optimal, as obtaining a fully representative and entirely independent dataset would demand significant additional field efforts.

4.1. Nano-hotspots within massifs

In this study we identified a significant number of hotspots of plant richness within a set of 93 MGRS 1 km^2 squares through the analysis of the total number of vascular plants during targeted field research conducted over two field seasons. A total of 18 actual nano-hotspots (Table 4) were identified, along with 57 potential nano-hotspots (Fig. 5; Table 6), which harbour more than 300 taxa within a single MGRS 1 km cell. Two nano-hotspots were identified, each with an actual diversity of more than 400 taxa in a single MGRS 1-km cell. It is acknowledged that the selection of different thresholds can be subjective and may influence the outcomes and

Table 4
The total number of vascular plants (TNVP) by basic Military Grid Reference System (MGRS) 1 km cells registered during the first and second years of fieldwork. Classes of richness: a) very rich = nano-hotspot (S > 300), b) rich (S 250–300), c) moderately rich (S 200–250), d) poor (S < 200).

MGRS_1 × 1_km	Massif	Poligon_id	TNVP	Classes of richness
CP7548	Tara	Beli Rzav, Kaskade	429	a
FN5681	Stara	Garište	415	a
CP7451	Tara	Oštrelj I	379	a
DN9598	Kopaonik	Vlajkovci, Orljak	347	a
CP7267	Tara	Gorušice-Grablje	340	a
CP7261	Tara	Konjska Reka	335	a
DN7497	Kopaonik	Karaula, Milovići	332	a
DN9698	Kopaonik	Vlajkovci	332	a
CP7450	Tara	Beli Rzav, Podstolac	332	a
FN2983	Stara	Dobrodolska reka	330	a
DP8606	Kopaonik	Jošanica, Katići	326	a
CP6666	Tara	Jokići II	326	a
CP7653	Tara	Timotijevići	314	a
FN3480	Stara	Krivi dol	314	a
DN8390	Kopaonik	Pojla	310	a
FN4779	Stara	Visočka Ržana	307	a
DN7396	Kopaonik	Pocesje	305	a
CP7364	Tara	Mitrovac	305	a
CP6661	Tara	Borovnjak	294	b
DN8991	Kopaonik	Mramor	291	b
CP6270	Tara	Tadići	289	b
DP8808	Kopaonik	Rokci II	287	b
FN5678	Stara	Senokos	287	b
FN4072	Stara	Kragujevac	287	b
FN4481	Stara	Rsovci	282	b
DN8793	Kopaonik	Ledenica	277	b
DP7602	Kopaonik	Pogrebina, Karaula	272	b
DP8707	Kopaonik	Rokci I	271	b
CP7268	Tara	Grablje-Perućac	262	b
FP3900	Stara	Javorska reka	261	b
CP6072	Tara	Veliki kraj	256	b
DP7600	Kopaonik	Kremići	254	b
CP7350	Tara	Tukelj	249	c
CP7754	Tara	Podsetnje, Iver	248	c
CP7260	Tara	Konjska Reka	247	c
DN8892	Kopaonik	Duboka	245	c
CP7766	Tara	Osluša	245	c
FP3402	Stara	Selište	241	c
DN8894	Kopaonik	Panićki Jelak	238	c
CP7366	Tara	Ravni-Kozja stena	238	c
CP7460	Tara	Sekulići	238	c
DN8794	Kopaonik	Metođe	236	c
FP3007	Stara	Golema reka II	236	c
FN3085	Stara	Nišor	235	c
CP7452	Tara	Oštrelj II	227	c
FP3103	Stara	Babin zub	227	c
CP7760	Tara	Dobro polje	227	c
FP3800	Stara	Golema njiva	226	c
FN4482	Stara	Vodenični del	226	c
CP6371	Tara	Drlije	224	c
CP6665	Tara	Jokići I	224	c
FP3501	Stara	Topli Do	220	c
DN7997	Kopaonik	Kukavica	219	c
CP7363	Tara	Krnja Jela	218	c
DN8799	Kopaonik	Saklamanska reka	215	c
DN8289	Kopaonik	Treska	213	c
DN8897	Kopaonik	Šiljača	212	c
DN8695	Kopaonik	Bele Stene	202	c
FP3205	Stara	Žarkova čuka II	202	c
CP7453	Tara	Oštrelj III	200	c
CP7767	Tara	Jokići	197	d
DN8699	Kopaonik	Saklamanska reka	192	d
FP3006	Stara	Kozarnička reka	189	d
FP3004	Stara	Crna Reka	188	d
CP7367	Tara	Grablje	187	d
DN8093	Kopaonik	Barska reka	184	d
DN8196	Kopaonik	Jankova Bara	184	d

(*continued on next page*)

Table 4 (*continued*)

