

Magyar Agrár- és Élettudományi Egyetem
Kertészettudományi Intézet

**A növénydiverzitás földrajzi eloszlásának vizsgálata a magyar gurgolya
(*Seseli leucospermum*) élőhelyein a Dunántúli-középhegység dolomit
sziklagyepeiben.**

**Biodiversity dimensions of dolomite outcrops across the geographic range
of *Seseli leucospermum* Waldst. & Kit. in the Transdanubian Mountains**

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Contents:

1. Introduction.....	2
2. Objective	3
3. Literature review	4
4. Material and methods	9
5. Results	16
6. Conclusions (discussion of results)	21
7. Summary.....	23
8. Bibliography	25
9. Acknowledgements	29
10. Attachments.....	30

1. Introduction

Biodiversity hotspots are crucial for the preservation of species and genetic diversity due to their exceptional concentrations of endemic species (Myers 1990). Globally, up to 44% of all species of vascular plants are confined to 25 hotspots comprising only 1.4% of the land surface of the Earth (Myers et al. 2000). Rocky outcrops are considered to be small natural features (SNF), meaning that even outcrops of smaller size have ecological roles extending beyond their area, much like keystone species but at an ecosystem scale (Hunter 2017). Dolomite outcrops represent such hotspots of biodiversity worldwide and in Hungary (Allison & Stevens 2001). These habitats are not homogenous, but naturally fragmented and often similar to islands (Csergő et al. 2014), a landscape feature which can influence their biodiversity patterns at local and regional scales. The effects of natural fragmentation on biodiversity have been shown to be both negative and positive. While the isolation of habitat fragments has been shown to play a major role in preserving high diversity e.g. of island floras (Whittaker et al. 2006, MacArthur et al. 1967), it is also known that small islands and habitat fragments can sustain only small populations (Triantis et al. 2010). Due to changing climate and increasing anthropic pressure on rock outcrops (Fitzsimons 2017), it is critical to understand the mechanisms that build the diversity of such hotspots and to identify threats that may disrupt these mechanisms.

We worked in dolomite grasslands home to *Seseli leucospermum* Waldst. & Kit., a relict “dolomite-endemic” species in the Transdanubian Mountains. This dolomite-endemism likely indicates refugial habitats well known for the high ability to preserve open grassland specialist species (dolomite-phenomenon (Zólyomi 1942)), many of which migrated here from the plains starting with the Younger Dryas until the end of the Atlantic period (Ősmátra theory, Borhidi 1997). At the same time, the small size of the fragments of *S. leucospermum* habitats may be able to support only a small number of species, and small populations of these species. This is recognized as an ecological process leading to a pattern called the species-area relationship (SAR). The SAR has been studied and used for decades to evaluate primarily the conservation value of islands – and later fragmented habitats –in connection with their area-dependent biodiversity. Consequently, in the highly fragmented landscape of the Transdanubian dolomites that includes multiple island-like outcrops as well as more contiguous rock habitats, the species accumulation, fragmentation and isolation events have been ongoing for over centennial timescales. These aspects made the Transdanubian Mountains well-suited candidate for testing local and regional biodiversity pattern-building mechanisms in biodiversity hotspots.

2. Objective

The overarching goal of my thesis was to understand the mechanisms that have built the high biodiversity of dolomite grasslands, using as model system the Transdanubian Mountains of Hungary. The specific objectives of the study were:

- 1) to investigate the effects of biogeographic factors (latitude, habitat patch area) and microhabitat conditions (slope, aspect) on species' diversity across the geographic range of the dolomite endemic *Seseli leucospermum*;
- 2) to investigate the effects of biogeographic factors (latitude, habitat patch area) and microhabitat conditions (slope, aspect) on the abundance distribution of *S. leucospermum*;
- 3) to seek for parallel patterns of species' diversity and the abundance distribution of *S. leucospermum*.

3. Literature review

Mountains as biodiversity hotspots

a) Biogeographic patterns in the Transdanubian Mountains Diversity patterns at the plant community level

The dolomite phenomenon

Compared to limestone, the dolomite is less affected by chemical erosion, instead being more prone to physical weathering. The latter causes the unique geomorphology of dolomite, which is key for the dolomite phenomenon (Zólyomi 1942). Due to external factors causing the physical weathering of dolomite, a thin layer of small debris forms on top, sometimes even comparable to sand. As a consequence, dolomite rarely forms large, cemented clusters, and the forming debris is easily washed down on even moderately steep slopes. This process of weathering leads to the formation of more or less deep valleys, which separate the mountaintops into highly variable smaller peaks ending in sharp slopes and ridges. The soil layer on top of these peaks is shallow, in a constant state of development, stuck in an immature stage, categorized somewhere between lithosoils/skeletal soil and rendzina. The highly variable morphology of these landscapes leads to a high variability of microclimate. Often the microclimatic effects are so strong that they may override role of the macroclimate (Zólyomi 1942).

Another consequence of the shallow topsoil layer is that forests cannot develop. Smaller trees can develop on gentle slopes or where the valleys separating adjacent peaks are wide enough. This natural bareness of dolomite is called biological karstification that has had a role in preserving relict plant species and communities, by stopping the encroachment of woody species. The species preserved here over long periods of time could evolve into dolomite-endemic species. Some of these species in the Transdanubian Mountains include *Sesleria sadleriana* (sometimes also found on limestone), *Dianthus plumarius subsp. regis-stephani*, *Thalictrum pseudominus* (sometimes found on other types of bedrock), *Linum dolomiticum* and most notably, *Seseli leucospermum* (Zólyomi 1942).

The dolomite phenomenon has been well studied and understood in the Middle Hungarian Mountains in connection with the Ősmátra-theory. While the North Hungarian Mountains are built of mostly volcanic rock (andesite) and limestone, the bedrock of the Transdanubian

Mountains consists of mostly dolomite and limestone, controlling the edaphic conditions. This bedrock difference along with climatic conditions forms the Middle Danubian flora line that separates the Transdanubian Mountains from the North Hungarian Mountains. This line is located within the Börzsöny Mountains, which makes the outcrop of Naszály part of the Transdanubian Mountains, despite being situated North of the Danube river (Zólyomi 1942)

The Ősmátra - theory (Migration to mountains)

Starting with the end of the Ice Age (Younger Dryas/Dryas III. stage), during the Holocene epoch, Europe has experienced rising temperatures that led to the migration of warm-tolerant species from Southern refugia towards North and the contraction of the geographic range of cold-tolerant species towards North and colder mountaintops (Csergő et al. 2009, Giesecke et al. 2019). According to the revised Ősmátra-theory (Borhidi 1997), the flora of all previous climatic periods accumulated on the low elevation mountains due to their high diversity of microclimates that could accommodate both cold- and warm-tolerant species in relatively small areas. Species with very different ecological tolerances found refuge in the most suitable microhabitats for survival, and were able to avoid competition by species promoted by dominant macroclimatic conditions. This phenomenon suggests that plant communities developed in the habitats of the relict-endemic *S. leucospermum* in the Transdanubian Mountains are partly composed of warm-tolerant species that survived the cold stages of the Pleistocene in the dolomite refugia, and some other that arrived during the warmer postglacial periods.

