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DISTRIBUTION MODELLING OF SELECTED RARE AND INVASIVE MOSS SPECIES IN SERBIA

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MODELOVANJE DISTRIBUCIJE ODABRANIH RETKIH I INVAZIVNIH VRSTA MAHOVINA U SRBIJI

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Abstract

Distribution modelling of selected rare and invasive moss species in Serbia

Bryophytes are sensitive to environmental changes, making climate change a major threat to their distribution and survival. In this study, Species Distribution Models (SDMs) were used to predict the distribution of selected mosses under changing climate. The three studied species differed ecologically: two rare halophytic mosses, *Entosthodon hungaricus* and *Hennediella heimii*, and one invasive moss, *Campylopus introflexus*. Data on species occurrences were combined with data on environmental variables to identify current suitable habitats, estimate model accuracy, select the most important environmental predictors, and predict future distribution using both single-algorithms and ensemble modeling. Ensemble models showed improved prediction reliability and reduced model uncertainty. The results showed that *E. hungaricus* has very limited suitable habitat in Serbia, projected to decrease by 75-92% under future climate scenarios due to changes in precipitation-related variables. Similarly, *H. heimii* will lose a considerable proportion of suitable habitat in Europe, becoming restricted to the northwestern coastal areas of the continent influenced by temperature stability. Regarding the investigated invasive species, climate change is also projected to have negative long-term effect on its European distribution by reducing its potential range and limiting further spread. The most important predictor of its distribution is the temperature seasonality. SDM proved to be an effective approach for modeling species with restricted range and/or narrow ecological niche, supporting conservation decision-making processes. The predicted decrease in range demonstrates the growing threat related to climate change and highlights the importance of focused monitoring and habitat conservation.

Key words: alien species, areal, bryophytes, prediction, climate change, conservation, ensemble modeling, threatened species, suitable habitats,

Scientific field: Biology

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Sažetak

Modelovanje distribucije odabranih retkih i invazivnih vrsta mahovina u Srbiji

Briofite su osetljive na promene u životnoj sredini, zbog čega klimatske promene predstavljaju pretnju za njihovu distribuciju i opstanak. U ovoj studiji korišćeni su modeli distribucije vrsta (SDM) za predviđanje distribucije odabranih mahovina u uslovima klimatskih promena. Istraživane vrste razlikuju se po svojim ekološkim karakteristikama: dve retke halofitne mahovine, *Entosthodon hungaricus* i *Hennediella heimii*, i jedna invazivna mahovina, *Campylopus introflexus*. Podaci o nalazima vrsta kombinovani su sa podacima o ekološkim faktorima radi identifikacije trenutno pogodnih staništa, procene tačnosti modela, određivanja najznačajnijih prediktora distribucije i predviđanja buduće distribucije primenom pojedinačnih algoritama i ansambl modelovanja. Ansambl modeli pokazali su veću pouzdanost predviđanja i smanjenu neizvesnost modela. Rezultati su pokazali da *E. hungaricus* ima veoma ograničena pogodna staništa u Srbiji, za koje se predviđa smanjenje od 75–92% u budućnosti usled promena varijabli povezanim sa padavinama. Slično tome, *H. heimii* će izgubiti značajan deo pogodnih staništa u Evropi, pri čemu će njen areal biti ograničen na severozapadna priobalna područja kontinenta, pod uticajem temperaturne stabilnosti. Kada je reč o ispitivanoj invazivnoj vrsti, klimatske promene će dugoročno imati negativan uticaj na njeno rasprostranjenje u Evropi, smanjujući potencijalni areal i ograničavajući dalje širenje. Najznačajniji prediktor njene distribucije jeste sezonalnost temperature. SDM se pokazao kao efikasan pristup za modelovanje vrsta sa ograničenim arealom i/ili uskom ekološkom nišom, predstavljajući osnovu za konzervaciju. Predviđeno smanjenje areala ukazuje na rastuću pretnju klimatskih promena i naglašava značaj ciljanog monitoringa vrsta i očuvanja staništa.

Ključne reči: alohtona vrsta, ansambl modeli, areal, briofite, klimatske promene, konzervacija, pogodna staništa, predikcija, ugrožene vrste

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1. INTRODUCTION

1.1 An Overview of the Mosses Ecology

Mosses are small-scale, non-vascular plants classified within the Plantae kingdom's Bryophyta division. They are amongst the earliest terrestrial plants, with fossil records dating back more than 400 million years to the Ordovician period (Newton et al., 2007). Division Bryophyta constitutes a group of terrestrial plants that have gametophyte dominance with rhizoids composed of multiple cells andsporophytes that still attach to the gametophyte following the emission of spores. The gametophyte generation is a plant that photosynthesize, whereas the sporophyte generation develops and relies on the gametophyte for nutrition and water, and disseminate spores. Bryophyte being a traditional term for any non-vascular seedless plant, consisting of mosses (phylum Bryophyta), liverworts (phylum Marchantiophyta), and hornworts (phylum Anthocerotophyta) exhibit significant ecological and morphological variety while lacking complicated tissue organization. In comparison to the majority of plants that bear seeds, they are very small and found all over the planet. Mosses, the most diverse bryophyte lineage, consist of over 12500 species (Crosby et al., 1999). Capsules with columellae and stomata, as well as the absence of elaters, separate them from the other two lineages (Frey & Stech, 2009).

Mosses are present in a vast variety of environments and are widely dispersed from pole to pole. They and their associated microfauna play critical roles in ecosystem function around the world, contributing to the production of above-ground biomass (Cornelissen et al., 2007; Wardle et al., 2012) and the regulation of abiotic conditions such as soil, temperature, and moisture (Longton, 1997), as well as being key drivers of ecosystem biogeochemical cycles (DeLuca et al., 2002; Turetsky, 2003; Lagerström et al., 2007). They also support a diverse range of microbes and invertebrates that form complex food webs which govern organic matter decomposition, carbon sequestration, and nutrient cycling, serving as a vital link between surface and underground ecosystem components (Wardle et al., 2012; Lindo & Gonzalez, 2010).

Mosses are characterised by absence of roots, thin cuticles and the leaves consisting of a single layer of cells (Proctor, 2000). Except for a few taxa, the great majority of mosses does not have enclosed transport tissues and therefore absorb water and nutrients over the gametophyte exterior. Thus, they are poikilohydric organisms that rely on the environment for water and lack mechanisms to resist desiccation, rendering them extremely vulnerable to changes in climate and precipitation regimes at both the micro- and macro-scales (He et al., 2016). While vascular plants prevent desiccation by through active regulation of internal water balance (i.e., homoiohydry) facilitated by morphological adaptations such as well-developed conducting tissues, leaf stomata, cuticle, and roots, mosses lack these traits. Instead, mosses adapt to drought by halting metabolism (controlled cessation) (Proctor et al., 2007). This poikilohydry used by mosses is not only the early stage of plants that lacked effective water balance, but a "highly evolved strategy of adaptation in its own right, optimal in some settings and at least a viable alternative in others." (Proctor & Tuba, 2002) When mosses are exposed to desiccation, their net assimilation rates drop fast as tissue hydration decreases under the level that is necessary to preserve complete turgor (Longton, 1988). Their cytoplasm may remain alive for lengthy periods of time with reduced water content and continue metabolic activity after rehydration.

As a result of their poor nitrogen-use productivity, strong cation exchange (resulting in nitrogen interception and retention), and delayed decay processes, mosses play an important role in nitrogen turnover and in maling nitrogen available for absorption by vascular plant (Malmer et al., 2003;

Turetsky et al., 2010). They influence plant-available nitrogen concentrations through regulating substrate thermal regime and moisture (Gornall et al., 2007). Mosses contribute significantly tophosphorus turnovet because they absorb phosphate and lower the amount of phosphate available for vascular absorption (Chapin et al., 1987). Crowley & Bedford (2011) have demonstrated that moss caused greater oxidised conditions in low-depth fen substrates, allowing for species to get more phosphorus. This emphasises the fact that, the interactions between mosses and vascular plants, can be either beneficial or detrimental. depending on the species and the prevailing abiotic conditions. Gornall et al. (2011) provided a model of the effects that layer of mosses has on vascular efficiency in which the detrimental impacts exceeded the favorable ones as the moss layer depth increases. Mosses contribute to the increase of ground peat and consequently soil carbon buildup in the long-term because of their impact on soil microclimate, net primary productivity (NPP), nutrient content, and decomposition rates (Turetsky, 2003). Major reserves of carbon are at present preserved in frozen mineral soils and frozen and unfrozen peatland soils. However, they are potentially vulnerable to soil heating and changes in disturbance regimes. These come due to as a result of slow accumulation of soil carbon the course of millennia (Grosse et al., 2011).

Mosses have a big influence on vascular plant recruitment and regeneration through influencing soil thermal and moisture regime and peat buildup. They regulate vascular regeneration indirectly since organic soils are poor seedbeds, especially for broadleaf species with small seeds (Astrup et al., 2008; Camill et al., 2010; Soudzilovskaia et al., 2011). In some circumstances, decrease in moss abundance decrease soil moisture, which might degrade wildlife habitat quality (Hodson et al., 2010). They are also important to food webs in an ecosystem as a source of food to some animals (Prins, 1982), regulate key habitat conditions such as soil climate, and represent verysignificant habitat for soil organisms included in detrital trophic network (Lindo & Gonzalez, 2010). Moreover, mosses and accumulated peat help in keeping the permafrost stable by protecting surface layers from fluctuating atmospheric temperatures. Temperatures of the soil surface are inversely proportional to the depth of organic layers of the soil throughout the vegetation period (Harden et al., 2006; Romanovsky et al., 2008).

The haploid, gametophyte generation is the permanent photosynthetic phase of the moss life cycle, which resembles that of hornworts and liverworts. Sporophytes are unbranched, monosporangiate, definitive in terms of growth, matrotrophic, and permanently linked to the female gametophyte, on which they rely in part at least for nourishment. The tiny, mostly perennial plants that make up moss gametophytes have either branched or unbranched shoot systems. In the wild, they are rarely discovered as lone, isolated individuals; typically, they are found in colonies in distinctive growth shapes encompassing structures such as cushions, turfs, or mats. Despite having similar overall life-history characteristics, mosses exhibit a wide range of morphological and anatomical diversity in the structure of their gametophytes and sporophytes. The five morphologically distinct superclasses into which mosses are now divided are as follows (Goffinet & Buck, 2004): Superclass I, which includes only Takakiopsida (*Takakia*); Superclass II, which includes Sphagnopsida (*Sphagnum* and *Ambuchanania*); Superclass III, which includes Andreaeopsida (*Andreaea* and *Acroschisma*); Superclass IV, which includes only Andreaeobryopsida (*Andreaeobryum*); and Superclass V, which includes all peristomate mosses in classes Oedipodiopsida, Polytrichopsida, Tetraphidopsida, and Bryopsida.