MGRS_1 × 1_km	Massif	Poligon_id	TNVP	Classes of richness
FP3002	Stara	Babin zub	181	d
DN8591	Kopaonik	Suvo Rudište	176	d
DN8290	Kopaonik	Novoselske Bačije	172	d
DN8795	Kopaonik	Bregovi	169	d
FP3003	Stara	Babin zub	160	d
CP7560	Tara	Sekulići	157	d
CP7860	Tara	Dobro polje	155	d
DN8494	Kopaonik	Crni Jelak	150	d
DN8492	Kopaonik	Kopaonik Centar	150	d
DN8194	Kopaonik	Hajdučka česma	147	d
FP3407	Stara	Golema reka	145	d
CP7264	Tara	Manita ravan	138	d
FN4382	Stara	Vodenični del	138	d
DN8595	Kopaonik	Gobelja	134	d
DN8297	Kopaonik	Suvi vrh	132	d
CP7263	Tara	Manita ravan	132	d
FP3104	Stara	Žarkova čuka I	131	d
DN8899	Kopaonik	Treštenica	126	d
DN9498	Kopaonik	Vlajkovci	125	d
DN8493	Kopaonik	Markov kamen I	124	d
DN8094	Kopaonik	Donji Babin grob	122	d
DN8491	Kopaonik	Sunčana dolina	115	d
DN8596	Kopaonik	Gobelja	112	d
FP3505	Stara	Midžor IV	102	d
FP3605	Stara	Midžor II	81	d
FP3408	Stara	Tupanar	79	d

Table 5

The validation metrics for each feature selection method employed for determining the optimal environmental factors (EFs). For clarification on the feature selection method, see the Material and Methods chapter.

Set of EFs	Feature selection method	Number of EFs	*RMSE*	R^2	*AICc*
1	**SR $p < 0.01$**	44	56.32	0.44	1160.05
2	**SR $p < 0.05$**	52	56.58	0.44	1175.88
3	**VIFSTEP**	30	60.39	0.36	1164.44
4	**CFS**	10	58.40	0.40	1055.84
5	**ES EFs**	20	57.53	0.42	1086.18
6	**All EFs**	97	57.18	0.43	1312.61

yield different conclusions. Nevertheless, the threshold values employed in this study were selected with careful consideration, taking into account the unique ecological, biogeographical, and historical characteristics of the research area. The majority of the identified potential nano-hotspots are situated in the deep river valleys, particularly in areas characterized by a pronounced canyon or ravine formation. Conversely, the lowest number of nano-hotspots was observed at the highest elevations of the mountain range, especially in regions where silicate substrates are prevalent. The concentration of the identified potential nano-hotspots in areas with pronounced canyon or ravine character is consistent with the findings of previous studies indicating that the most species-rich plots in the Balkan Peninsula are located in these refugial areas, as well as in the medium elevation of mountains (Mišić, 1984; Karadžić, 2018; Ilić et al., 2022; Sekulić et al., 2021, 2023). In addition to the generally high richness of vascular plant species, the gorges and canyons of the central Balkans are characterized by a large number of species belonging to the Mediterranean-sub-Mediterranean chorological group, as well as a significant number of Tertiary relicts (Mišić, 1984). The high concentration of species in these parts can be attributed to a number of factors, including the favourable conditions of a temperate humid mountain or ravine climate, the great diversity of microhabitats resulting from the significant heterogeneity of the microrelief, the large occurrence of carbonates and the low impact of agriculture. Furthermore, the relatively weak and localized glaciation that occurred during the Pleistocene climate fluctuations (Bognar et al., 1991; Milivojević et al., 2008) provided suitable environmental conditions for the long-term survival of various taxa, which contributed to high species diversity.

4.2. *Environmental factors (EFs) analysis*

The lack of dominantly better group of EFs resulting from the application of different feature selection methods can be attributed to several different factors. Firstly, the employed random forest method also performs feature selection internally, where more informative predictors end near the root node during the growing (training) of decision trees. Therefore, the additional EFs exert a relatively week influence on the model performance, whereas their exclusion can result in a significant reduction in performance. This is particularly evident since the use of all EFs results in a slight reduction in performance than the top-performing one, whereas some