Influence of the Submediterranean climate

The Hungarian climate has been divided into two main climatic groups (namely “C” arid, and “D” continental) of the Köppen climate classification (Réthly 1933, 1941, Keöpeczi 1934). Zólyomi (1942) realized that within the range of the Middle Hungarian Mountains, the Middle Danubian flora line aligns with the line that separates the two climatic groups, defined by the - 2 °C January isotherm. The origins/ancestry and relatives of the endemic species of the two separated sides of the mountain range may also indicate this macroclimatic effect.

The influence affects the whole Transdanubian Mountains, and the western range of the North Hungarian Mountains up until West-Cserhát Mountains to a varying degree (Kun et al. 2005, Bauer 2014). This influence can differentiate the role and importance of the more Southerly

dolomite outcrops in the Transdanubian Mountains from the ones located at more Northerly geographic positions, where the climate is different. The influence also has an effect on the geoelement composition of the flora, that makes possible the presence of Submediterranean species in the Southern part of the mountain range. For example, *Ruscus hypoglossum* and *Lathyrus venetus* both reach their northern limit of distribution inside of Hungary in the Old Bakony Mountains microregion (Dövényi 2008), while the geographic range of *Aethionema saxatile*, *Convolvulus cantabrica* and *Artemisia alba* subsp. *saxatilis* reach the Vértes Mountains (Isépy 2002). Other characteristic Submediterranean species of our studied habitats include: *Thalictrum minus* subsp. *pseudominus*, *Globularia punctata* and *Thymus praecox*.

Dolomite outcrops as ecological islands

Over the last decades, research and conservation of fragmented habitats has been guided by the Theory of Island Biogeography (MacArthur and Wilson 1967), which has been developed for true oceanic islands, i.e. terrestrial habitats surrounded by a saltwater matrix and lack of physical connection with the mainland. According to the theory, the balance of three processes govern the assemblage of species occupying an island: “(1) Extinction rate is expected to be lower on larger islands due to reduced demographic drift in larger populations, (2) Increased isolation, here understood as the distance to the nearest possible species pool (e.g., continent, other islands), should lead to reduced immigration rates, and (3) Speciation rate is expected to be higher on larger and more isolated islands due to increased environmental heterogeneity and reduced gene flow. Dolomite outcrops, mountaintops and other rocky outcrops can be regarded as ecological islands and can be analogous to true islands in many respects (Martín-Queller et al. 2017). Mountaintops have been regarded as ecological islands because of their apparent spatial isolation (Steinbauer et al. 2016, but see Flantua et al. 2020). Mountaintops have also preserved elevated levels of species diversity because the colonization events that happened over centennial timescales were not followed by notable extinctions particularly on larger mountain ranges, and were simply additive. While local extinctions have been more frequent at lower elevations, species often survived by escaping extinction via upward contraction of the geographic range towards higher slopes and peaks (Wells 1983).

Although terrestrial fragments of habitats such as the rock outcrops are similar to true islands, there are major differences stemming from a better connectivity in space and time (Csörgő et al. 2014, Flantua et al. 2020). The matrix surrounding the fragments is potentially more

permeable for species' movement than the saltwater, influencing the immigration rates between fragments. The nature of the matrix can also directly affect the enclosed habitat and the demography and survival of its local populations (e.g. invasive species in surrounding matrix). Further, while true islands have a long-term biogeographical history and development, some of the fragmented habitats on the mainland are comparatively more recent, sometimes due to anthropogenic effects. Additionally, the local environmental conditions like strong winds or salinity can also be influential on species richness of the individual islands. These major differences lead the recognition of the importance of adapting the island rules to ecological islands and recent habitat fragments for the purpose of biodiversity conservation (Martín-Queller et al. 2017).

The species-area relationship

The Species-area relationship (SAR) describes the relationship between the size of a habitat and the number of all existing species in that same area. It is one of the most frequently studied and fundamentally important patterns in ecology and is crucial for both ecological biogeography and conservation biogeography. The increase in species richness with area is general, but not universal in all circumstances. In practice SAR is not a single form of construct, but rather an important class of related macroecological patterns. Grasslands habitats that act like ecological islands can have very different outcomes regarding SAR because of other factors (e.g. biogeographic, micro-habitat) that can modify the slope of species accumulation. The size and configuration of these habitat patches can have effects on their hosted communities through several mechanisms. Fewer species may be able to colonize small, isolated patches, and small patches may also have higher extinction rates (MacArthur and Wilson 1967). Habitat quality may also decrease as the edge-to-area ratio increases, leading to species loss in small habitat fragments (Laurance 2008). The difference in patterns under particular circumstances is key to understanding the impact of anthropogenic change (e.g. habitat change/loss, climate change) on biodiversity (Whittaker et al. 2012). In cases where SAR is strong and positive (Csörgő et al. 2014), species accumulation increases with increasing area, making the protection of more habitats with larger surfaces a priority; on the other hand, in cases where the SAR is not significant (Deák et al. 2020) the species richness is not changing regardless of the size of the fragments, making conservation prioritization different because even the smallest of islands can be of equal value.

In difference to SAR, the Endemics-area relationship (EAR) only measures the number of endemic species in different sized habitats (Hobohm et al. 2019). Using this approach can be useful if we only want to estimate endemic species extinctions in relation to habitat loss, because non-endemic species that might go extinct in an area can still persist elsewhere in other habitats.

Although area-based approaches are used often to evaluate certain habitats or to estimate the extinctions of species in conservation science, many of these approaches are influenced by lots of different underlying environmental and ecological factors aside from the area size. Species loss as a result of habitat loss estimates made using SARs and EARs have been shown to be influenced by coexistence-mechanisms, the spatial distribution of environmental conditions and the pattern of habitat loss (Matias et al. 2014). Other estimates focusing on ISARs (island species-area relationships), used in the case of evaluating habitats that function as islands such as true geographical islands or natural habitat isolates surrounded by a contrasting non-water matrix, can be modulated by the island type (a variable linked to matrix type). Species' habitat requirements can also influence the SAR, for example the inclusion of generalist species in evaluations may mask the impact of habitat loss on specialists (Matthews et al. 2016).

Fahrig (2013) argued for a revision of using the SAR approach on habitat fragments, saying that investigating this relationship on the patch level (island or fragment) was inappropriate, because of the high-immigration rates individuals from small, but well-connected patches while individuals located in large patches may actually interact with far fewer individuals than those within their patch due to dispersal limitation. In addition, individuals of different species may perceive the landscape differently due to their different habitat requirements and dispersal abilities (Martín Queller 2017).

b) Biogeographical patterns at the species level

Peripheral populations and the Centre-Periphery Hypothesis

Peripheral populations occur near the boundary of the geographic range of a species. For several decades, the biogeographical ecologists stated that a species' abundance is typically greatest at the centre of its geographical range and uniformly low toward the edges (Pironon et al. 2017). This lays on the assumption that near the centre, the habitats tend to be more frequent and larger in area, whereas near the periphery the suitable habitats become more scarce, and

isolated/fragmented. This pattern can be observed in the Transdanubian Mountains in the distribution of dolomite outcrop habitats across the geographic range of the dolomite-endemic species *S. leucospermum*. It is expected that the central Bakony, Balaton Uplands and Vértes areas would host dolomite outcrops with the most abundant *S. leucospermum* populations.