Despite being referred to as “tiny” plants, the approach used by mosses to thrive in the arid aerial environment is different from that of vascular plants. While some mosses are only found in aquatic habitats, others can withstand desiccation (Mishler & Oliver, 2009). In mosses, poikilohydry-related selective pressure has affected the morphology, biochemistry, and life cycle. Their organs are thin and small, and lignin is not needed to maintain them against gravity or the negative pressures

created during transpiration since surface absorption and diffusion regulate the cellular water status (Mishler & Oliver, 2009). The protonemal filaments produced by haploid spores in the majority of mosses extend by apical division and tip growth. Diffuse growth causes the buds produced by the filaments to mature into leafy gametophores (Figure 1). According to Schumaker and Dietrich (1998), diploid sporophytes, which grow from eggs fertilised by swimming sperm at the gametophore apex, create haploid spores. Gametophytes of mosses have a variety of cell types despite having a simple structure. After differentiation, the protonema produces caulonemal cells and chloroplast-rich chloronemal cells, which stretch threefold more quickly (Menand et al., 2007). Protonemal cells undergo programmed cell death when they are subjected to dehydration stress. They then divide again and differentiate into thick-walled, dehydration-tolerant brachycytes and subtending tmema cells (Decker et al., 2006). Rhizoids, axillary hairs, leaves, and a stem are examples of gametophores. Conducting cells, thin-walled parenchyma cells, and tiny, thick-walled epidermal and subepidermal cells usually make up the stem. Similar in function to xylem and phloem, the conducting cells are composed of hydroids and leptoids (Buck & Goffinet, 2000). Though they lack thick lignified secondary cell walls, hydroids are dead at maturity and connected by holes, just like tracheary elements (Hebant, 1977). With the exception of the midribs and edges, which may include several layers of differentiated cells, leaves are normally only one cell layer thick. Photosynthetic chlorocytes and hyalocytes with complex cell wall thickenings are seen in *Sphagnum* species' leaf cells. Papillae and other surface elaborations are examples of further leaf cell specializations. The gametangia, gametes, and sterile paraphyses are formed by other differentiated cell types. Specialised cell types, such as stomata (Sack & Paolillo, 1983), are also present in the spores, sporangium, and sporophyte stem (Buck & Goffinet, 2000). Despite having a similar body plan and poikilohydric ecological strategy, mosses have evolved specialised morphological and biochemical adaptations as a result of diversification and habitat colonisation. These features must be taken into account when drawing conclusions about their patterns of evolution from studies comparing them with vascular plants.

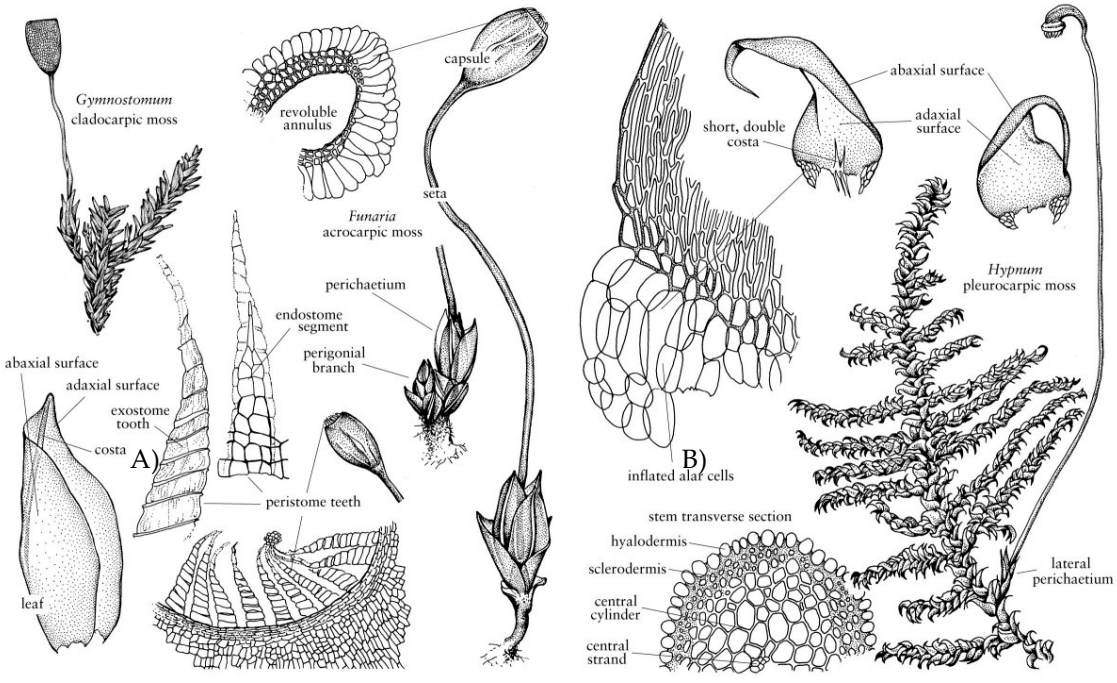

Figure 1. General morphological characteristics of acrocarpous mosses *Gymnostomum* and *Funaria* (A) and pleurocarpous moss *Hypnum* (B). Taken from Crandall-Stotler & Bartholomew-Began, 2007.

Researchers assess that bryophyte are among the oldest plants in the world, they were believed to develop from seaweed approximately 300 million years ago (Alimbetov & Kamalova, 2020). According to the most recent phylogenies (Qiu et al., 2006), the mosses split off from the land plant lineage between the hornworts and liverworts, which are sister to the vascular plants. The aquatic Sphagnales, the desiccation-tolerant rock-dwelling Andreales, and the morphologically varied Polytricales are three early divergent and ecologically specialised lineages that are part of the moss lineage, along with the "true mosses" (Mishler & Oliver, 2009). Although poikilohydry has allowed mosses to maintain basic features of their cell wall composition and structure, they have also developed unique cell wall adaptations that allow them to colonise a variety of environments.

1.2 Mosses' Life Cycle

Vascular plants and mosses have quite different life cycles. A succession of sexual and asexual phases as well as ploidy is experienced by all plants during the alternation of generations. In vascular plants there is typically a non-dominant (sexual reproductive) stage and a dominant (vegetative body), as well as having a dominant sporophyte (diploid) stage and a non-dominant gametophyte (haploid) stage (Naramoto et al., 2022). Mosses exhibit the opposite pattern (Figure 2), with the sporophyte phase being non-dominant and the gametophyte phase prevailing (Naramoto et al., 2022). One of the distinctive characteristics of bryophytes that no other plant has is this dominant gametophyte stage.

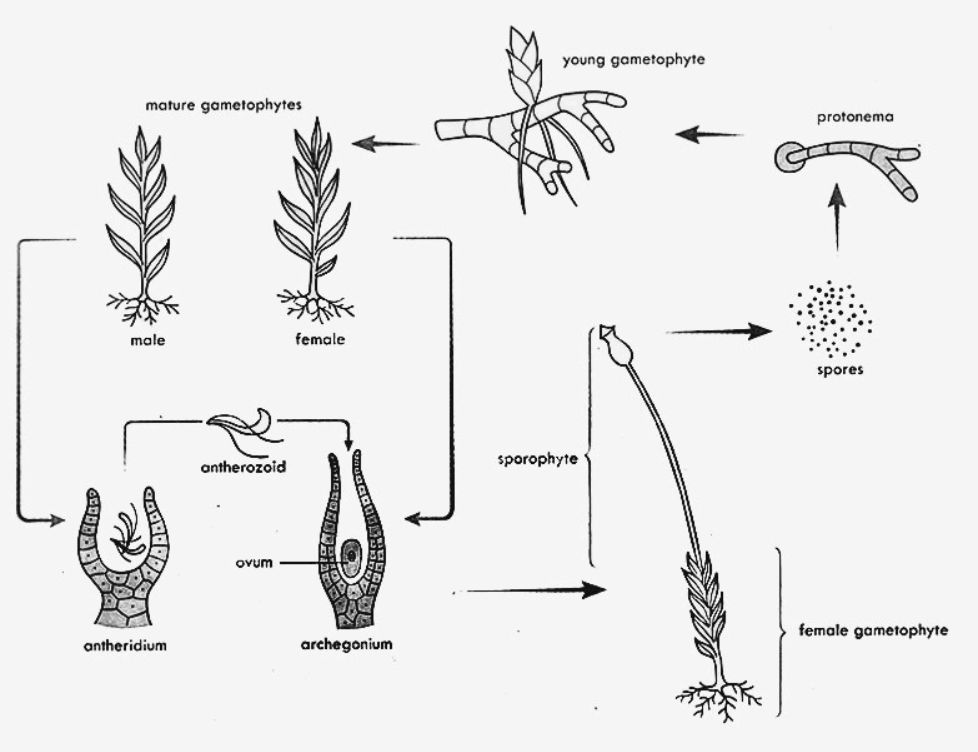

Figure 2. Moss's Life cycle. Downloaded from https://www.notesforshs.com/2022/11/mosses.html

1.2.1 Reproduction

Mosses have the ability to reproduce asexually or sexually, and each strategy has advantages in certain contexts. Asexual reproduction has a significantly greater establishment success than spores that are produced sexually (Longton, 2006) which is beneficial for immediately growing a cluster of moss

and/or sustaining the colony's population (Frey & Kürschner, 2011). Propagules produced asexually are unable to spread far enough to form new colonies. However, mosses that must rapidly grow in sparse populations would devote a greater proportion of their energy reserves to asexual propagation than to sexual reproduction due to their significantly better success rate compared to sexually produced spores (Longton, 2006).

Mosses reproduce asexually using a variety of techniques. They reproduce asexually by cloning, fragmentation, or the regeneration of specialised parts of plants, such as leaves or branches (Frey & Kürschner, 2011). Although they cannot spread as far as spores, mosses contain specialised structures called gemmae that resemble spores. The gemmae are propelled from the parent plant by water, usually in one droplet of water cascading into the moss. Gemmae come in eight different varieties; however, they all perform the identical task of asexually developing a new bud that is distinct from the maternal plant (Frey & Kürschner, 2011). It is advantageous to reproduce sexually while starting a new colony. Because they are so small they can be transported aerially to long distances - far from the parent plant. Thus, spores typically form when the cushion does not have to develop and it can devote its resources to spreading farther away. However, spore establishment rates are low (Longton, 2006).