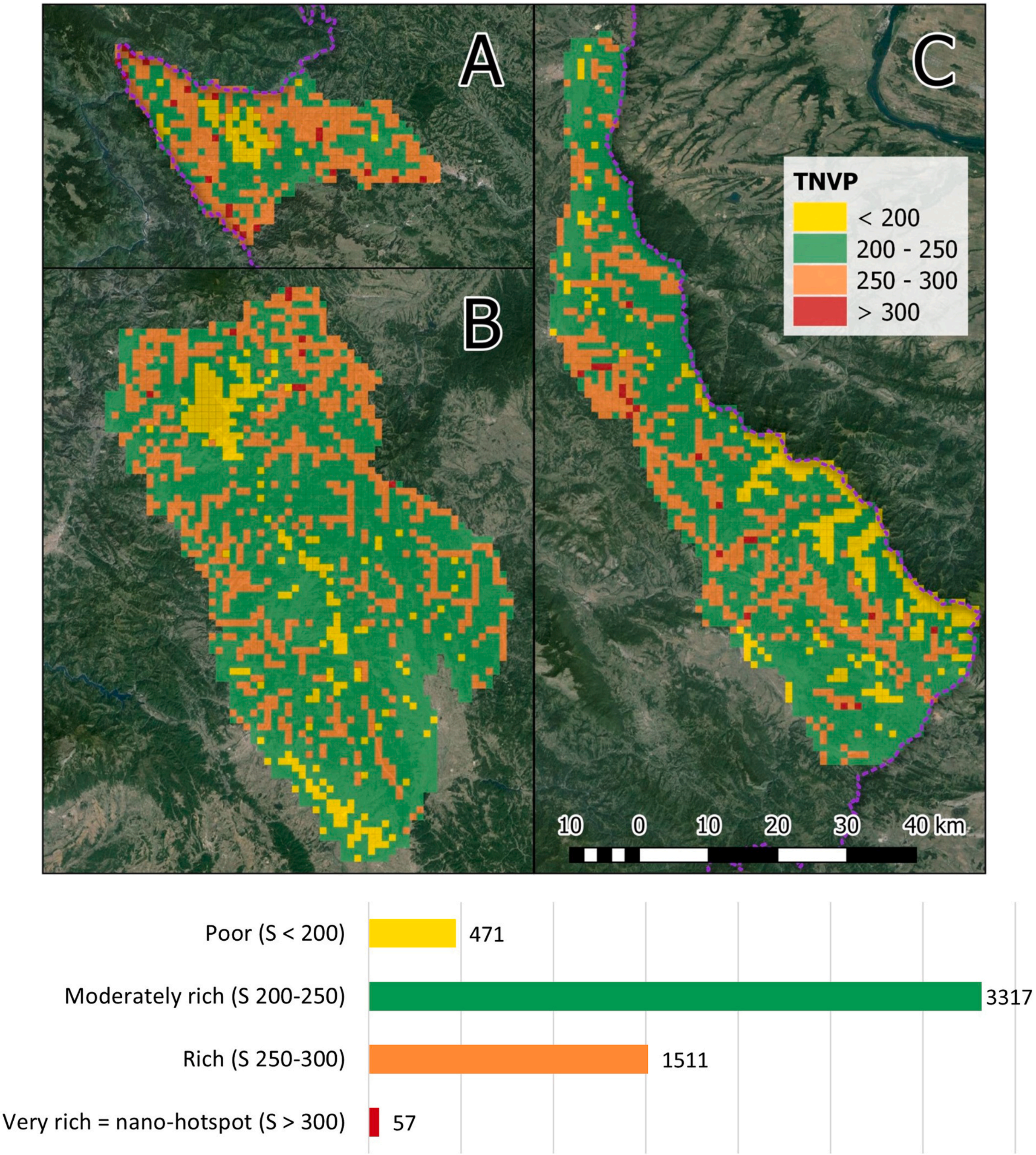

Fig. 4. Distribution of predicted total number of vascular plants (TNVP_rf) in the Tara (A), Kopaonik (B) and Stara massifs (C). Red cells symbolize the identified potential nano-hotspots.

feature selection methods (like VIFSTEP) have identified EFs that have a markedly deteriorating effect on performance. Secondly, all of the employed feature selection methods are based on similar principles, namely statistical significance and correlation value. In combination with the random forest, the close performance metrics are no surprise. Lastly, it should be noted that the dataset used for feature selection is relatively limited in size, comprising 93 MGRS grids with TNVP values. The utilization of larger and more diverse datasets will facilitate more pronounced benefits from feature selection, thereby enabling the full potential of different methods to be realized and enabling more effective differentiaton between them.

Table 6
The number of Military Grid Reference System (MGRS) 1 km grid cells belonging to different classes of floristic richness based on the predicted total number of vascular plants (TNVP_rf).

Richness class	MGRS cell numbers	% of MGRS cell numbers
a) very rich = nano-hotspot (S > 300)	**57**	**1 %**
a) very rich = nano-hotspot (S > 300) | Tara	21	0.4 %
a) very rich = nano-hotspot (S > 300) | Kopaonik	13	0.2 %
a) very rich = nano-hotspot (S > 300) | Stara	23	0.4 %
b) rich (S 250–300)	**1511**	**28 %**
b) rich (S 250–300) | Tara	279	5.2 %
b) rich (S 250–300) | Kopaonik	706	13.2 %
b) rich (S 250–300) | Stara	526	9.8 %
c) moderately rich (S 200–250)	**3317**	**62 %**
c) moderately rich (S 200–250) | Tara	253	4.7 %
c) moderately rich (S 200–250) | Kopaonik	1736	32.4 %
c) moderately rich (S 200–250) | Stara	1328	24.8 %
d) poor (S < 200)	**471**	**9 %**
d) poor (S < 200) | Tara	46	0.9 %
d) poor (S < 200) | Kopaonik	198	3.7 %
d) poor (S < 200) | Stara	227	4.2 %

4.3. Hotspots and environmental factors

The patterns of species richness observed at large spatial scales are traditionally understood to be a function of the current environment, particularly climatic conditions, as well as evolutionary and migratory history, latitude and area size (e.g. Currie and Paquin, 1987; Francis and Currie, 2003). In contrast, at the small spatial scales, patterns of species richness are influenced by a number of additional factors, including meso- and microclimate, elevation, physico-chemical properties of the soil, geological substrates, habitat types and biotic factors (Tsiftsis et al., 2008; Djordjević et al., 2016). The significance of habitat heterogeneity and landscape context for fine-grained patterns of species richness is further substantiated by the prevalence of calcareous substrate and the ruggedness of the terrain (Janišová et al., 2014; Divíšek and Chytrý, 2018; Večeřa et al., 2019).