4. Material and methods

Seseli leucospermum biology, distribution and ecology

S. leucospermum is a glabrous herbaceous perennial (Hemicryptophyte), reaching heights between 30-100 centimeters. The plant has a conic taproot characteristic of Apiaceae, and can be woody at the base. The stem is cylindrical, bare or slightly grooved. Its leaves are pinnatisect, consisting of usually around 20-60 lobes, linear-setaceous in shape, longer than 2 centimeters in length, less than 0.5 millimeters in width. Bracts barely exist (0-1); bracteoles connate at base, puberulent. Individuals can flower from July until October. Flowers have white colored petals and form compound umbel inflorescences. The schizocarp fruit is 3-4 x 2-2.5 mm, ovoid globose, sparsely puberulent.



Figure 1.: Pictures of a dolomite outcrop on Csóka-kő, Keszthely Hills (left), and a *Seseli leucospermum* individual on Csóka-kő (right).

The species is an iconic dolomite endemic of the Transdanubian Mountains of Hungary, and it is considered to be near threatened according to IUCN Red List of Threatened Species (Király 2013, IUCN 2022). In a paper discussing the co-existence of protected plant species growing in dry grasslands of the Carpathian Basin, the species has been shown to be indicative of the presence of *Festuca pallens* (Csontos 2007). Furthermore, *S. leucospermum* and *Paronychia cephalotes* were significantly mutually indicative of each other within Hungary. The mentioned paper discusses the idea of transplanting *S. leucospermum* to habitats where *P. cephalotes* already exists as a method of conserving the species, based on the observation that the two rare, protected species have similar ecological requirements because of their demonstrated coexistence.

Syntaxonomy of the habitats of *Seseli leucospermum*

The habitats of *S. leucospermum* in Hungary have been classified as rocky grassland-steppe complexes (*Seseli leucospermi-Festucetum pallentis*, *Fumano-Stipetum eriocaulis*, *Chrysopogono-Caricetum humilis*) (Bauer 2009).

The rupicolous pannonic grasslands containing these complexes are protected under the EU Habitats Directive (listed habitat 6190 "Rupicolous pannonic grasslands (*Stipo-Festucetalia pallentis*)") (Commission of the European Communities 2009). We include a short description of these plant-communities according to the syntaxonomical system of Hungary (Borhidi 2016).

Class: Festuco-Brometea Br.-Bl. et R. Tx. ex Klika et Hadač 1944

~ Dry and semi-dry rocky grasslands and steppes

Order: Stipo pulcherrimae-Festucetalia pallentis Pop 1968

~ Subcontinental rocky grasslands

Group: Bromo-Festucion pallentis Zólyomi 1966

~ Submediterranean limestone-dolomite outcrops

This group of plant associations are rocky limestone-dolomite outcrops showing Submediterranean influence and found in the Transdanubian Mountains, Limestone Alps, and northern regions of the Carpathian Mountains. These loose-structured grasslands are mostly dominated by shortgrasses like *Festuca pallens* or *Stipa eriocaulis*, and sedges like *Carex humilis*. The only taller grasses that can be found are *Bromus pannonicus* and *Chrysopogon*

gryllus, but they don't form the usual tall, closed colonies. The signature species in this group are usually protected, relict, or endemic species. Rosette-forming dicots species of alpine origin, which include *Aethionema saxatile*, *Anthyllis vulneraria* subsp. *alpestris*, *Biscutella laevigata* agg. *Bromus pannonicus*, *Carduus glaucus*, *Coronilla vaginalis*, *Dianthus regis-stephani*, *Draba lasiocarpa*, *Galium austriacum*, *Hornungia petraea*, *Leontodon incanus*, *Primula auricula* subsp. *hungarica*, *Stipa eriocaulis*, *Thalictrum pseudominus* and *Seseli leucospermum* are also characteristic. Six plant associations are categorized within this group, of which I only mention the ones that are hosting *S. leucospermum*.

1. *Seselio leucospermi-Festucetum pallentis* Zólyomi (1936) 1958

~ Open dolomite rocky outcrop grasslands

Thermo-xerophilous calciphytic rocky grasslands situated in significantly sunny, dry rocky slopes of Southern aspect in the submountains of the Transdanubian Mountains. Due to the special weathering of dolomite, usually no proper soil layer develops on these rocky surfaces, and the inhabitant plants grow root in the dolomite gravel directly. Not many species can adapt to the extreme microclimatic conditions and the missing soil layer. Characteristic plants that live here include drought-tolerant grasses, subshrubs, succulents and ephemerals. Cemented boulder surfaces are usually covered by lichens. The most dominant species is *Festuca pallens*, but *Carex humilis* must also be mentioned. The highly ranked characteristic of the association is the species *S. leucospermum*. Other notable plants include: *Hornungia petraea*, *Draba lasiocarpa*, *Sorczonera austriaca*, *Aethionema saxatile*, *Paronychia cephalotes*, *Onosma visianii*, *Jurinea mollis* var. *dolomitica*, *Astragalus vesicarius* subsp. *albidus*. Many species live that here can also be found in sandy outcrops like *Fumana procumbens*, *Alyssum tortuosum*, *Viola rupestris*, *Gypsophila arenaria*. Some noteworthy endemic subspecies are: *Thalictrum minus* subsp. *pseudominus*, *Euphorbia segueriana* subsp. *minor*, *Dianthus regis-stephani*. Some more common rocky grassland species include *Helianthemum canum*, *Teucrium montanum*, *Alyssum montanum*, *Jovibarba hirta* and *Iris pumila*. *Poa badensis* can be dominantly found on slightly eroded or secondary surfaces. Spring ephemeral species like *Saxifraga tridactylites*, *Thlaspi perfoliatum*, *Erophila verna*, *Cerastium semidecandrum* and *Veronica arvensis* can also live here.

2. *Chrysopogono-Caricetum humilis* Zólyomi (1950) 1958

~Dolomite rocky slope steppes

Edaphic grasslands situated on sunny, rocky slopes with southern aspect in the sub mountains of the Transdanubian Mountains. The slow weathering of dolomite and the warm and dry mesoclimate impedes the encroachment by woody species. The grassland consists of drought tolerant narrowleaf grasses. The more or less closed communities are separated by bare rocky surfaces of varying size, which host rocky outcrop patches. The most typical grasses building up the communities are *Carex humilis* and *Chrysopogon gryllus*, but *Festuca rupicola*, *Festuca valesiaca* and *Stipa capillata* can also be found in areas with deeper soils. Some species characteristic of dry steppe grasslands include *Pulsatilla grandis*, *Adonis vernalis*, *Veronica spicata*, *Aster linosyris*, *Centaurea sadleriana*, *Hippocrepis comosa*, species typical on dolomite include *Jurinea mollis*, *Onosma visianii*, *Dianthus regis-stephani*, *Scorzonera austriaca* and the endemic *Astragalus vesicarius* subsp. *albidus*. This phytocoenosis also gives home to the endemic *Vincetoxicum pannonicum* in the Buda Hills. Species typical to rocky outcrops like *Poa badensis*, *Helianthemum canum* and *Teucrium montanum* can repopulate eroded surfaces. Submediterranean geoelements indicate connections to Western Balkan rocky outcrops: *Convolvulus cantabrica*, *Serratula radiata*. Species indicative of sand steppes (*Iris humilis* subsp. *arenaria*, *Onosma arenarium*, *Ephedra distachya*) are remnants of the mass-migration of flora from sand steppes onto mountains, as described by the Ösmátra-theory.