In sexual reproduction, sperm fertilise an egg encased in an archegonium (female reproductive organ), producing a diploid (2n) sporophyte (Figure 3). Only water can carry sperm to the egg (Kimmerer, 2003). The sperm cannot reach the egg if there is a breach in the water. A capsule is produced at the end of a seta by the sporophyte, which grows after fertilization. Inside the capsule, haploid spores are created and subsequently dispersed. Mosses live for a variety of lengths of time. Some can live for thousands of years, while others only live for a year (During, 1979). Because of their extended growth period, mosses can be challenging to restore once a population has been vanished.

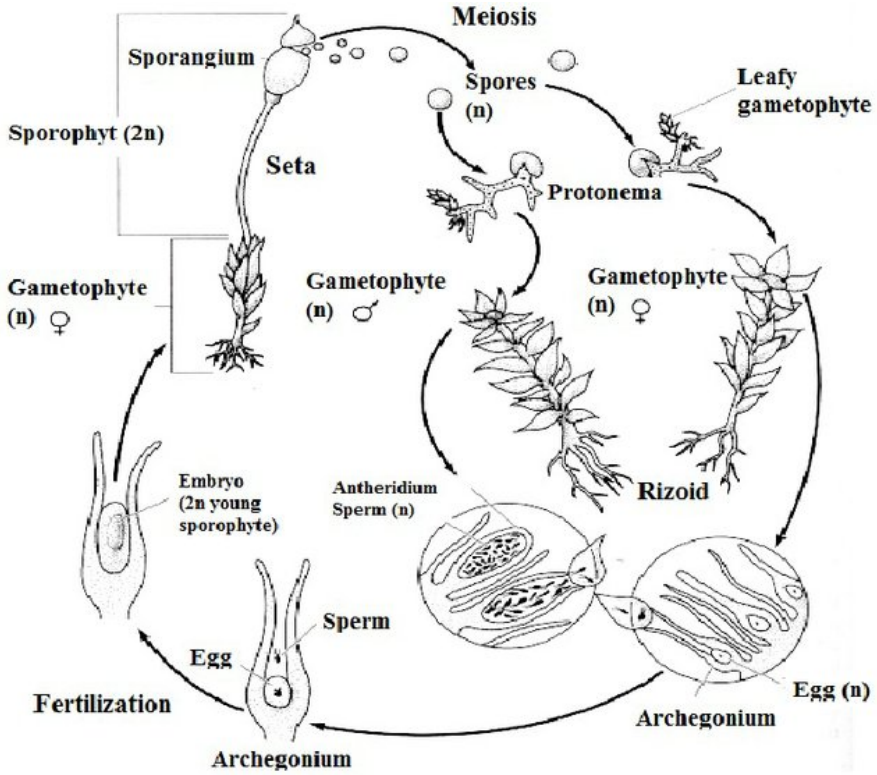

Figure 3. Mosses's Reproduction Process. Taken from Ursavaş & Çetin, 2013.

1.3 Impact of Mosses in Ecosystems

Mosses play a variety of functions within the ecosystems. These functions involve providing microhabitats for micro- and macroinvertebrates, establishing habitats, fixation and cycling nutrients, acting as a pollution gauge, and acting as a significant reservoir for carbon (Bahuguna et al., 2014). Because they are often pioneer species, mosses are very significant. According to Bahuguna et al. (2014), they are one of the the earliest plants to colonise inhospitable areas, such as porous, nutrient poor, mineral soil, and rocks, gradually transforming the area into a more livable space for species that need more water and nutrients. In areas lacking both, mosses can thrive because they can withstand desiccation and get the nutrients they need from the air and water (Bates, 1992).

Mosses can create a structure that allows soil to build up by creating a gathering spot. This eventually creates a solid layer of soil that can withstand runoff and produce more debris by accumulating organic materials from the moss. They not only collect organic matter but also offer cyanobacteria that fix nitrogen a great place to live (Bahuguna et al., 2014; Rousk, 2022), which helps the soil absorb nitrogen. Water retention increases over time as soil and organic matter accumulate. Together with the higher level of nutrients, this produces a microhabitat that is conducive to other plant species recruitment and germination. According to Rehm et al. (2019), bryophytes are particularly crucial in restoration sites where older woody litter and nursing logs might not be accessible for seeds to sprout in. They aid in the establishment of seedlings in some ecosystems, such as tropical forests. Mosses create a crucial structure known as a soil crust, which is also made up of bacteria, lichens, fungi, and cyanobacteria (Wang et al., 2023). They cover 12 percent of the earth's terrestrial area and can prevent soil degradation on barren ground by up to 135% (Wang et al., 2023). Soil crusts are found in most exposed ground areas that receive sunlight, although they are particularly common in arid regions like deserts that have little vegetative ground cover (Belnap, 2006). In between patches of mosses and lichens, the majority of soil crusts with high moss and lichen populations collect sediments, organic materials, and water, all of which can help seeds germinate and establish (Belnap, 2006). Given that areas that retain water and nutrients are particularly crucial for the germination of seeds and further development, this is particularly crucial in arid conditions.

Sphagnum moss-dominated peatlands are among the world's greatest stores of carbon (Yu, 2012). Although they only make up around 3% of the earth's surface, peatlands store about 600 Gt of carbon, or about 30% - almost the amount of atmospheric carbon (Clymo, 1998; Oke & Hager, 2020). Substantial amounts of organic matter are found in peatlands, which are frequently flooded and have extremely low oxygen levels, which prevent the organic matter from decomposing (Oke & Hager, 2020). Because organic matter keeps building up in these peatlands, significant amounts of carbon are trapped there. Peatlands are suffering from human activity, like many other ecosystems. It is mostly unknown what processes determine whether a degraded peatland will act as a source or sink of carbon. However, whether carbon is stored or released in the degraded peatland is known to depend on the rate of pre-degradation wetland decomposition as well as the rate of input and breakdown of incoming organic matter (Laiho, 2006). There is no justification for draining peatlands or avoiding conservation and restoration initiatives just because some may not eventually become a source of carbon. Numerous creatures that depend on the integrity of intact peatlands can be found in these uncommon habitats. Even while degraded peatlands might not be as significant a source of carbon as previously believed, their preservation and restoration are still important because they offer other advantages beyond carbon sequestration.

In addition to macroinvertebrates such as insects, spiders, and molluscs, mosses are home to a wide variety of microinvertebrates, together with rotifers, nematodes, protozoa, and tardigrades

(Bahuguna et al., 2014). Although the significance of mosses as an invertebrate habitat may vary by species and ecological system, it is reasonable to infer that removing or degrading the mosses in the habitat may lead to a reduction in nutrient cycling and decomposition, which would have an impact on the ecosystem as a whole.

The presence of contaminants in surroundings has a significant influence on mosses. According to Bahuguna et al. (2014), while certain taxa can tolerate pollutants, as a whole, their populations tend to drastically decline when exposed to them. However, different species react differently to specific pollutants. Additionally, mosses can reveal information about the site, including the concentrations of various metals and minerals in the soil (Bahuguna et al., 2014). Moss population loss may be a sign of environmental contamination prior to other organism reductions.

1.4 Rare Species

A key component of the conservation and long-term growth of humanity is biodiversity. But due to biological invasion, habitat destruction brought on by human activity, environmental pollution, land-use change, and global climate change, it is more threatened than ever. Understanding the biological characteristics and patterns of distribution of rare taxa is crucial for conservation and management in various regions (Leitão et al., 2016).

Rare species frequently face extinction due to human activities or local ecological, often climatic, changes that may result in the depletion of suitable habitats (Purvis et al., 2000). Multiple investigations have made an effort to address this issue, with a number of them focusing on bryophytes (Heinlen & Vitt, 2003). Based on how rarity is defined, rare species can make up as much as 35 percent of the flora in numerous locations (Newmaster et al., 2005). Because rare plant species are valuable in terms of ecology, politics, and intrinsic value, conservationists and land managers fight to safeguard them. According to Gaston (1994), a significant number of species are uncommon, meaning they have small populations and frequently have limited geographic distributions. Despite the fact that different types of rarity have been identified in relation to the processes via which species go extinct (Hartley & Kunin, 2003), it is believed that all rare species are extremely susceptible to overexploitation (Dulvy et al., 2003), changing climate (Sekercioglu et al., 2008), ecosystem loss (Lavergne et al., 2005), and competitive relationships with exotic species (Jelks et al., 2008). Because the extinction of rare species contributes disproportionately to the current sixth extinction crisis, conservation biologists have given these species significant attention (Van Calster et al., 2008). Ecosystems' biogeochemical and dynamic characteristics may change as a result of this biotic impoverishment (Naeem et al., 2012). Therefore, the preservation of ecosystem functioning has emerged as a potent defense to stop the loss of biodiversity, transcending aesthetic, cultural, and moral considerations (Loreau et al., 2001). In fact, the loss of ecosystem services carried out by certain species poses a threat to the majority of important ecological processes, including productivity, bioturbation, bioerosion, and organic matter degradation (Bellwood et al., 2012). It has historically been believed that their disappearance will have little effect on ecosystem processes at short-term and at a local scale (Grime, 1998). However, since the extinction of rare species can impact regional ecosystem functions, this theory has been contested (Bracken & Low, 2012), and rare species can have a major role in the long-term and enormous scale performance of ecosystems (Lyons et al., 2005), ultimately offering ecological insurance under conditions where biodiversity levels fluctuate over time (Floder et al., 2010). According to Lavergne et al. (2003), uncommon species may provide supplementary functions to those of other species, including closely related species, due to their unique functional characteristics. Accordingly, those rare species may boost local communities' functional diversity (Richardson et al., 2012), sustain the ecosystem processes

(Mouillot et al., 2011), and offer functional traits capable of supporting the primary ecosystem processes in the event of potential environmental shifts (Floder et al., 2010).

Not many studies worldwide investigated landscape patterns of moss diversity in relation to moss co-occurrence and environmental diversity drivers. In Belgium, Vanderpoorten & Engels (2003) conducted an analysis of edaphic conditions and topographic characteristics within a Walloon Brabant province to elucidate the correlation between the diversity of rare mosses and these ecological factors. Orbán (1992) identified variations in the percentage of colonists and perennial perseverer species when comparing the developmental histories of endangered bryophytes in Hungary with those of the entire flora. The majority of these studies have concentrated on habitat or associated environmental factors in order to describe the observed presence of rare mosses; however, none of them have analysed the patterns of rare moss distribution on landscapes by taking into account regional climatic factors.