Given the focus of our research on identifying the fine-grained patterns of species richness, we have conducted an in-depth analysis of the impact of a multitude of environmental factors, classified into seven groups: hydrography, land cover, substrate, topoclimate, topography, vegetation diversity and vegetation types. The models developed for the extraction of environmental factors that favour high species richness demonstrated that the best predictors belong to the EF categories hidrography, topography and vegetation diversity. Conversely, the substrate category was identified as having the lowest importance for predicting the distribution of floristic richness in the study area, which was an unexpected result. The EF: Elevation minimum, Elevation maximum, % cover of running water and Edge density of running water demonstrated the greatest predictive potential when considered individually. In addition to the aforementioned four key factors, the following EFs also demonstrated high predictive significance: Slope maximum, Slope range, Slope standard deviation, Heat Load Index (HLI) range, Compound Topographic Index (CTI), minimum (dem_twi_min), Number of land cover types, Shannon index of vegetation type and # Cumulative plant species riches per vegetation types. Some of the predictor variables demonstrated a statistically significant positive correlation with TNVP, while others exhibited a negative correlation with TNVP. In general, the TNVP demonstrated a positive correlation with the elements of topography, the variability of topoclimatic elements, the intensity of the hydrographic network, diversity of vegetation and land cover, the proportion of thermophilic deciduous forests and scrub, and the proportion of carbonate bedrock.

The results of our study highlight the importance of the hydrographic factor as one of the main drivers of species richness patterns. Furthermore, the results of our study reinforce the importance of other factors that have been demonstrated to be pivotal in previous studies, including terrain ruggedness, topoclimate, elevation, geological substrate, and vegetation types.

4.3.1. Elevation and species richness

A decline in general biodiversity is frequently observed from middle to high elevations in mountain systems throughout the globe (Sanders and Rahbek, 2012; McCain and Grytnes, 2010; Timsina et al., 2021). These patterns can be explained by two factors: the influence of climatic factors and by the relationship between species and area. The climate gradient hypothesis posits that species richness reaches its maximum at a specific elevation where a combination of growth conditions is optimal for the species (Lomolino, 2001; Körner, 2007; Djordjević et. al., 2022). The concept of the species-area relationship suggests that the maximum species richness is observed in the altitudinal zones encompassing the largest area (Acharya et al., 2011; Trigas et al., 2013).

The results of our study indicate that minimum elevation and maximum elevation are the most important factors influencing plant species richness (Table 7; Fig. 4). The MGRS 1 km grid cells that exhibit the highest species richness are situated in areas of medium elevation. This finding is consistent with the results of previous studies that have demonstrated a correlation between species richness and mid-elevation zones, where the species richness of particular plant groups or the entire flora tends to decline with increasing elevation (Grytnes et al., 2006; Hemp, 2002; Tomović et al., 2014; Djordjević et al., 2022). It is assumed that this pattern along the altitudinal gradient is primarily determined by climatic factors and the breadth of the climatic niche of the species forming the species pool in the study area. It is assumed that most species tolerate the moderate environmental conditions at medium elevations better

Table 7
Bivariate relationships between the total number of vascular plants (TNVP) and the environmental factors (EFs) determined as optimal predictor variable by SR $p < 0.01$ method - results of the simple regression analyses: R^2 - coefficient of determination; R^2_{adj} - coefficient of determination adjusted for the number of explanatory terms in a model; F - F statistics; p - significance of the coefficient of the single explanatory variable being non-zero; RF importance - random forest variable importance based on variance of the responses. Average values for F and RF importance for each EF category are shown in bold. For the environmental variables see Table 2.