3. *Festuco pallenti-Brometum pannonicum* Zólyomi 1958

~Closed dolomite rocky outcrop grasslands

Edaphic plant-communities situated in the upper-third part of cold, humid slopes and their escarpments. The slopes have predominantly northern aspect and are located on the dolomite bedrock of the sub mountains of the Transdanubian Mountains. The habitat conditions of these outcrops are very similar to that of the *Seslerietum sadlerianae* dolomite outcrops, which they replace outside the geographic range of the endemic relict species *Sesleria sadleriana*. The grassland is closed by mesophilic broadleaf, and drought tolerant narrowleaf grasses, and bare rocky surfaces are sparse. Dicots living here are mesophilic broadleaf species, or those living in rocky habitats or meadows. The lowest layer of the turf hosts a rich moss flora. The three dominant species are *Bromus pannonicus*, *Festuca pallens* and *Carex humilis*, but species characteristic of meadows (*Briza media*, *Anthoxanthum odoratum*) and rare, dealpine relicts (*Festuca amethystina*, *Calamagrostis varia*, *Carduus glaucus*, *Primula*

auricula subsp. *hungarica*) can also occur here. *Anthericum ramosum* lives here in greater numbers. This phytocoenosis preserved the dolomite-endemic *Linum dolomiticum* on the Kis-Szénás hill and gives home to *Thlaspi montanum* in Pilisborosjenő. Some more species in common with rocky outcrops of the Alps include: *Polygala amara*, *Galium austriacum*, *Phyteuma orbiculare*, *Coronilla vaginalis*, *Daphne cneorum* subsp. *cneorum*, *Globularia punctata*, *Biscutella laevigata* and *Teucrium montanum*. Many other steppe-living species like *Koeleria cristata*, *Centaurea sadleriana*, *Pseudolysimachion spicatum* and *Scabiosa ohroleuca* can also be found here.

Vegetation data collection

We collated a vegetation database of 112 phytosociological relevés recorded in *S. leucospermum* habitats throughout the species' geographic range, where the species was present. The work started in the summer of 2021. The database included four phytosociological relevés recorded personally on the Csóka-kő outcrop (SW Keszthely Mountains), another four relevés recorded in Keszthely-mountain with the help of Assoc. Prof. Judit Bódis, as well as phytosociological relevés published in the literature from the Balaton Uplands (Bauer 2014.), Keszthely-Mountains (Bauer 2014), Bakony-Mountains (Bauer 2014), and Naszály Mountain (Pintér et al. 2010). To complement the database, we extracted further phytosociological relevés from the CoenoDat Hungarian Phytosociological Database (GIVD ID EU-HU-003; Csiky et al. 2012) based on the presence of *S. leucospermum*. In each plot recorded personally, we estimated the presence and the cover of each vascular species following Hortobágyi (1974), as guided by Assoc. Prof. Judit Bódis. The size of these plots was between 1-4 m², depending on the accessibility and the size of the grassland patches. We further extracted the size of each published vegetation plot from the literature sources and from CoenoDat. The source of the relevés is presented in Table 1.

Taxonomy and nomenclature

The nomenclature of plant taxa follows the New Hungarian Herbal (Király 2009).

Biogeographic factors and microhabitat conditions

Geographic coordinates of the vegetation plots

The GPS coordinates (latitude and longitude) of the relevés recorded personally were registered using the Locus Map 4 Outdoor Navigation application. The geographic location of the rest of the vegetation plots was extracted from the literature and from CoenoDat respectively, if available. Plots with missing coordinates were not included in the database, except for the locations that could be identified with sufficient precision based on the description of data collection.

Identification and area calculation of dolomite patches

To define the individual dolomite bedrock outcrops on which *S. leucospermum* occurred, we exported the georeferenced geological map of Hungary available from MBFSZ (<https://map.mbfisz.gov.hu/>) with the QGIS (QGIS Development Team 2016) software into Photoshop (Adobe Inc. 2020) and color selected only the soils that contained dolomite in some form. In QGIS we georeferenced and stacked the dolomite bedrock map, the MÉTA quadrats indicating the known distribution of *S. leucospermum* extracted from the map of the Hungarian Flora (<http://floraatlasz.uni-sopron.hu/>) and the geographic location of the *S. leucospermum* vegetation plots in our database. We also referenced the microregions map of Hungary to identify the geographic individuality of the dolomite mountains. This approach allowed us to examine if the collected vegetation plots were located in areas with dolomite bedrock and known occurrences of *S. leucospermum*. Next, we identified the individual dolomite patches that lacked physical connection with other similar patches, and contained our vegetation plots, but we made minor adjustments to include non-connected patches according to the microregion map and floristic map of *S. leucospermum*. Thus, each vegetation plot was assigned to a dolomite bedrock patch. We tried to adjust the area of the patches to account for dolomite regions unavailable to the studied plant-communities due to afforestation and human land-use, by using a satellite-based map. All other bedrock patches were deleted from the final dolomite bedrock-map. Using QGIS, we converted the layer of our selected patches from raster to vector format to be able to calculate the area of the individual patches using the *dissolve* function. The size of the studied patches was recorded in hectares.

Microhabitat conditions

For the relevés recorded personally we used a compass to determine the aspect of the slope, and we estimated visually the slope angle, guided by a clinometer app on the mobile phone. For the rest of the relevés we extracted the slope aspect and angle from the literature and the CoenoDat

database. We also calculated the heat load of each relevé using their aspect, slope and latitude. This was done in accordance with a paper published by Mccune & Keon (2002).

Calculation of biodiversity indices

We expressed the vascular plant diversity as (1) species richness (number of species) and (2) species diversity (Inverse Simpson Diversity [=1/Simpson's diversity]), within each 4 m² plot, calculated using the *vegan* package (Oksanen et al. [2013](#)) in R-4.2.0.

Statistical analyses

For data analysis we selected vegetation plots of 4m² plot size to avoid biases resulted from comparing values resulted from plots of different sizes. We tested the effect of biogeographic factors (latitude, patch area) and microhabitat conditions (slope, aspect) on species richness and species's diversity using linear mixed effects models (LMM), using the nlme package (Pinheiro et al. 2022), and on the abundance of *S. leucospermum* using mixed model with binomial error distribution using the lme4 package (Bates et al. 2015) in R. In another set of models we replaced the aspect with the heat load and analysed the two sets of models comparatively. Fixed effects were latitude, estimated patch area, aspect, aspect squared (when needed), slope, heat load (where applied) and random effects were the number of plots in each patch (to factor out the differences in diversity due to different sampling effort across the patches). All fixed variables were scaled to mean and unit variance, and the patch area and the number of species in each plot were used on a logarithmic scale. We also investigated the correlation between the abundance of *S. leucospermum* and species' diversity with a similar linear mixed effect model, but where the abundance of *S. leucospermum* was the only fixed effect. Residuals were checked for normality (normality plots) and heteroskedasticity (residual plots). Residuals were checked for spatial autocorrelation (Moran's I) and statistical models were updated accordingly with the spatial correlation term when needed. To estimate the effect of each independent variable, we applied ANOVA tests (Chi-squared test) refitted with maximum likelihood on the LMMs, comparing the full model with the reduced model from which the variable of interest was removed. We conducted all analyses in RStudio (RStudio Team 2022).