According to Leitao et al. (2016), nature reserves were created in regions where rare and sensitive listed species were highly prevalent (Pimm et al., 2001) in order to preserve its biodiversity. Nonetheless, managing nature reserves that contain several rare species might be difficult. Finding the best course of action to safeguard populations might be aided by evaluating the many forms of rarity. According to Rabinowitz (1981), rare species can have broad or restricted habitat specificity depending on whether they are locally commmon with limited ranges, or locally uncommon with big geographic ranges. A species' life history traits, including reliance on a particular pollinator or a disturbance regime, may also contribute to species rarity (Bissessur et al., 2019). With a single population or possibly a single individual, species ranges may be on the outskirts of protected area due to their varied life histories (U.S. Fish and Wildlife Service, 2015). The limited population sizes of these species alone make them vulnerable to extinction or inbreeding (Rodrigues, 2019). Movement of rare species is hindered by the increasing fragmentation of protected areas caused by agricultural or urban expansion, and a high density of invasive species, activities involving unauthorised trail use, and increased vulnerability to fires caused by humans; these are some of the risks that exist at a reserve's perimeter (Radeloff, 2005). Trails and roads could have a negative effect on the persistence and shifting of rare plants and can introduce invasive species into the habitat of rare species (Thomson, 2005). There are some highly species-rich nature reserves close to densely populated areas of people (Seabloom et al., 2006). Additionally, Syphard et al. (2017) found that these regions are more susceptible to longer fire return intervals, which has a detrimental effect on rare species (Lawson et al., 2012).

To make management decisions, land managers must curate and consider the available data in light of the risks and difficulties associated with maintaining rare plants (Margules & Pressey, 2000). In an effort to conserve rare species, scientists and botanical organizations have created lists of species that aid in ranking species according to their rarity and the challenges they face in certain regions. The occurrence of rare species can then be incorporated into databases created from these lists to help guide conservation strategy (Viciani et al., 2018).

National lists of rare species have become the standard in conservation biology, and form basis for the preparation of red lists, as well as for the definition of significant areas for protection (Pantović, 2018). In Great Britain, for example, very rare taxa are those that appear in 1–15 10 × 10 m squares, and as rare those that appear in 16–100 such squares (Prescott, 2016). In Serbia, nearly 30% of moss flora (174 species) is considered threatened, while another 20% is considered Data Deficient (DD) (Sabovljević et al., 2024). However, these findings emphasize the necessity of for field investigations into species distribution and biology. Given that such research is extremely demanding in terms of time, money, and other resources, species distribution modelling analyses are highly important for

defining potential species distributions, identifying suitable habitats, and planning appropriate conservation measures.

1.5 Invasive species

It has been well known that invasive species can have adverse effects on native plant taxa, ecosystems, and communities (Simberloff et al., 2013). Globally, invasive plant species are considered one of the key contributors of the loss of biological diversity and an important driver of the worldwide shift (Vitousek et al., 1996, 1997; Didham et al., 2007). According to Pearson et al. (2018), invasive plant species have the potential to disrupt the establishment of autochtonous taxa, which in turn can impact the structure and assembly of plant communities. In the end, they can jeopardise the conservation of biodiversity (Pejchar & Mooney, 2009), and human wellfare by threatening biodiversity and causing extinctions (Bellard et al., 2016), altering soil properties (CastroDíez et al., 2019), nutrient cycling (Vilá et al., 2011), fire regimes (Brooks et al., 2004), and hydrology (Levine et al., 2003). Invasive plant species represent a major challenge to the restoration of native ecosystems and can substantially alter the structure and composition of natural communities (D'Antonio & Meyerson, 2002).

Important studies on the ecology, mechanisms of dissemination, and management of imported species have been prompted by their near-ubiquity across habitats. Ecologists are constrained by their inability to measure and include these species in a comprehensive and significant manner, despite the fact that their influence on ecosystems is perhaps the most significant issue (Byers et al., 2002). While we should not undervalue the economic effects of invasive species, we should all focus on the ecological effects from the standpoint of conservation and ecosystem service protection (MA, 2005). Therefore, factors that contribute to alien plant species' invasiveness are a crucial area of study in ecology and invasion biology, with significant practical implications.

Although it is highly probable that invasiveness is encouraged by functional qualities of species, such as physiology, biomass allocation, growth rate, size, and fitness (Van Kleunen & Richardson, 2007), the hunt for traits that confer invasiveness has not advanced very far. With few exceptions (Mason et al., 2008), the majority of research on species traits linked to invasiveness (Pysek & Richardson, 2007) have focused on relatively simple traits, such as plant height and growth form, which are easily accessible for a large number of species from databases, including floral compendia. To quantify many potentially significant functional features for invasiveness, however, invasive and non-invasive species cultivated in similar environmental settings must be compared. Native plant species frequently experience decreases in dominance and abundance due to intense competition with invasive plants, and in some situations, localised extinctions (Sax et al., 2007).

In addition to affecting taxonomic elements and abiotic conditions, alien species invasions affect biological diversity by altering the composition of functional groups, for instance (Wu et al., 2009). Thus, invasive alien plants possess the capacity to significantly affect individual ecosystem services (Villa et al., 2010) and alter multiple ecosystem functions (Pritekel et al., 2006).

Approximately 139 species of bryophytes have been identified as aliens globally (Essl & Lambdon, 2009). However, this number is significantly lower than that of seed plants, particularly considering that only three species of bryophytes have a significant, acknowledged socio-economic impact, and seven more pose an imminent danger to biodiversity (Essl et al., 2013). Sometimes a dense layer of bryophyte can actually prevent the herb and shrub layers from regenerating. Even a thin layer of moss can stop seedlings from emerging in relatively dry areas like grasslands and heathlands. This is because it prolongs the time that seeds remain above ground, increasing the likelihood that they will be

destroyed by fire and predators, and it creates an environmental barrier that prevents seeds from germinating (Zamfir, 2000).

1.6 Bryophytes and Climate Change

Bryophytes are a common component of photosynthetic biomass in terrestrial ecosystems (Gunnarsson, 2005; Turetsky et al., 2010). However, they are often overlooked in assessments of biodiversity and ecosystem function, even in systems where they are the dominant vegetation, despite making a substantial and possibly disproportionate contribution to ecosystem processes such as the cycling of water, carbon (C), and nitrogen (N) (Turetsky, 2003; Eldridge et al., 2023). Unfortunately, it has been demonstrated that bryophyte survival and function can be negatively impacted by climate change (Tuba et al., 2011; Alatalo et al., 2020). A thorough analysis of how changing climate will affect bryophyte-mediated impacts on water, carbon, and nitrogen cycling is necessary, as ongoing changes in climate (temperature and moisture availability) will influence how all plants interact with hydrological and biogeochemical cycles.

Global warming-related climate change is anticipated to be most noticeable at high latitudes – a phenomenon reffered to as Arctic amplification (IPCC, 2021). According to Huttunen et al. (2005), experimental research has shown that *Sphagnum* species react to increased UV light by slowing growth. Certain arctic bryophytes, such as *Polytrichum hyperboreum* on the Svalbard tundra, reproduce sexually and develop sporulating sporophytes. At higher Antarctic latitudes, sexual reproduction is more common in Antarctic mosses (Lewis-Smith & Convey, 2002). Rising nitrogen deposition occurs alongside increasing emissions of nitrogenous air pollutants over the northern hemisphere (Bouwman et al., 2002). Estimates of the effects and possible outcomes of global changing climate are highly uncertain. The rise in atmospheric CO_2 is the only aspect of global climate shift that can be regarded as certain. According to Houghton et al. (1990), it might double or possibly surpass its current concentration by the end of the 21st century (600-700 μmol/mol 1).

Compared to aquatic bryophytes, terrestrial bryophytes have higher thermal optima and tolerance (Carballeira et al., 1998). As heat stress typically occurs when gametophytes are dehydrated, the development of dry heat tolerance in bryophytes is expected to be more strongly selected than wet heat tolerance (Meyer & Santarius, 1998). This is not same case in vascular plants, which have the highest wet heat tolerance among terrestrial plants, and the great majority of which cannot completely desiccate (Nobel et al., 2006). High temperatures cause membrane structural changes, increased permeability and fluidity, and ultimately cell death (Deltoro et al., 1998). Moss sporophytes are more vulnerable to extreme temperatures than gametophytes, which can exhibit extremely high heat tolerance when desiccated (Meyer & Santarius 1998). However, in one research two sporophytic embryos of desert mosses showed a phenological pattern of over-summering, which allows them to survive extended periods of heat stress despite desiccation (Bonine, 2003).

Over the past 200 years, the amount of atmospheric CO_2 has elevated from approximately 280 ppm in pre-industrial era to approcimately 410 ppm in 2019 (Arias *et l.,* 2021). In the coming century, it is predicted to exceed twice its pre-industrial level (Houghton et al., 1990). The posibble impact of changing climate on bryophyte taxa has been insufficiently studied, despite their importance, compared to its influence on other plant groups with higher economic value such as trees, crops, and grasses (Korner & Bazzaz, 1996).

Bryophytes are considered shade plants with generally low chlorophyll a:b ratios, even in those found in open, exposed environments. Species found in open, well-lit environments, exhibit

photosynthetic saturation at relatively low irradiances, about 20% of full sunlight (Marschall & Proctor, 2004).

Since the majority of bryophytes are dehydrated and metabolically inactive during bright, dry, sunny weather, it makes sense that poikilohydric organisms are acutally adapted to photosynthetise at relatively low light availability. The majority of their photosynthesis occurs in gloomy or rainy conditions, when irradiance may be less than 20% of that in full sunlight. In arid environments, the primary physiological requirement for bryophytes is likely photoprotection rather than energy absorption during brief exposures to intense sunlight when the plant dries. Bryophytes found in mires, springs, and other humid habitats, which typically stay continuously moist even in the conditions of full sun, might appear to be the best adapted to photosynthesise in high light (Proctor, 2000; Goffinet, 2008).

Ozone in the stratosphere has altered the solar energy that reaches the Earth surface at UV-B wavelengths of 280–315 nm, resulting in a 60% increase in UV radiation during spring at subarctic latitudes (Taalas et al., 1995). According to Rozema et al. (2002), the UV-B adaptation of moss species is likely consequence of their evolutionary age, as they predate vascular plants. As the ozone layer gradually accumulated, mosses may have adapted to the increasing UV-B intensities, compared to those that exist today. UV protection and reflection protection mechanisms vary among different bryophyte groups. For example, ectohydric mosses have a slender lipid stratum and lack wax on their surfaces to shield them from radiation, while the surfaces of several endohydric species are covered with cuticles and wax deposits.

Although there are some exceptions, such as *Marchantia* and Polytrichaceae, the essentially undifferentiated basic structure of bryophytes makes them susceptible to UV-B damage. The ability of Antarctic bryophytes to adapt to increasing UV-B radiation is critical for their survival during ozone loss. Photosynthetically active radiation is transmitted by pigments that absorb UV-B energy. Rather than relying on repair mechanisms, which require an active metabolism, the accumulation of these pigments is significant for arctic and boreal bryophytes during physiologically inactive phases such as desiccation or freezing, due to their passive UV-B absorption capacity (Glime, 2017).