Environmental factors (EFs)	R^2	R^2_{adj}	F	p	RF importance
Topography					
dem_curvature_sd	0.08	0.07	8.42	0.0046	9904.45
dem_elevation_max	0.38	0.37	55.20	0.0000	33207.07
dem_elevation_min	0.38	0.37	55.49	0.0000	42063.02
dem_slope_max	0.22	0.21	25.26	0.0000	12519.87
dem_slope_min	0.10	0.09	9.93	0.0022	7246.74
dem_slope_range	0.24	0.23	28.78	0.0000	14530.85
dem_slope_sd	0.21	0.20	24.25	0.0000	13057.87
dem_tri_max	0.17	0.16	18.92	0.0000	10499.06
dem_tri_range	0.18	0.17	19.90	0.0000	11492.99
dem_tri_sd	0.18	0.17	19.74	0.0000	14037.83
Topoclimate					
dem_hli_min	0.18	0.18	20.65	0.0000	14962.74
dem_hli_range	0.20	0.19	22.20	0.0000	15945.19
dem_hli_sd	0.17	0.16	18.78	0.0000	14994.78
dem_tci_max	0.09	0.08	8.60	0.0043	5343.14
dem_tci_range	0.09	0.08	8.60	0.0043	6139.37
dem_tci_sd	0.19	0.18	20.99	0.0000	8626.00
dem_twi_max	0.10	0.09	10.60	0.0016	6817.32
dem_twi_min	0.21	0.20	23.84	0.0000	11873.81
dem_twi_range	0.13	0.12	13.49	0.0004	10496.26
Substrate					
Ca	0.12	0.11	11.91	0.0008	3965.02
Ca_2	0.09	0.08	9.14	0.0032	3543.67
krecnjaci_perc	0.15	0.14	15.65	0.0002	5426.58
Si	0.16	0.15	16.89	0.0001	3223.44
Si_1	0.12	0.11	12.73	0.0006	984.09
Hydrography					
rw_edge_density	0.25	0.24	29.86	0.0000	19993.92
rw_perc	0.24	0.23	28.83	0.0000	22164.10
Land cover					
lc_edge_density	0.09	0.08	9.13	0.0033	6470.46
lc_mean_patch_area_ha	0.09	0.08	8.68	0.0041	5765.21
lc_shannon	0.13	0.12	13.87	0.0003	18545.86
lc_summary_perc_2	0.17	0.16	18.17	0.0000	6691.20
lc_summary_perc_5	0.11	0.10	11.08	0.0013	14944.19
lc_types	0.25	0.24	30.01	0.0000	3305.42
Vegetation types					
gkass_summary_perc_3	0.16	0.15	16.92	0.0001	15849.78
gkass_summary_perc_6	0.10	0.09	10.02	0.0021	6154.99
gkass_summary_perc_7	0.12	0.11	12.60	0.0006	4288.96
gkass_summary_perc_10	0.12	0.11	12.90	0.0005	13882.27
gkass_summary_perc_11	0.11	0.10	11.16	0.0012	5826.54
gkass_summary_perc_13	0.09	0.08	8.56	0.0043	4471.66
gkass_summary_perc_18	0.11	0.10	10.73	0.0015	6125.94
gkass_summary_perc_27	0.24	0.23	28.83	0.0000	21921.38
Vegetation diversity					
veg_edge_density	0.09	0.08	9.36	0.0029	6722.03
veg_S_klasa	0.15	0.14	16.44	0.0001	9871.80
veg_shannon	0.20	0.20	23.42	0.0000	17868.35
veg_types	0.23	0.22	27.00	0.0000	8834.17

than extreme environmental conditions at low and high elevations, in terms of precipitation, relative humidity, temperature, ultraviolet radiation, partial pressure of all atmospheric gases and air pressure (Lomolino, 2001; VanderMeulen et al., 2001; Körner, 2007; Djordjević et. al., 2022). It may be posited that the reduced species richness observed in high-elevation regions is also attributable to the diminished diversity of their pollinators (Arroyo et al., 1982; Jacquemyn et al., 2005) and a reduced pollen load of pollinators (Bingham and Orthner, 1998).

4.3.2. Terrain ruggedness and species richness

The strong influence of terrain ruggedness and our finding that the largest number of plant species is found at places with pronounced rugged terrain and consequently shallow soil are consistent with the pattern that rugged terrain tends to harbor more species than flat or slightly hilly landscapes (Večeřa et al., 2019; Ilić et al., 2022). The primary factors responsible for the influence of terrain