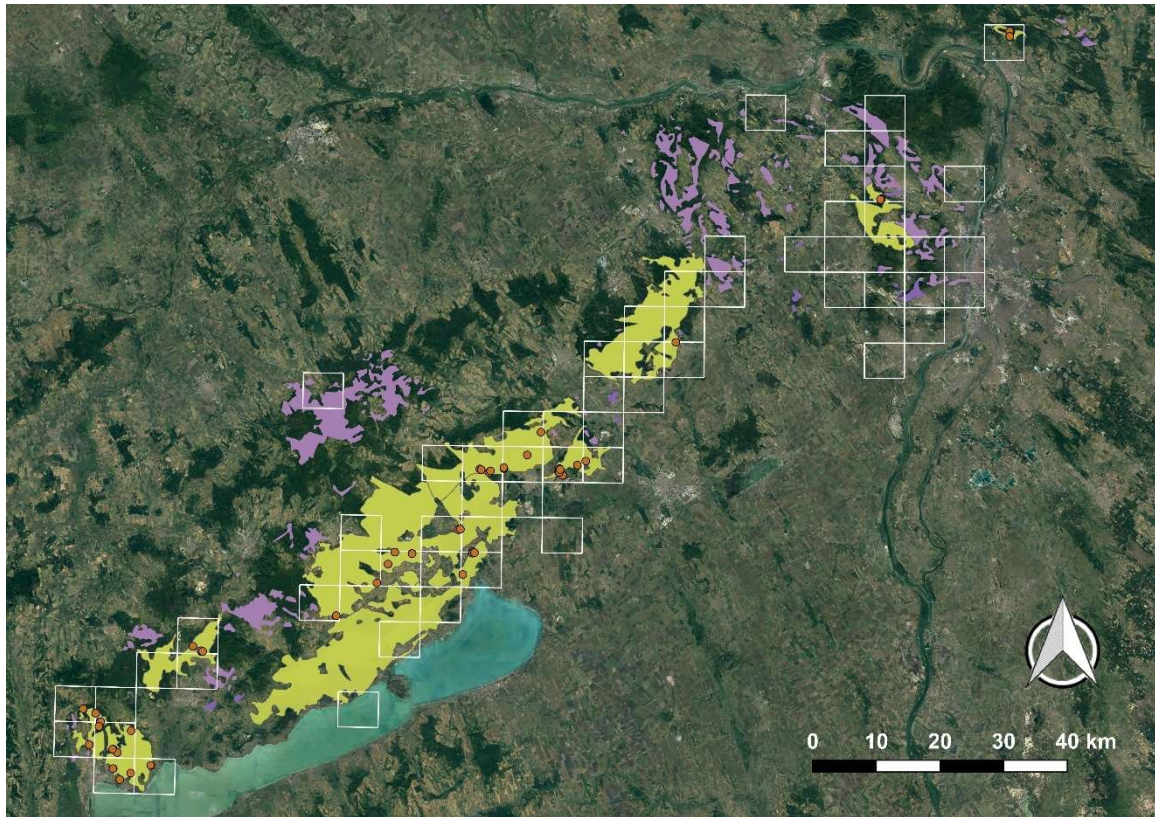


Figure 2.: Map showing the dolomite bedrock of the Transdanubian Mountains (purple and green), the selected patches (green), the distribution of *S. leucospermum* (white quadrants) and the position of the relevés (orange).

5. Results

a) Descriptive statistics

Our vegetation data collection yielded a total of 112 relevés, of which 101 were of use to us due to their 4m² size (Table 1, Table 2). We collected 203 species across all relevés, with 20.51 species/relevé on average. According to the average number of species in each patch, Vértes had the largest number of species with 35 species, followed by Naszály with 27.3 species, Balaton Uplands with 22.5 species and Southern Keszthely Hills with 21.15 species, although Vértes had only one relevé in our data collection. The most dominant species were *Carex humilis* with an average abundance of 9.84%, *Stipa eriocalis* with 8.26%, *Festuca pallens* with 6.24% and *Seseli leucospermum* with 3.14% across all relevés. The less abundant species were *Galium verum*, *Hieracium sabaudum*, *Leucanthemum margaritae* and *Valeriana officinalis subsp. collina* with an average abundance of 0.00893% each. The average slope was 29.93°, but *S. leucospermum* occurred on slopes as steep as 80 degrees.

b) Exploratory plots

Most relevés containing *S. leucospermum* were recorded on higher heat loads, where species richness, species diversity and the abundance of *S. leucospermum* had a wide range. In contrast, all values decreased at lower heat load values (Figure 3.)

Relevés that were located at higher latitudes had consistently higher heat load values while those at lower latitudes had a larger range of heat load values (Figure 4). This probably indicates the influence of the Submediterranean climate on Southern locations, while at higher latitudes the studied plant-communities might need the higher heat loads to compensate for the increasing influence of the continental climate.

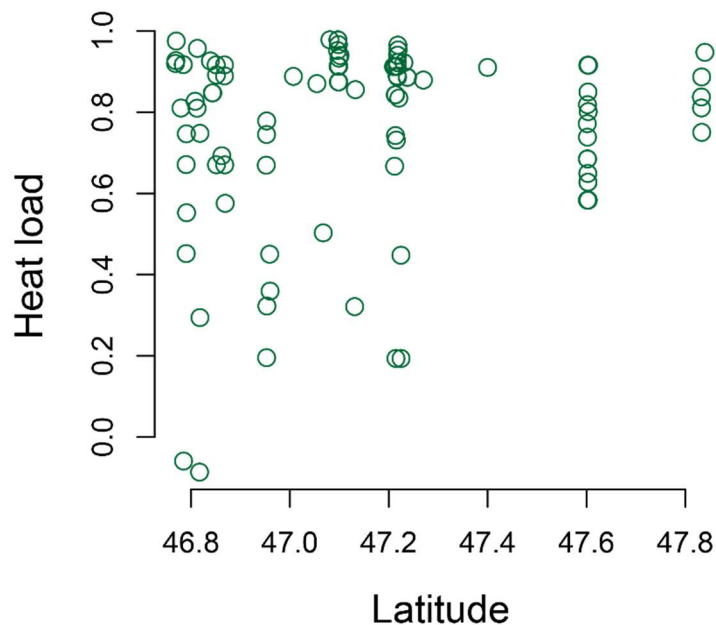


Figure 3.: Exploratory plot showing the position of the relevés and their respective heat load values across the latitudinal gradient.

c) Species richness (total number of species)

Biogeographic factors:

The effect of patch area on species richness was not significant ($p = 0.460$). The value of the regression coefficient (β) was 0.02, which is much lower than the median z value corresponding to habitat islands (0.22). Latitude had no significant effect on species richness either ($p = 0.712$) (Table 3).