According to Mayaba and Beckett (2003), desiccation disrupts plants in a number of ways, including membrane leakage of ions and electrolytes, pH shifts, solute crystallisation, protein denaturation, and the production of reactive oxygen species. Barker et al. (2005) state that these disruptions lead to reduced growth, chlorophyll degradation, and decreased regeneration potential. In moss habitats, where rapid drying events are frequent, desiccation damage of bryophytes is highest when the period of hydration is brief (Proctor, 2004). Bryophytes display a wide range of desiccation tolerance. For example, desert moss species may restore its maximum photosynthetic activity as fast as only one hour of rehydration after extremely prolonged drying. On the other hand, certain species of *Sphagnum* cannot survive a sole dessication period. Additionally, desert mosses can tolerate a variety of consecutive wet and rapid dry conditions (Stark et al., 2005).

Numerous techniques, including protein synthesis response (Oliver et al., 2004), pigment concentrations (Newsham, 2003), chlorophyll fluorescence (Takacs et al., 2000), and membrane permeability (Beckett et al., 2000), have been used to investigate the desiccation tolerance of bryophytes.

There is no doubt that the range of bryophytes will shift as a result of the warmer and drier climate caused by global warming. The water table will drop as a result of increased evapotranspiration, which will drive most of these changes. Many bryophytes are useful indicators of

climate because they are sensitive to factors such as temperature, precipitation, and evapotranspiration ratios. Therefore, species response surfaces in climatic space and the consequent indicator communities offer intriguing opportunities for measuring the effects of global warming on both their own distribution patterns and those of their associated ecosystems.

1.7 Distribution Modelling in Bryology

As a useful statistical tool, species distribution models (SDMs), including the models commonly known as habitat suitability models or climate envelope models, are being used more and more in order to characterise relationship between species and habitat, describe species distributions, and forecast how species react to changing environmen with the aim to facilitate conservation and management policies (Zurell et al., 2022). At their most basic level, SDMs forecast species distributions by using statistical techniques to link species behavior, occurrence, or abundance to environmental and spatial factors. SDMs are fitted using a variety of techniques, such as machine learning algorithms, decision trees (such as boosted regression trees), spatiotemporal ("geostatistical") models, generalised linear and additive models (GLMs and GAMs), maximum entropy models, and more. The fundamental presumptions and workings of the various modelling techniques vary, and the type of data as well as research question frequently influence the modelling approach selection (Elith & Leathwick, 2009).

Species distribution modelling is frequently used to answer fundamental and practical problems in the core fields of biogeography, such as historical biogeography, studies of species distributions, diversity patterns, biome and ecoregional typology, conservation evaluation, and the effects of global change (Guisan & Thuiller, 2005). Whether SDM is a method or a subdiscipline is debatable, but regardless, it provides a fresh perspective on biogeography, bolstered by "big biodiversity data," the growing environmental mapping of remotely sensed data (He et al., 2015), and geographical instruments for analysis of data (Franklin et al., 2016; Wüest et al., 2020). In addition to more recent sources, big biodiversity databases now incorporate many of the traditional biogeographic data sources (natural history collections, pollen, charcoal, and other palaeodistribution or palaeoenvironmental data, phylogenies) (Callaghan et al., 2021; Sueur & Farina, 2015; Williams et al., 2018).

According to Vanderpoorten et al. (2010), several bryophyte species have a range of distribution that crosses many continents. However, there is a wide range of information available about the distribution of European bryophytes, from comprehensive atlases to more fragmentary data from checklists, local floras, databases, and herbaria. Different approaches have been taken to address this problem, which is typical of distribution data (Araujo & Guisan, 2006; Mateo et al., 2011). For all except the rarest species, Linder et al. (2012) cautiously extrapolated range maps from point data. The fact that many bryophyte species have distinct niches in various biogeographic regions has long been recognised (Shaw, 1985; Vanderpoorten & Durwael, 1999). Additionally, the idea that populations of bryophytes that are continentally disjunct share the same habitats is being challenged by an increasing amount of evidence that suggests significant rates of cryptic speciation in bryophytes (Vanderpoorten & Shaw, 2010).

Correlative species distribution models (SDMs) have garnered significant attention in recent decades and are well recognised by ecologists, evolutionists, biogeographers, and conservationists (Franklin, 2023). Numerous theoretical and practical applications employ SDMs to map the spatial distribution of species and comprehend the interaction between them and their surroundings (Guisan & Thuiller, 2005; Franklin, 2010). Real-world management choices like planning and conservation priority are frequently supported by them (Guisan et al., 2013; Whitehead et al. 2017). It's crucial to determine how models function on the kinds of data that are commonly available because modelers

frequently have to compile existing data as opposed to obtaining costly survey-based samples (Powney & Isaac, 2015; Johnston et al., 2020). Furthermore, SDM forecasts may differ based on the model that is fitted (Hallgren et al., 2019), which may cause significant adjustments to the choices that are made in response to their predictions (Muscatello et al., 2021). In order to determine whether some modelling techniques generally outperform others, there is continuous motivation in evaluating the predictive performance of various modelling techniques. In the past, a number of researches have examined different models (Elith et al., 2006; Bahn & McGill, 2013; Shabani et al., 2016). Nonetheless, a number of novel modelling techniques have surfaced in recent years, highlighting the need for ecologists to have a current evaluation of their overall effectiveness (Elith et al., 2020).

The selection of background data, the choice of modelling algorithms, the appropriateness of underlying model assumptions, the tuning of model parameters and complexity, the availability of species data, and environmental predictors are just a few of the many factors that must be taken into account when creating an SDM (Araújo et al., 2019). Predictions may be significantly impacted by these factors. Because there are numerous approaches accessible, the modelling algorithm selection is frequently the most important of these factors. Finding broad patterns in prediction performance across methodologies is of continuous interest because different methods have varying predictive achievement (Pearson et al., 2006; Thuiller et al., 2009).

Covariates associated with a species' abundance and distribution are usually identified when species distribution modelling is applied successfully. Latitude, longitude, altitude, substrate type, season, and other properties are examples of relatively constant covariates. Other covariates may be more dynamic environmental features. These dynamic measurements can provide a moment in time of the ever-changing environment, including the current physical circumstances, water quality, and biological traits, which can differ greatly over time and place. In order to understand and quantify the intricate combination of behavioral preferences, predatory/competitive restrictions, physiological requirements, and stochastic processes that determine a species' location in space and time, species distribution modelling is used. Effective use of species distribution modelling can therefore be used to estimate habitat quality and appropriateness. Future distribution patterns or distribution in areas that were not previously sampled can be predicted using the fitted species-environment correlations, if they are strong, in conjunction with additional environmental data (Guisan & Thuiller, 2005; Elith & Leathwick, 2009).

1.7.1 Models based on Regression

In species distribution modelling, the two most used regression techniques are Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs). GLMs model the response-predictor relationship using parametric functions, such as linear or higher-degree polynomials. To account for nonlinearity in the fitted functions, GAMs employ nonparametric smooth functions.

Generalized Linear Model fitting can be done in a number of ways, and contemporary regularization techniques frequently yield good results (Reineking, 2006). The coefficients are penalised in Lasso regression and ridge regression (L1 and L2 regularization, respectively), which decrease them in the direction of zero (Friedman et al., 2010). Because of this shrinkage, the regression model's variance (i.e., stability across various data samples) is decreased, potentially improving the fitted model's generalization. Lasso can, in contrast to ridge regression, set the coefficient of variables to precisely zero, thus eliminating those variables and producing sparser models (Hastie et al., 2009). According to a recent analysis, penalised regression operates similarly to MaxEnt (Gastón & García-Viñas, 2011). Predicting species distributions may benefit from these regularization techniques, as MaxEnt is frequently seen to have good predictive ability. With piecewise linear basis functions in

place of smooth functions, Multivariate Adaptive Regression Splines (MARS) are a versatile nonparametric regression that is comparable to GAMs (Elith & Leathwick, 2007). Fast, built-in internal cross-validation techniques are used to determine how many of these piecewise linear functions are fitted across each predictor variable, which determines the model's complexity. When given the opportunity, MARS fits interactions (Leathwick et al., 2006).

Specifically designed for modelling presence-only species data, MaxEnt is a well-liked modelling technique for species distribution prediction (Phillips et al., 2006). According to Renner & Warton (2013) and Renner et al. (2015), it has established connections to regression techniques, specifically point process approaches. Complexity is managed through the selection of regularization settings and the application of modified characteristics of the predictor variables, such as linear, quadratic, product, hinge, and threshold (Elith et al., 2011). Driven by fresh insights into the connection between MaxEnt and Poisson point process models (Renner & Warton, 2013), MaxNet is a new, alternative version of MaxEnt (Phillips et al., 2017). It is created as an R package that does not require any additional software that fits the MaxEnt model using infinitely-weighted logistic regression (Fithian & Hastie, 2013). Similar to Lasso, MaxEnt and MaxNet both employ L1 regularization (Elith et al., 2011) though they may have more adaptable fitted functions (via modified features).

1.7.2 Tree-based models

Nonlinear (and nonparametric) models, such as classification and regression trees, iteratively divide the predictor space into regions with comparable response variable values (Elith, 2019). A few benefits of this theoretically straightforward approach include the ability to automatically model interactions between covariates and the consistent selection of significant covariates (Strobl et al., 2009). Single trees are high-variance techniques that vary depending on the training data set. They're not very good at estimating smooth functions, either. Despite this limitation in their predictive capabilities, they are frequently employed as the basis learner in tree ensembles and are frequently very successful at making predictions (Hastie et al., 2009). Machine-learning models are frequently defined as tree-based models.

Stochastic gradient boosting is used in Boosted Regression Trees (BRT) to build the models, and the approach concentrates on the weakest regions of the model by fitting each new tree to the residuals of the previously fitted trees (Elith et al., 2008; Friedman, 2002).

A novel and slightly different approach to gradient boosting, the XGBoost algorithm (Chen & Guestrin, 2016) has a number of features designed to increase scalability and reduce over-fitting (Prasad, 2018). As demonstrated by Doren & Horton (2018), Huang et al. (2019), and Herdter (2019), XGBoost is rarely used in species distribution modelling, despite its effective use in other fields (Chen & Guestrin, 2016). According to Muñoz-Mas et al. (2019), this could be because XGBoost is very new and has a lot of hyperparameters that require careful tweaking because of its great degree of flexibility.