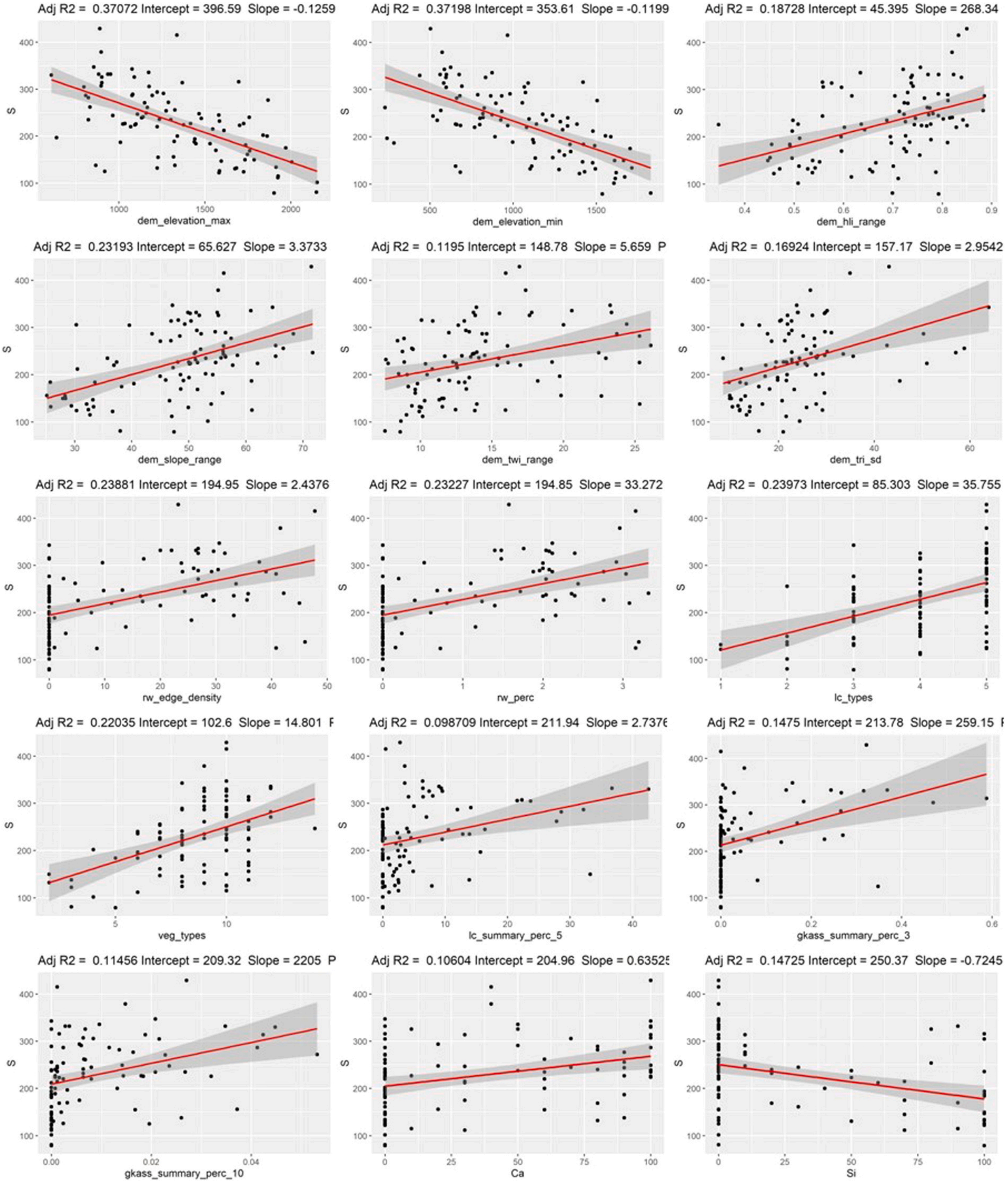

Fig. 5. Linear regressions between the environmental variables (EFs) explaining the greatest proportion of total vascular-plant richness, from dataset including all massifs.

ruggedness on species richness are habitat heterogeneity and spatial mass effects (Zelený et al., 2010), locally buffered climate change and associated refugial effects in times of macroclimatic variability (Sandel et al., 2011), as well as poor accessibility and low human management intensity (Ewald et al., 2008).

4.3.3. Topoclimate and species richness

The diversity of the topoclimate (i.e., local climate conditions influenced by topography, as defined by Buttrick et al. 2015) is directly correlated with the diversity of the relief. Consequently, topoclimatic elements exert a strong influence on species diversity in our model. In principle, sites with highly heterogeneous relief, characterized by a high degree of terrain roughness, are also rich in microclimatic niches. This generally leads to increased species diversity (Kerr, 1997) and increases the probability of species persistence over a longer period of time (Weiss and Weiss, 1998; Luoto and Hekkinen, 2008). Areas characterized by high topoclimatic diversity are likely to offer a greater number of localized habitats that are conductive to the dispersal of individuals within a species. Furthermore, these areas provide a greater diversity of niches, which in turn facilitates evolutionary adaptation and the process of speciation (Buttrick et al., 2015).

4.3.4. Geology and species richness

The richness and abundance of plant species are determined by a number of factors, including geological substrates and soil properties (Fenu et al., 2014; Hahm et al., 2014; Djordjević and Tsiftsis, 2019). It is known that soil pH, concentrations of basic cations (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) and acidic cations (H^{+}, $Al3^{+}$) exert a significant influence on the composition of plant communities (Ewald, 2003). All predicted nano-hotspots in the studied area are located in areas dominated by limestone or other carbonate bedrock types. This finding is consistent with the results of numerous studies on alpha-diversity of vascular plants in Europe and the Balkan Peninsula. These studies have demonstrated that the relationship between vascular plant species richness and base-rich and calcareous soils in Europe is often positive and represents one of the most consistent gradients of species richness (Pärtel, 2002; Ewald, 2003, 2008; Brković et al., 2015; Ujházyová et al., 2016; Večeřa et al., 2019; Djordjević and Tsiftsis, 2019; Ilić et al., 2022, 2023). This pattern can be explained by the physical and chemical properties of the soil, the evolutionary history and the size of the species pool (Zobel et al., 1998; Pärtel, 2002; Ewald, 2003). Indeed, it has been suggested that the high species richness observed on calcareous soils in Europe may be attributed to the widespread occurrence of carbonate substrates during the Quaternary period, which has influenced the evolution of numerous plant species adapted to high pH soils. This hypothesis offers a potential explanation for the observed high species richness on calcareous soils in Europe (Grubb, 1987).