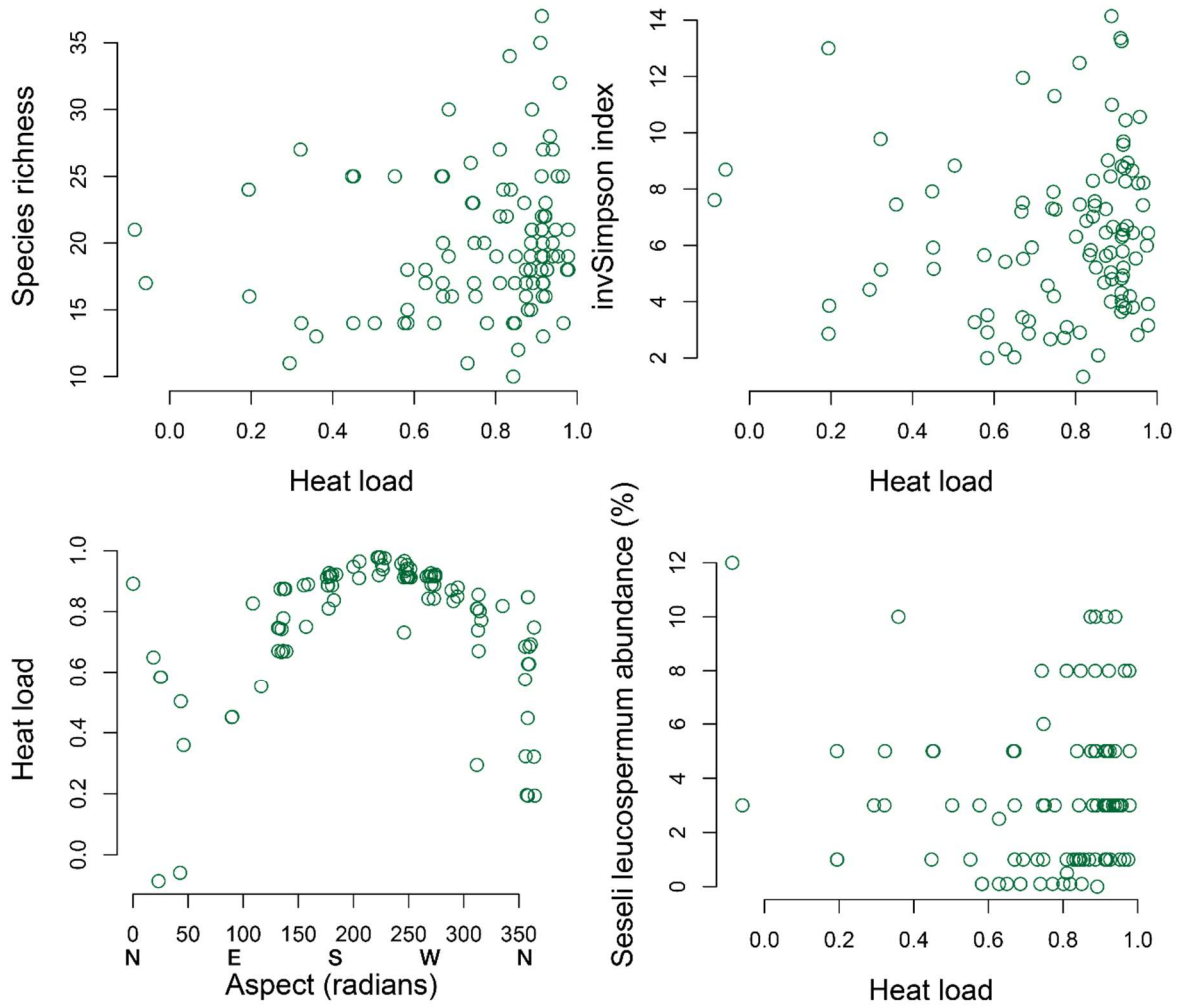


Figure 4.: Exploratory plots showing the relationship between the heat load value corresponding to the relevés and species richness (upper left), species diversity (upper right), aspect (bottom left) and the abundance of *S. leucospermum* (bottom right).

Microhabitat conditions:

The number of species increased significantly as the aspect increased from North through East to South-Southwest ($\beta = 0.202$, $p = 0.004$, Table 3), where it flatlined towards Western and North-Western positions (Figure 5).

While the sign of the estimated coefficient for the slope was negative, it was not significant ($p = 0.333$, Table 3.).

Heat load had no significant effect on species' richness ($p = 0.503$, Table 3).

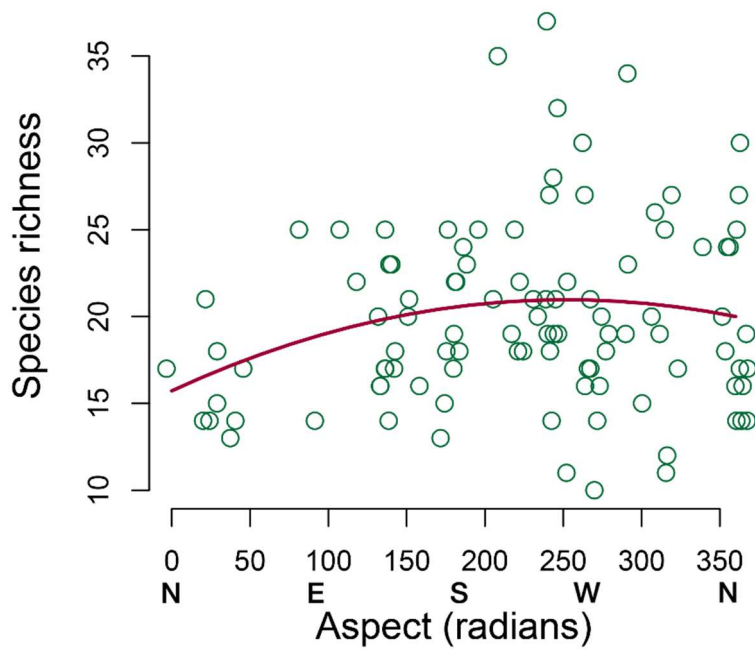


Figure 5.: The effect of slope aspect on species richness.

d) Species diversity (Inverse Simpson index)

Biogeographic factors:

Patch area did not influence significantly the species' diversity expressed as the inverse Simpson index ($p = 0.854$, Table 3). We found a significant negative effect of latitude on species' diversity, i.e., the values of the inverse Simpson index decreased towards Northern latitudes ($p = 0.045$) (Figure 6). Because the Moran's I index indicated significant spatial autocorrelation in the diversity patterns ($p = 0.01$), we fitted models corrected for the spatial autocorrelation. Following this correction, the effect of latitude was still marginally significant ($p = 0.057$).

Microhabitat conditions:

Neither the aspect, nor the slope had a significant effect on the inverse Simpson index ($p = 0.483$, and respectively, $p = 0.993$, Table 3).

We found no significant effect of heat load on the inverse Simpson index ($p = 0.203$, Table 3). The inverse Simpson index increased significantly with increasing abundance of *Seseli leucospermum* ($p = 0.041$, Figure 6, Table 3).