For SDMs, Random Forests (RF) (Breiman, 2001) has gained popularity. In contrast to BRT, this modelling technique uses bagging (bootstrap aggregation) to join several trees rather than a stagewise strategy for ensemble construction. According to Strobl et al. (2009), bagging entails selecting several bootstrap samples from the training data, fitting a tree to each sample, and calculating the average prediction across all fitted trees. Special to this approach, RF grows each tree using just a random subset of the predictor variables on each split. By doing this, decorrelated trees are produced and the final model's variance is decreased, improving its predictive performance (Hastie et al., 2009). Random Forests's lack of sensitivity to model parameter modification is one of its advantages over

comparable techniques like BRT and XGBoost (Strobl et al., 2009; Freeman et al., 2016). Because of these features, RF is now a somewhat popular SDM strategy (Mi et al., 2017; Harris et al., 2018).

A variation of RF known as Conditional Inference Forest (cforest) uses a distinct type of decision tree known as ctree (Hothorn et al., 2006). This technique was initially created to address well-known issues with popular splitting techniques for recursive binary partitioning, specifically the selection bias in favor of predictor variables with missing values or a large number of alternative splits. Unlike RF, cforest uses a stopping criterion rather than growing trees to their maximum size. In order to determine variable relevance objectively, the forest model additionally employs subsampling without replacement rather than bootstrap sampling (Hothorn et al., 2006; Strobl et al., 2008). Due of the high cost of ctree fitting, it is computationally expensive to create ensembles of several ctrees in a forest.

1.7.3 Alternative models

With the increased use of SDMs in ecology, the accuracy and uncertainty of species predictions have come under scrutiny. It has been shown that the reliability of predictions varies depending on the species. Furthermore, the outcomes derived from alternative single models could be so different that chould affect the decision-making in species conservation managemement (Araújo & New, 2007; Guisan et al., 2007; Buisson et al., 2010). Therefore, different models should be selected for each species carefully (Segurado & Araujo, 2004; Luoto et al., 2005; Barbet-Massin et al., 2012).

Another common method for reducing the uncertainty of model predictions is the use of ensemble models, which combine the predictions of several single models to improve overall performance, accuracy, and precision compared to single models. One of the common ensemble techniques is model averaging (Dormann et al., 2018). In order to reduce forecast uncertainty resulting from method selection, it has been common practice for SDMs to average predictions from many approaches (Araújo & New, 2007). Biomod, a computer program, was created especially for modelling species distributions, constructing ensembles using a variety of modelling techniques (Thuiller et al., 2009). Ten algorithms are included, some of which were employed in our study (such as GAM, GLM, BRT, RF, and MaxEnt). The predictions of these models are combined for example, via weighted averaging of the predictions. Although the biomod model is widely used, its prediction performance has not received as much specialised research as it might (Hao et al., 2019).

1.8 Environmental Factors Influencing Moss Distribution

Among the first terrestrial plants, bryophytes have special survival techniques for adjusting to land conditions. Their tiny shape and dependence on ectohydric (external water conduction) rather than interior water-conducting cells, set them apart from other embryophytes (Vitt et al., 2014). They are distributed throughout different ecosystems worldwide due to their strong reliance on moisture and specific physiological characteristics that allow them to flourish in harsh environments (Tuba et al., 2011).

Mosses are incredibly adaptable and may live in a variety of environments, including urban areas, lush woods, and parched deserts. An analysis of the effects of topography, soil chemistry, temperature, and precipitation are necessary to comprehend moss ecology (Alataş et al., 2023).

By influencing environmental factors like light intensity, moisture retention, and soil properties, topographical features like mountain ranges, valleys, and different kinds of landforms not only directly affect the ecological niches and resources that bryophytes can access, but they also indirectly influence their growth and distribution (Kruckeberg, 2004). For example, mosses can grow in microenvironments

that are favored by the damp conditions of valleys and the shading effect of mountains (Zhao et al., 2023). Furthermore, the degree and length of sunshine exposure for bryophytes are determined by the slope and direction of various terrains, which impacts their growth patterns and photosynthetic efficiency (Scherrer & Körner, 2011; Man et al., 2022).

The distribution and diversity of bryophytes have been shown to be significantly influenced by climate conditions, especially temperature and humidity (Amatulli et al., 2019; Karger et al., 2012). Mosses' survival and capacity for reproduction are directly impacted by climatic factors like temperature and humidity, which also have an impact on physiological functions including photosynthesis, water absorption, and nutrient exchange (Glime, 2013). For example, temperature variations can affect moss plants' seasonal growth patterns and metabolic processes, while humidity variations can affect their drought tolerance and water-use efficiency (He et al., 2016). Additionally, factors that impact moss diversity include solar radiation and light intensity. According to Yin et al. (2023), mosses have adapted to microclimatic zones, exploiting ideal light conditions for photosynthesis, despite the hard conditions in Antarctica.

As a physical substrate, soil is a dynamic and complex media that supports mosses (Seppelt et al., 2016). According to Raggio et al. (2017) and Kutnar et al. (2023), it is essential for regulating the availability of water and nutrients, which are vital for the metabolic processes and overall health of these non-vascular plants. The diverse reactions of moss plants to various soil types demonstrate the complex interaction between soil characteristics and moss physiology. For example, whereas compact, nutrient-poor soils may restrict the spread of moss, nutrient-rich, well-draining soils can promote moss growth (Diekmann et al., 2023; Rola et al., 2021). The pH of the soil has a major impact on the distribution of moss species; some species prefer acidic while others prefer alkaline environments (Tyler & Olsson, 2016). The mosses' resistance to metal ions and other soil-borne compounds, which varies with pH, is sometimes attributed to this predilection. Furthermore, because mosses have few means of retaining water, soil moisture—a variable that is greatly impacted by both internal soil characteristics and external climatic factors—is a crucial element in determining moss survival and spread (Oishi, 2018).

Anthropogenic activity and biotic interactions have a major impact on moss ecology. Epiphytic moss communities are influenced by the presence of particular tree and vegetation species (Perdrizet & McKnight, 2012). Mosses live on a variety of surfaces in urban settings, adapting to changes in temperature, humidity, and light caused by human activities (Cruz et al., 2023). According to Gornall et al. (2007), disturbances can alter ecological functioning by affecting moss presence and ecosystem processes, mostly through adjustments to soil temperature and moisture equilibrium.

1.9 Biology of Investigated Species

Three moss species were selected for the research in this dissertation: two rare species *Entosthodon hungaricus* and *Hennediella heimii*, which are considered facultative halophyte species, and *Campylopus introflexus,* an invasive moss species spreading further into south-Eastern Europe.

1.9.1 *Entosthodon hungaricus* (Boros) Loeske (fam. Funariaceae)

Synonyms: *Funaria hungarica* Boros, *Physcomitrium maroccanum* Meyl, *P. martianovii* Broth., *Entosthodon. maroccanum* (Meyl.) Hebr.

Entosthodon hungaricus was first described from Hungary in 1924 (Ignatova and Ignatov, 2005). It is a xerophilic, photophilic, halophytic moss that grows on salty alkaline soils. This species is considered a facultative halophyte; it can establish on salty soils, but its optimum is in a low-salt environment (Sabovljević & Sabovljević, 2007). However, it is a poorly competitive species, easily outgrown by other mossess, and therefore inhabits saline habitats where other salt-intolerant species are absent (Sabovljević et al., 2018).

Entosthodon hungaricus is a European sub-endemic species, found in specific localities, such as dry steppes and salt marshes (Figure 4), and therefore its distribution is significantly discontinuous (Pisarenko et al., 2001). The distribution of this species in Europe spans across the Mediterranean to Central and Eastern Europe, analogous to other xerothermic species (Pocs et al., 2004).

Figure 4. Natural habitat of *Entosthodon hungaricus* - saline grasland in Special nature reserve Selevenjske pustare in northern Serbia. © Jovana Pantović.

Hodgetts (2015) and Ellis et al. (2016) noted that this species was found in the Canary Islands, Hungary, Serbia, Montenegro, Romania, Slovakia, Greece, Russia, Moldova, Austria, Germany, Malta, Portugal, and Sicily. It is also known outside of Europe from Israel, Kazakhstan, Kirgizia, and Morocco (Pisarenko et al., 2001).

Although some research has been done on the biology and ecology of *Entosthodon hungaricus* in Serbia (Sabovljević et al., 2012, 2018; Ćosić et al., 2020), its local distribution is still considered insufficientlly known. This species is rare in the country and endangered because of its specific ecological requirements (Papp et al., 2016) and habitat degradation, making it difficult and time-consuming to discover in the field due to its small size and seasonality (Figure 5a). A further factor in the species' extinction concern is the extreme sensitivity and fragility of saline ecosystems, which are impacted by human activity and climate change in general. Due to their low agricultural value, these saline environments are especially vulnerable, they are frequently utilised as low-class land for construction and/or waste deposits, or occasionally as overgrazing pastures, which further compromises the survival of rare species in these areas (Papp et al., 2016; Sabovljević et al., 2018). The survival, phenology, and development of these species are impacted by severe climate change, which also affects the particular water regime (Sabovljević et al., 2018).

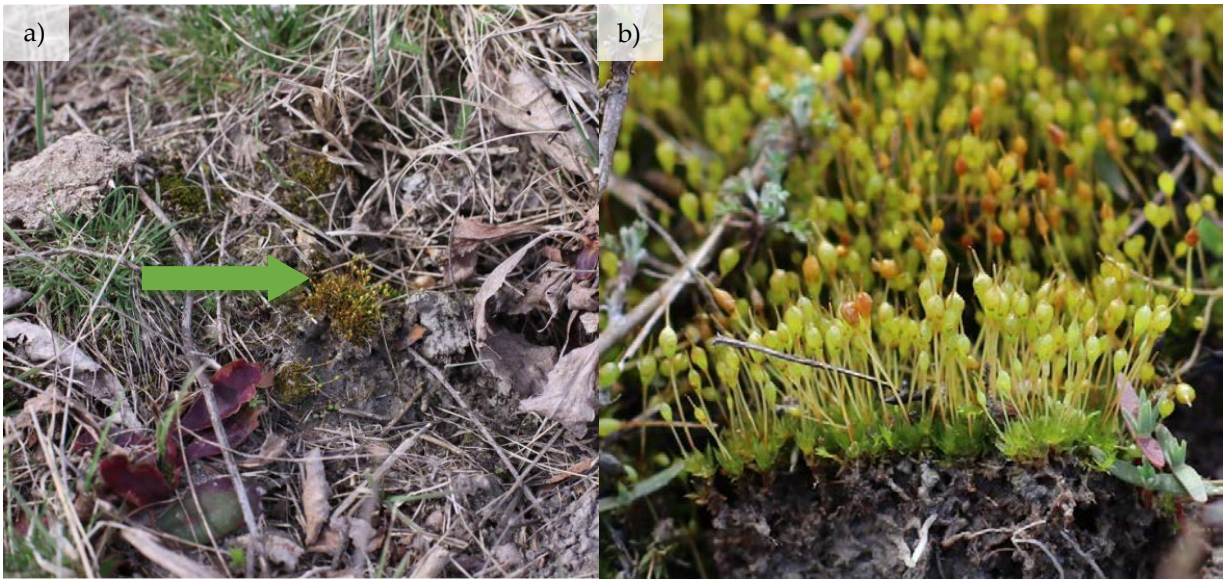

Figure 5. Characteristic appearance of *Entosthodon hungaricus* in the field (a), with numerous capsules that develop in the spring (b). © Jovana Pantović.