The results of our study indicate that a markedly reduced number of species was observed in the squares dominated by acidic igneous rocks (granite, granodiorite, quartz latite and quartz monzonite). This phenomenon may be attributed to the presence of free (dissolved) heavy metal ions, particularly iron and manganese, in acidic soils with a $pH < 4.5$, which also exhibit elevated concentrations of harmful Al^{3+} ions (Brunet et al., 1996; Tyler, 2003). Consequently, habitats developed on acidic soils are inhabited by a smaller number of taxa, primarily because the majority of species are unable to tolerate high concentrations of Al^{3+}, which disrupts cell division and prevents further plant growth. This is not, however, due to the low amount of calcium carbonate present in these soils (Tyler, 2003). Despite the reduced species diversity, the siliceous substrates within the study area represent significant habitats, supporting a considerable number of boreal and Central European species (Vukojičić et al., 2014; Djordjević et al., 2016, 2020).

As anticipated, our results indicated that species richness increases with an increasing proportion of carbonate rock and decreases with an increasing proportion of silicate rock. However, the summarising effect of geological substrate was found to have the least significance for predicting the distribution of floristic richness in the study area, which was an unexpected outcome. The lack of significance of geological substrate in our model for predicting the distribution of floristic richness can be attributed to several factors. Firstly, the input geological maps are of insufficient resolution (1:100 000 and 1: 300 000) to adequatly address the geological variations observed at the MGRS 1 km grid scale. Secondly, these datasets were created by scanning and vectorizing original paper maps, which inevitably resulted in a certain degree of reduction in their original spatial accuracy. Lastly, the input 93 MGRS 1 km grid cells were relatively geologically homogeneous, thus further complicating the task for models attempting to determine and capture patterns. As a result, the MGRS 1 km grid was insufficiently detailed to fully capture the influence of the geologic substrate on species richness. It is anticipated that the utilization of more comprehensive and precise geological maps would enhance the predictive capacity of the model, thereby underscoring the pivotal role of the geological substrate in species richness. Additionally, it is essential to consider geological heterogeneity when planning fieldwork, ensuring the inclusion of diverse geological features in the data used for model training.

4.3.5. Diversity of vegetation and land cover and species richness

The significance of habitat heterogeneity and landscape context in shaping fine-grained patterns of species richness has been acknowledged as a pivotal predictor (Divíšek and Chytrý, 2018; Janišová et al., 2014; Večeřa et al., 2019). Studies investigating the effect of landscape structure (percentage cover and diversity of surrounding habitats/vegetation) on different components of species diversity revealed that alpha diversity was influenced by both the percentage cover and the diversity of different habitats in the surrounding area. Alpha diversity was found to increase with an increasing proportion or diversity of different natural and semi-natural habitats, and to decrease with an increasing proportion or diversity of non-natural habitats in the surrounding landscape (Janišová et al., 2014).

By analyzing the land cover and vegetation data for each 1 km^2 square, we were able to identify 45 elements which were divided into three groups of EFs (land cover, vegetation types and vegetation diversity) and correlate them with the TNVS data for each square. The results of our models demonstrated that, on average, land cover and vegetation types exhibited moderate to low predictive potential, whereas vegetation diversity elements demonstrated high predictive potential. The highest individual predictive potential was identified for the EFs: No. of land cover types and cumulative plant species riches per vegetation type, which is also consistent with the pattern observed in previous work (Janišová et al., 2014; Večeřa et al., 2019).

In contrast with the findings of the previous study, which indicated that high alpha diversity was best predicted by a high proportion of grassland in the surrounding area (Janišová et al., 2014), our results demonstrated that, in addition to aquatic and wetland vegetation associated with watercourses, a high proportion of xerophilous deciduous forests (% cover of "Quercion frainetto") exerts a significant influence on the increase in species richness. This is an unsurprising result, given that xerophilous deciduous forests in the Balkans are primarily distributed at low and medium elevations, they are characterised by a remarkable diversity of vascular plant species and a greater number of plants than other forest communities at higher elevations (Lakušić, 2005b; Čarni et al., 2016).

4.3.6. Hydrography and species richness

Our models for the extraction of environmental factors that favour high species richness demonstrated that Edge density of running water (rw_edge_density) and % cover of running water (rw_perc) are among the most effective explanatory variables (EFs with the strongest predictive potential). In fact, the TNVP was observed to increase with increasing hydrographic network intensity, particularly by increasing of Edge density of running water and % cover of running water. This is not surprising when one considers that the presence of a highly branched hydrographic network, especially in the context of highly complex relief, significantly increases the heterogeneity of favorable habitats, which in turn leads to an increase in overall biodiversity. It is also noteworthy that the diversity and richness of aquatic and wetland vegetation in Serbia is considerable (Lakušić, 2005b). Given the relatively limited number of common species between these syntaxa and their azonal character of distribution, it is evident that the hydrographic network exerts a profound influence on the TNVP.