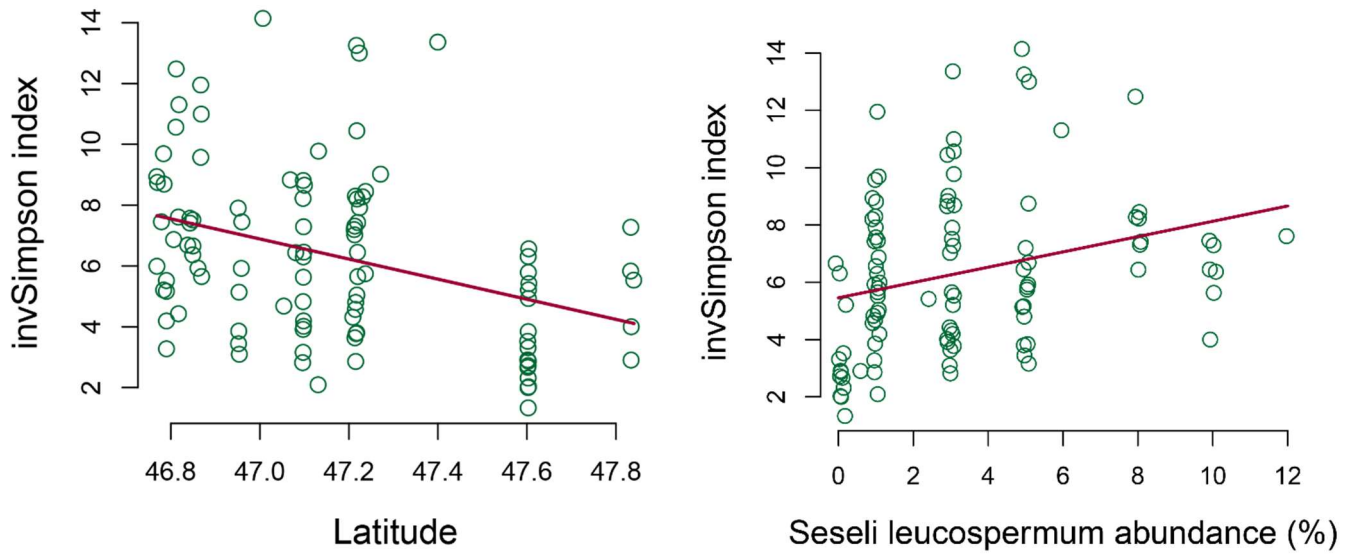


Figure 6.: The effects of latitude (left) and the abundance of *S. leucospermum* (right) on species diversity (inverse Simpson index).

e) Abundance of *Seseli leucospermum*

Biogeographic factors:

The area of dolomite habitat patches and latitude had no significant effect on *S. leucospermum* abundance ($p > 0.424$, Table 3).

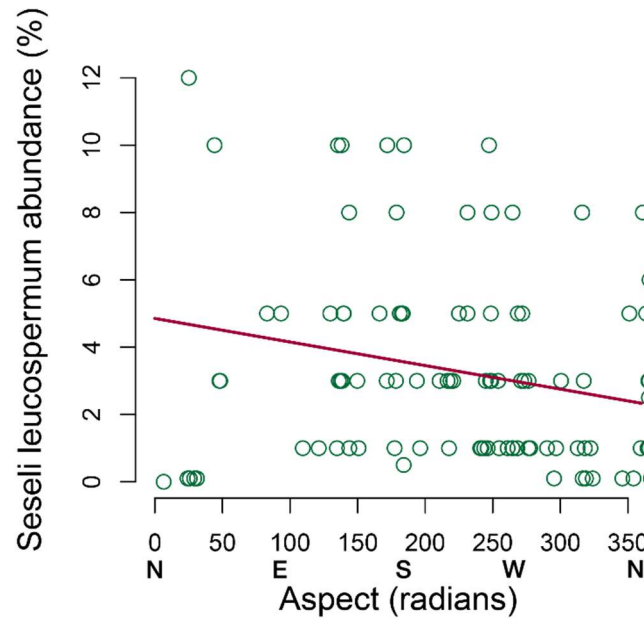


Figure 7.: The effect of the slope aspect on the abundance of *S. leucospermum*

Microhabitat conditions:

We found a significant negative effect of aspect on the abundance of *S. leucospermum* ($p = 0.0008$, Table 3, Figure 7). Slope ($p = 0.385$) or heat load had no significant effect on this variable ($p = 0.796$) (Table 3).

6. Conclusions (discussion of results)

a) Discussion of results

The species-area relationship of the studied dolomite outcrops was weak, with a rather low value of the regression coefficient (Table 3) and a non-significant effect of area on the species richness. This result suggests that even small patches can preserve a large number of species in the studied dolomite grasslands. Indeed, Naszály had on average 27.3 species on 381 hectares of patch area, comparable to the average of 19.5 species of Bakony with 30904.267 hectares. This result is similar to the findings of Deák et al. (2020), who found no significant effect of area on the species richness on burial mounds (kurgans) in the Hungarian Great Plain. The abundance of *S. leucospermum* was not affected significantly by the area of the patches either, suggesting the ability of small outcrops to retain high local abundances of endemic species as well as high species richness. On the other hand, the dolomite patches identified by us according to the geological map probably have lower surface dolomite outcrop areas, due to the encroachment of woody species and human land use, and more refined analyses are needed to ascertain the non-significant effect of habitat area on the number of species. Our analyses were also limited by the low number of relevés in each patch and the uneven sampling effort per patch, despite our efforts to harness vegetation data from the available resources. Further efforts and a systematic sampling of the *S. leucospermum* habitat is needed before a thorough species-area relationship can be established in the area.

Latitude had a significant, negative effect on the inverse Simpson index, indicating an increase in the relative abundance and a proportional decrease in the species richness of the dolomite grasslands at more Northerly geographic positions. This result may indicate the influence of the Submediterranean climate in the Southern outcrops of the Transdanubian Mountains, which may increase the species pool of the dolomite grasslands (Borhidi 2016). Indeed, species like *Ruscus hypoglossum*, *Lathyrus venetus*, *Aethionema saxatile*, *Convolvulus cantabrica* and *Artemisia alba subsp. saxatilis* (Dövényi 2008, Isépy 2002) reach their Northern limit of distribution at different latitudes of the Transdanubian Mountains. Our earlier analysis on the most Southern dolomite outcrop of these mountains, on Csóka-kő, indicated that the habitats of *S. leucospermum* hosted 10% percent of Submediterranean geoelements (Szijj and Csergő 2021). Interestingly, the geographic position had no significant effect on *S. leucospermum* abundance, suggesting no difference between geographically central, Southern or Northern peripheral population local abundances. This finding contradicts the expectations of higher abundance in the geographic range center according to the Centre-Periphery hypothesis,

suggesting a high value of peripheral outcrops for the conservation of *S. leucospermum* populations.

The significantly increased species richness on Southwestern slopes indicated that a large number of thermophilous and drought tolerant species find optimal conditions on the slopes of dolomite outcrops more exposed to sun radiation. Interestingly, the heat load had no significant effect on species richness or inverse Simpson index. This result reinforces the tenet of the Ösmátra theory, according to which these habitats served as a refuge for thermophilous plant species during colder periods (Borhidi 1997) but which may need to be complemented with other ecological requirements of the same species, such as light requirements or competitive abilities. Such species were *Carex humilis*, *Festuca pallens*, *Thymus praecox*, *Fumana procumbens*, *Potentilla arenaria* and *Seseli leucospermum*. In a similar way, the abundance of *S. leucospermum* decreased from Southern towards Northern aspects, and it was not affected significantly by the heat load, suggesting similar effects of the microhabitat conditions on the demographic processes of thermophilous species.

The slope angle had negative effects on species richness, however it was not significant. We expected that on steeper slopes significantly fewer species will be able to persist while on mild slopes the deeper soils may support a greater number of species. It is likely that good competitor species such as *Carex humilis* and *Stipa erocalis* are preventing the establishment of poor competitor, but stress-tolerant species, which on the other hand are able to persist under the stressful conditions of the higher slopes. This may have been the case of *S. leucospermum*, the abundance of which was not influenced significantly by the slope angle.

b) Conclusion

Species accumulation and *S. leucospermum* abundance was not affected by the size of the dolomite outcrops, indicating that all studied dolomite outcrops can be of equal conservation value, regardless of their size.

The Submediterranean influence had an amplifying effect on species diversity (inverse Simpson index), suggesting that habitat fragments located near the Southern periphery of the Transdanubian Mountains are of increasing importance due to their higher diversity. At the same time, the abundance of *S. leucospermum* was not lower in peripheral populations, reinforcing the high conservation value of both the Southern and Northern habitats of the species.