The *E. hungaricus* habitat types in Serbia are exceptionally significant from an ecological and conservation standpoint. According to Papp et al. (2016), these habitats are highly valuable for protection not just for *E. hungaricus* but also as a home for certain birds, insects, plants, and fungus that are of conservation concern. Moreover, these hallophyllous habitas are rare and thus endangered in Serbia. The species is categorized as VU (Vulnerable) in the most recent Red List of Moss species of Serbia (Sabovljević et al., 2024) based on recent distributions and species biology, whereas it was classified as EN (Endangered) under criterion B in the previous Red List of bryophytes in Serbia (Sabovljević et al., 2004). Finding possible species distribution areas is made easier with the help of SDMs, particularly in uncharted regions of the nation. Furthermore, this species' monitoring and conservation management can be better understood using the prediction models.

As an ephemeral species, *E. hungaricus* phenological optimum occurs from April to May (exceptionally, it can be found from March to July), as determined by the percipitation in early spring. During this time, it actively produces abundant sporophytes (Figure 5b) so that it can swiftly colonise suitable unoccupied habitats as well as escape unfavorable climate conditions (e. g. cold winters or dry and hot summers). The new generation typically arises in November during the autumn rains (Papp et al., 2016). It usually thrives in extreme salt conditions, where it is thought to have a competitive edge over non-halophytic plant (Sabovljević et al., 2018). In Serbia, *E. hungaricus* thrives in frigid winters and highly warm, arid summers, as well as in saline soils. It uses a short-lived life approach to avoid highly severe circumstances. Also, it is commonly found in continental inland salt steppes, primarily in the eastern Pannonian regions of Austria, Romania, Hungary, Slovakia (Zechmeister, 2005), and in Serbia as well. They represent habitat types with exceptional ecological and conservation importance that are rare and endangered in Serbia.

Although it has a wide distribution area throughout Europe, the populations are vastly dispersed and fragmented, hence its range is severely uneven. According to the new European Red List of Mosses, Liverworts and Hornworts it is classified as Least Concern (LC) (Hodgetts et al., 2019). However, due to its range features, ephemerality, peculiar ecology, specificity of the substrate and vulnerability of its habitats, it is red-listed in several European countries: it is considered CR in Slovakia, NT in Hungary and Spain, and rare (R) in Germany (Hodgetts, 2015).

In literature, this species has only been mentioned in two historical sources for Serbia, both of which come from the geographical areas of Bačka and Banat in northern province of Vojvodina (Guelmino, 1970, 1972). Afterwards, it hasn’t been discovered in nearly 40 years until its collection in 2010 (Papp et al., 2016), which confirmed these several locations in northern Serbia.

Existential risks of this species come from habitat destruction and the deterioration of its particular substrate requirements. Because of its unique ecology and decreased capacity for environmental adaptation, targeted conservation efforts are needed. Due to a decrease in population, the species is included on both national and international conservation lists. In Serbia, it is classified as Vulnerable (VU), indicating its limited range and high ecological requirements (Sabovljević et al., 2024). The fact that the moss has been placed on red lists by several European nations is evidence of its declining numbers (Papp, 2008; Soltes et al., 2002; Sergio et al., 2006; Sauer & Ahrens, 2006; Sabovljević et al., 2004). Its populations exhibit discontinuities and fragmentation despite its broad distribution across Europe. Because of its short life cycle, unique ecological requirements, and particular substrate requirements relating to gypsum and saline content, there is a substantial risk of both local and long-term extinction.

1.9.2 *Hennediella heimii* (Hedw.) R. H. Zander (fam. Pottiaceae)

Synonyms**:** *Desmatodon heimii* (Hedw.) Mitt, *Gymnostomium heimii* (Hedw.) Sp. Musc. Frond, *Pottia heimii* (Hedw.) Hampe

Moss *H. heimii* is a hyperboreal species according to Hodgetts et al. (2019a). The area it covers in Europe extends from the Massif Central in France north to Iceland and Svalbard, along the Atlantic and Baltic coasts. It is found in central Europe, although the population is dispersed there because of significant habitat damage (salty grassland type). According to Blockeel et al. (2014), *H. heimii* occurs beyond Europe in northern Asia, with a few locations also known in central Asia, Japan, North America, southern South America, Tasmania, New Zealand, the Subantarctic Islands, the Antarctic Peninsula, and south to New Mexico and Newfoundland.

From an ecological perspective, *H. heimii* can be classified as a salt-tolerant bryophyte (Blockeel et al., 2014). It flourishes in grazed turf, on walkways, and on disorganised surface in upper marshes, making it a particularly distinctive bryophyte of salt marshes (Blockeel et al., 2014). Additionally, it is common in coastal habitats, such as the sand or muddy ground between beach boulders, the soil at the base of sea walls and cliffs, the banks of tidal rivers and dykes, rock ledges and crevices, and short turf on cliff tops and slopes (Hodgetts et al., 2019a). It typically lives along the edges of salty grasslands, salt flats, or pools near salt springs or lakes in central Europe. In rare instances, it has been observed inland in habitats that are ruderal and seemingly non-saline, like alongside salted roads (Figure 6) (Tipper, 2007). Capsules are plentiful and typically mature between February and May, though they are observed all year long (Figure 7a).

Figure 6. Salt-tolerant moss species *Hennediella heimii* colonizing roadside verges influenced by salt usage during winter periods. © Robin Stevenson. Downloaded from https://www.britishbryologicalsociety.org.uk/learning/species-finder/hennediella-heimii/

Although the species occurs in fragmented habitats, its overall population size in the Europe appears to be large; therefore, it is not currently red-listed for Europe (Hodgetts et al., 2019b). However, local extinctions have been reported in Austria, Spain, and the Lorraine region in northeastern France (Mahévas et al., 2010; Garilleti & Albertos, 2012; Hodgetts et al., 2019a).

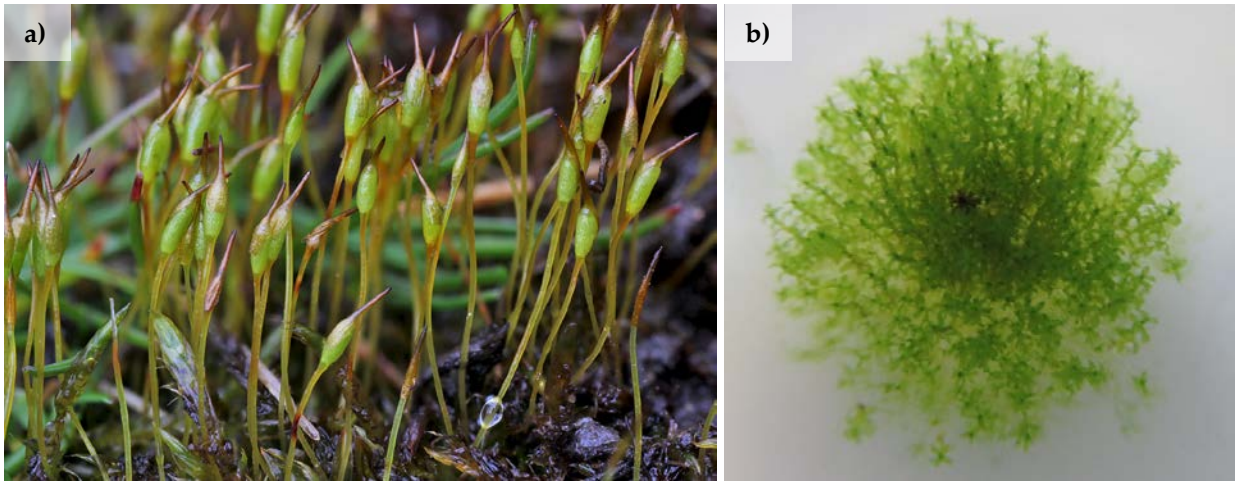

Figure 7. **a)** Distinctive appearance of moss *Hennediella heimiii* in natural habitat, characterised by long-setae and abundant immature capsules © Barry Stewart. Downloaded from https://www.westglamorganflora.org.uk/bryophytes/hennediella-heimii/30145/ and **b):** *H. heimii* growing in *in vitro* culture in the Botanical garden "Jevremovac" in Belgrade, Serbia. © Marko Sabovljević.

According to Checklist and country status of European bryophytes (Hodgetts & Lockhart, 2020), *H. heimii* is considered Vulnerable (VU) in Switzerland, Endangered (EN) in Hungary and Romania, and Critically Endangered (CR) in Slovakia. Furthermore, it is also considered threatened and red-listed in Austria (Highly Endangered), Ukraine (Rare), Germany (Near Threatened), and Poland (Indeterminate). It is listed as a Data Deficient (DD) species in Italy, Slovenia, and the Czech Republic, and as Regionally Extinct (RE) in Spain.

In the literature, there are no recent records of *H. heimii* from the Balkan Peninsula. While there are some quite old findings of this species, all records are more than 70 years old, and not-confirmed in later field studies of the area. For example, the only known record of *H. heimii* in central Serbia dates back more than a century ago, from Pčinjski district in the Southern Serbia (Pantović et al., 2021). Considering the species' ecology and habitat preferences, this record is unlikely to be reliable, and the specimen may have been misidentified. This cannot be confirmed with certainty without checking the original specimen, which to our knowledge is not preserved in the herbarium collection.

Because so few salt-tolerant bryophyte has been studied before, the species is intriguing to study from both an ecological and eco-physiological (Figure 7b) standpoint. It is additionally of great conservation concern. When it comes to adapting to salt stress, the species exhibits some very intriguing traits, such as quick ontogenesis and alterations in biochemistry and physiology (Ćosić et al., 2020a, b, 2021).

Increased temperatures globally threaten the survival of global ecosystems which have been affecting biodiversity across regions (Dawson et al., 2011). Climate change causes species to shift their ranges by moving to colder areas (He et al., 2019), and as species relocate to higher elevations, species of conservation interest that have restricted geographic ranges, small populations and narrow niche face

extinction as their ranges diminish (Daskalova et al., 2020). Thus, understanding how these taxa react and adapt to changing climate is necessary in order to evaluate biodiversity vulnerability and plan conservation efforts.