The influence of the hydrography suggests that habitat moisture is an important factor influencing patterns of vascular plant diversity in the study area. Some studies have indicated that the moisture gradient significantly determines the distribution pattern of herbaceous communities, species richness and species composition of vascular plants (Diez and Pulliam, 2007; Zelnik and Čarni, 2008; Hettenbergerová et al., 2013; Moeslund et al., 2013). The importance of the soil moisture gradient can be attributed to its influence on not only plant growth and water availability, but also alkalinity, nutrient availability, soil conditions that regulate oxygen concentration, and soil thermal properties, including heat capacity and conductivity (Araya et al., 2013).

While a significant portion of the regional variation in TNVP can be statistically explained by a few environmental variables, it is important to acknowledge that the current state of biodiversity is not merely the consequence of the immediate effects of individual environmental factors. Instead, it is largely shaped by their collective impact and historical dynamics (Gaston, 2000). It has been demonstrated that climate and geological history have a significant impact on the distribution patterns of species, especially endemics (Jansson, 2003; Chytrý et al., 2003; Ewald, 2003; Ohlemüller et al., 2008; Canadas et al., 2014; Večeřa et al., 2019). This demonstrates the necessity for the improvement of models for the prediction of species distribution and the detection of potential hotspots through the incorporation of historical ecological factors. In many cases, it is not possible to understand the current relationships between species in space without such factors. A highly robust and efficient method for incorporating elements of environmental history as predictive variables was employed to analyse the alpha diversity of vascular plants in European forests (Večeřa et al., 2019). Given the suitability of this approach at the regional scale, and the fact that we focused on fine-grained patterns of species richness in a historically and biogeographically uniform area, the inclusion of environmental history elements in our predictive models was deemed unnecessary.

In conclusion, our research highlights the necessity of an integrative methodology for the investigation of fine-grained patterns of species richness. This approach must encompass multiple environmental factors, including elevation, topography, hydrography, geological substrate, and vegetation types, while accounting for their interactive effects, which can be either synergistic or antagonistic. The collective influence of these factors determines the final species richness under diverse environmental conditions (Michalet et al., 2024).

4.4. Implications for conservation

It is well documented that the identification of narrow hotspots can be a valuable tool for identifiying gaps in protected area networks. Therefore, this approach can yield valuable insights into the representativeness of protected areas, which may have implications for the identification of priority areas for conservation (Laffan et al., 2013; Canadas et al., 2014). The identification of several nano-hotspots within the zones of maximum protection provides a good basis for enhancing the planning within protected natural areas. At the same time, a significant number of the identified nano-hotspots are situated beyond the boundaries of any designated protected area. This represents a compelling argument for the designation and declaration of new protected natural areas. Furthermore, the availability of funding may also be a contributing factor to the accuracy and reliability of the data, given that it is a critical element in the decision-making process (Wilson et al., 2007). In addition, an understanding of the key factors that determine the occurrence of nano-hotspots is crucial for elucidating the specific threats to biodiversity loss, which is a priority in conservation (Brooks et al., 2006).

The identification of nano-hotspots in deep river valleys, especially in areas with a pronounced canyon or ravine character, renders them particularly resilient to climatic changes. This makes this type of landscape highly promising for the in-situ protection of biodiversity at the regional, but also on a global scale. This is related to the data indicating that a rapid increase in temperature has a major impact on species migrations, which can often result in a notable loss of species, especially endemic species (Le Roux and McGeoch, 2008; La Sorte and Jetz, 2010; Canadas et al., 2014). In light of the fact that the gorges and canyons of the study area exhibit the greatest richness of vascular plants and therefore possess a high conservation value, it is imperative to carefully plan the construction of hydroelectric power plants on mountain rivers and to generally establish long-term monitoring of the hydrographic state. The potential for the biodiversity of gorges and canyons throughout the Central Balkans to be jeopardised is high, given that the number of planned hydropower plants on Balkan rivers is around 3000 (Huđek and Schwarz, 2021; Pavlakovič et al., 2022; Carolli et al., 2023). Given the pivotal role of the hydrographic factor and the minimum elevation in shaping vascular plant diversity, it is imperative to implement robust protective measures in light of the impending effects of global warming.

Finally, this novel modeling approach based on GIS has the potential to enhance the efficiency of the urgent biodiversity protection. It is now widely accepted that mapping species distribution is essential for a comprehensive understanding of global biodiversity. The provision of accurate and cost-effective information on biodiversity represents a fundamental basis for biodiversity conservation, ecosystem preservation and climate change mitigation (Jiang et al., 2016; Bouchard et al., 2019; Modzelewska et al., 2020). While traditional field survey methods facilitate the accurate inventorying of species, they are inherently time-consuming and require significant manual input. Advances in modeling approach based on GIS techniques are attempting to address these limitations by reducing the time and effort required without compromising accuracy and information richness (Sheeren et al., 2016; Madonsela et al., 2018; Grabska et al., 2019; Kovačević et al., 2020).

Ethics statement

Not applicable: This manuscript does not include human or animal research.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03630.

Data Availability

Data will be made available on request.

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