Microhabitat conditions such as slope aspect have a key influence on both species' diversity and abundance of *S. leucospermum* in dolomite grasslands, however the amount of heat may not be as important factor as previously thought.

The parallel between the abundance of *S. leucospermum* and the inverse Simpson index of plant communities in the same habitats may be indicative of the similar ecological processes influencing the presence and abundance of plant species living in these habitats. Consequently, the management for conservation of *S. leucospermum* can result in the protection of the whole biodiversity of its habitats.

7. Summary

Dolomite outcrops have a significant species-preserving effect (dolomite-phenomenon) resulting in high species richness and diversity. Due to natural fragmentation and isolation, they usually host many endemic species as a result of longer periods of speciation. These factors make them not only biodiversity hotspots, but also refuges of rare endemic and relict species that confer the habitats a high conservational value. Many of the most notable dolomite outcrops of Hungary exist within the geographic range of the endemic *Seseli leucospermum*, within the Transdanubian Mountains. These habitats have been studied both at the community-level and on a biogeographic scale, and many influencing factors (dolomite-phenomenon, Submediterranean influence) have been well-documented and understood. As far as we know, investigating these fragmented habitats as ecological islands from the perspective of the Species-Area relationship (SAR, MacArthur et al. 1967) was not in the focus of geobotanical studies, and the Centre-Periphery hypothesis (CPH, Pironon et al. 2017) has not been tested on endemic species of the area.

We investigated the SAR as well as the CPH, along with biogeographic and microhabitat influences for species' diversity of these habitats and for the abundance of *S. leucospermum*, across the full distribution range of the dolomite specialist *S. leucospermum*.

Our results showed that the SAR was not significant, and the z-value was much lower compared to classical "true" islands or habitat islands on the mainland, indicating high values of species richness even on small dolomite outcrops. Instead, we found positive effects of the Submediterranean climatic influence on the species diversity of the more Southerly dolomite outcrops. Species richness increased significantly on warmer slopes (S-W), indicating the key role of microhabitat conditions on the biodiversity of the grasslands, as also suggested by the dolomite-effect and the Ósmátra-theory.

The lack of a strong relationship between the abundance of *S. leucospermum* and the geographic position and area of the dolomite habitat patches rejected the hypothesis of a higher abundance of *S. leucospermum* in central areas of the Transdanubian Mountains (CPH), and the hypothesis of higher abundance of *S. leucospermum* in larger habitat patches. Importantly, we found important parallels between the species diversity and *S. leucospermum* abundance pattern, which suggests that on dolomite grasslands similar processes can influence population processes and species presence.

Our results indicate that even dolomite outcrops of the smallest size could be of great conservational value, especially those located in the most Southwestern peripheral areas of the mountain range (e.g. those found in Keszthely Hills), where the Submediterranean influence is strongest. Furthermore, the management for conservation of *S. leucospermum* can result in the protection of the whole biodiversity of its habitats.

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10. Attachments

Table 1.: References of the collected relevés and their amounts

Reference	Number of relevés
Own collection	8
Bauer 2014	76
CoenoDAT	17
Pintér, Tímár 2010	10
Jakucs 1968	1

Table 2.: Names of our studied patches and the number of relevés in each designated patch.

Patch name	Number of relevés
Northern Keszthely Hills	15
Southern Keszthely Hills	19
Sümege–Tapolca Plateau	7
Balaton Uplands	8
Southern Bakony	11
Eastern Bakony	24
Vértes	1
Szénás Hills	17
Naszály	10

Table 3.: Model structures and results:

Structure of the model	Variables	β	SE (β)	Chi test (Likelihood ratio)	Anova p (for full model/model with removed variable)
Total number of species					
m5c <- lme(fixed = log(count)~scalearealog+scalelat+scaleaspect+scalespectsq+scaleslope, data = dat, random = ~1 scalearea/no_plots, method = "ML")					
	(Intercept)	2.958	0.025		
	scalearealog	0.020	0.028	0.546	0.460
	scalelat	0.009	0.026	0.137	0.712
	scaleaspect	0.201	0.102	4.087	0.043
	scalespectsq	-0.173	0.102	3.029	0.082
	scaleslope	-0.025	0.026	0.939	0.333
m5ch <- lme(fixed = log(count)~scalearealog+scalelat+scaleheatload+scaleslope, data = dat, random = ~1 scalearea/no_plots, method = "REML")					
	(Intercept)	2.959	0.031		
	scalearealog	0.033	0.032	1.281	0.258
	scalelat	0.017	0.032	0.143	0.705
	scaleheatload	0.016	0.033	0.449	0.503
	scaleslope	-0.016	0.033	0.228	0.633
Inverse Simpson index mixed					
invmodel <- lme(fixed = log(invSimpson)~scalearealog+scalelat+scaleaspect+scaleslope, data = dat, random = ~1 scalearea/no_plots, method = "ML")					
	(Intercept)	1.743	0.064		
	scalearealog	-0.011	0.063	0.034	0.854
	scalelat	-0.172	0.065	4.038	0.045
	scaleaspect	0.030	0.043	0.493	0.483
	scaleslope	-0.0004	0.046	0.0001	0.993
invmodelb <- lme(fixed = log(invSimpson)~scalearealog+scalelat+scaleaspect+scaleslope, data = dat, random = ~1 scalearea/no_plots, method = "ML", correlation = corRatio(form = ~ lat + lon, nugget = T))					
	(Intercept)	1.801	0.048		
	scalearealog	-0.012	0.046	0.071	0.790
	scalelat	-0.104	0.054	3.636	0.057
	scaleaspect	0.035	0.037	0.585	0.444
	scaleslope	-0.010	0.043	0.054	0.816
invmodelh <- lme(fixed = log(invSimpson)~scalearealog+scalelat+scaleheatload+scaleslope, data = dat, random = ~1 scalearea/no_plots, method = "REML")					
	(Intercept)	1.750	0.076		
	scalearealog	-0.008	0.073	0.053	0.819
	scalelat	-0.169	0.078	5.111	0.024
	scaleheatload	0.057	0.056	1.618	0.203
	scaleslope	0.033	0.057	0.593	0.441
modelsimpes <- lme(fixed = invSimpson~Seseli.leucospermum, random = ~1 scalearea/no_plots, data = dat, method = "REML")					
	(Intercept)	5.776	0.610		
	Seseli.leucospermum	0.188	0.093	4.183	0.041
Abundance of Seseli leucospermum					
seselimodelbinom <- glmer(binom~scalearea+scalelat+scalexexposition+scaleslope+(1 no_plots), data = dat, family = binomial)					
	(Intercept)	-3.395	0.114		
	Scalearea	0.102	0.107	0.829	0.363
	Scalelat	-0.089	0.108	0.641	0.424
	Scaleaspect	-0.194	0.057	11.233	0.0008
	Scaleslope	0.051	0.059	0.756	0.385
seselimodelbinomh <- glmer(binom~scalearea+scalelat+scaleheatload+scaleslope+(1 no_plots), data = dat, family = binomial)					
	(Intercept)	-3.366	0.116		
	scalearea	0.086	0.109	0.000	1.000
	scalelat	-0.089	0.112	0.000	1.000
	scaleheatload	-0.019	0.072	0.067	0.796
	scaleslope	0.036	0.076	0.000	1.000