1.9.3 *Campylopus introflexus* (Hede.) Brid. (fam. Dicranaceae)

Synonyms: *Dicranum introflexum* Hedw.

Campylopus introflexus (Heath Star Moss), commonly known as Heath Star-moos (Figure 8), is a neophytic species from the southern hemisphere. It is native in South America, South Africa, and Australia (Hassel and Söderström, 2005). It is the most widespread invasive moss species in Europe, having spread throughout Europe and North America around the mid-twentieth century. The earliest known discovery in Europe occurred in 1941 in the United Kingdom (Richards, 2013) subsequently in 1954 within French Bretagne region (Størmer, 1958). It is also likely that the moss appeared in Europe from multiple locations at multiple time points (Richards, 2013).

Figure 8. Characteristic apperance of Heath Star-moss, showing reflexed, hyaline hair points when dry. © Claire Halpin. Downloaded from https://www.britishbryologicalsociety.org.uk/learning/species-finder/campylopus-introflexus/

Among adventive mosses worldwide, *C. introflexus* is arguably the most dangerous. Dispersal of vegetative propagules allows for its local dispersal, while spore formation facilitates long-distance dispersal (Miravet et al., 2021). This method makes it a pioneer species and coloniser; it may rapidly takeover areas that are accessible and unsettled (Figure 9). While *C. introflexus* thrives in a variety of environments, it favors decalcified, nutrient-poor substrates and disturbed sites, such as dunes, bare peat, mining sites, roadsides, and substrates that have been altered by humans (Mikulášková et al., 2012). Its thick carpet could also prevent seed germination of many vascular plants and exclude native moss and lichen communities, particularly on sandy soils found along the shore (Equihua and Usher, 1993). According to reports from the Netherlands (Biermann and Daniëls, 1997) and coastlines in Germany (Biermann, 1999), the invasion of *C. introflexus* has caused great reduction in the abundance of herbaceous vascular plants and the rich lichen diversity.

Hodgetts & Lockhart (2020) report that *C. introflexus* is known to occur in 39 European countries. The CABI database (CABI, 2016) offers a comprehensive review of research on the start of spreading in European countries. By the end of the 1960s, *C. introflexus* was established all over Western Europe and, throughout the decades that followed, in numerous Central and Northern European countries. Despite it was observed in Latvia and Russia (Kaliningrad Province) in 2000, originally it was noted in Eastern Europe (Poland) in the 1980s. Poland has a widely reported potential for its expansion towards eastward (Górski et al., 2016). Numerous countries in southern (Portugal, Spain, Italy), central (Germany, the Czech Republic, Hungary), and eastern (Poland, Latvia, Russia)

Europe have reported cases of *C. introflexus*. Southeastern Europe has also recently reported increased spreading of this invasive species (Alegro et al., 2018). The first *C. introflexus* record in southeastern Europe was reported from Slovenia (Ellis et al., 2014), followed by Croatia (Alegro et al., 2018), and Serbia (Sabovljević et al., 2023). First record of *C. introflexus* in Serbia is from 2019, when it was discovered in the Pešter Plateau in southwestern Serbia (Sabovljević et al., 2023). Moreover, Slovenia and Croatia reported several new records and further spreading within the countries (Sabovljević et al., 2020; Strgulc Krajšek et al., 2023; Šegota et al., 2021, 2026). These populations represent southeastern border of the invasion of *C. introflexus* in Europe.

Figure 9. Cushions of alien species *Campylopus introflexus* prevailing in the landscape in Penygroes, UK. © Barry Stewart. Downloaded from https://www.westglamorganflora.org.uk/bryophytes/campylopus-introflexus/30570/

Researchers have been examining the ecological characteristics of *C. introflexus's* invasion of various ecosystems and its capacity for competition since the 1980s. Unlike most alien bryophytes, which typically colonise environments that have been disturbed by humans (such as gardens, roadsides, and walls), *C. introflexus* has established itself in vegetation that is close to natural, including pine forests, bogs, and coastal dunes (Essl & Lambdon, 2009). The formation of spores and seeds of different species may be adversely affected by the dense, compact cushions formed by *C. introflexus* (Equihua & Usher, 1993). Native populations that have been invaded may become colonies with a high concentration of *C. introflexus* and very few mosses or lichens. In sandy regions of the Netherlands, where virtually no other bryophyte or lichen species can thrive, this species is known to develop incredibly dense turfs that cover dozens of square meters (Sparrius & Kooijman, 2011). Spiders and carabid beetles are examples of organisms that suffer from alterations in the vegetation's structure (Schirmel et al., 2011). Among invasive bryophytes, the effects of *C. introflexus* have been researched the most (Essl et al., 2014a).

However, little is known about the biology and extent of its spread across the majority of Europe. The species exhibits distinct behaviors throughout Western and Central Europe. According to

the data currently available, *C. introflexus* can form dense mats and colonise a variety of environments in Western Europe, which includes countries with an oceanic climate, such as the Netherlands, Belgium, and Germany (Sparrius & Kooijman, 2011; Mikulášková et al., 2012). The harmful impact of *C. introflexus* invasion had originally been noted for the Netherlands' coastal dunes (Van der Meulen et al., 1987). Because it poses a threat to autochtonous vegetation, majority research in Western Europe has concentrated on sand habitats and nutritionally deficient grasslands (Sparrius & Kooijman, 2011).

Through soil stabilization, leaf litter binding, decay rate alteration, and the creation of microhabitats that impact the makeup of microfaunal communities, *C. introflexus* may change the makeup of the ecosystem and how dunes function (Pehle & Schirmel, 2015). According to Mikulášková et al., (2012), the Czech Republic has the most data on Central Europe. The national distribution of *C. introflexus* spans from the colline to the montane belt (210–1140 m). Among the most commonly invaded habitats are the edges of pine and spruce plantations, forest areas, and bare regions with damaged peat bogs. Human activity has an impact on all of these conditions, such as bare acidic soils that are conducive to *C. introflexus* growth since there is little competition from vascular plants. Nonetheless, research from Hungary (Csiky et al., 2015) indicates that human activity is not required for colonisation because animal disturbance or biological processes can frequently produce bare, acidic soil surfaces that are ideal for colonisation.

According to Razgulyaeva et al. (2001), the species was found in small patches on decomposing litter in an open *Betula pendula - B. pubescens - Pinus sylvestris* forest near the easternmost frontline of the invasion (Kaliningrad Province, Russia). Repečkienė et al. (2015) concluded that *C. introflexus* could possibly have a detrimental effect on Lithuanian peatlands' fungal diversity, seasonal succession, and fungal community structure, all of which may have an adverse effect on the plant cover's natural recovery. *Campylopus introflexus*, on the other hand, is a typical pioneer species in vacuum-harvested peatlands, has no effect on vegetation variety, and is not harmful to peatlands, according to the research on peatlands in Latvia (Priede & Mežaka, 2016).

The ecology of *C. introflexus* is poorly understood, despite the fact that it is recognised as one of the emblematic invasive species in Europe (Daisie, 2009). Although it can grow in a variety of environments, it is primarily a successful early invader in open spaces and gaps where vascular plants do not pose a threat (Żarnowiec et al., 2019).

Understanding this species' potential impact on and threat to native communities in southeast Europe is thus worthwhile. Serbia is an excellent example of a newly occupied area in central-southeastern Europe where *C. introflexus* is already widespread.

Even though Heath Star-moss is known as one of the archetypal invasive species in Europe, little is known about its ecology (Daisie, 2009). It is therefore important to comprehend the potential threat and effects of this species on native communities in southeast Europe. Because of its rapid growth and the paucity of regional research in the area, SDMs provides a solid scientific basis for predicting its ecological impact. This work can support biodiversity conservation and invasive species management in Serbia and elsewhere by filling in these research gaps.

According to available data, 27.18% of Serbia's moss flora, which includes 174 taxa, is at risk of extinction (status 2024). According to Sabovljević et al. (2024), 5.16% (33 species) of the moss flora are classified as Near Threatened (NT), and almost 20% (129 species) are classified as Data Deficient (DD). These results unequivocally show that fieldwork and species biology studies are urgently needed to identify the main threats and implement effective conservation strategies.

Rare or endangered species ecological preservation is of international concern, especially in light of the growing effects of modern human activity on the environment (Díaz et al., 2019). It is very difficult to conserve and manage these species because environmental disturbance, particularly human changes, frequently has the most detrimental effects on them. It is common for rare species to be both the ones that require robust inductive reasoning about growth rates and state variables, and also the ones for which obtaining such data is most challenging (MacKenzie et al. 2005). Unexpectedly, considering the theory that rare species have more limited core niches (i.e., physiological tolerances) than common species, it has been discovered that the physiological tolerance of rare moss species is significantly wider than the horizon of environmental conditions in which the species originated.

It is commonly known that rarity depends on scale (Rabinowitz, 1981). Therefore, only a small number of world-wide rare species, or species that are very widespread or even invasive in other regions, may be included in regional lists of rare species. Until recently, it was believed that maintaining a few high-productivity species would be enough to keep the ecosystem functioning. However, recent research has shown that rare species also play an important role in maintaining ecosystems functions (Chapin et al., 2000; Lyons et al., 2005). Therefore, preserving local biodiversity helps strengthen ecosystems by maintaining ecological interactions, improving ecosystem stability, and increasing resilience to environmental change (Tilman et al., 2014).

The world's biodiversity is seriously threatened by invasive plant species (Sala et al., 2000). Plant invasions contribute to a homogenised flora on an extensive scale, and invasive plants frequently create uniform and dense stands at the commune level (Hejda et al., 2009). As a result of their influence, alien plants alter terrestrial environments on nutrient cycles and soil conditions (Weidenhamer & Callaway, 2010), plant diversity (Ketner-Oostra & Sykora, 2004), microclimate conditions (Schirmel et al., 2011), and vegetation composition (Hejda et al., 2009). Nature's organism’s arrangement and food web formation are thus impacted by invasive alien plants (Petillon et al., 2010). For example, the invasion by the moss *C. introflexus* in European acidic coastal dunes (grey dunes) has a detrimental effect on ground-dwelling arthropods, demonstrating that even small-scale invasions can affect the native fauna (Schirmel et al., 2011).

2. RESEARCH AIMS

2.1 Research Objectives

Main goal of this doctoral dissertation was to provide experimental evidence on the use and importance of species distribution modelling in conservation biology, especially in the case of poorly studied taxa and/or regions. The specific objectives of this research were to:

- Analyse the present range and preferred habitats of three selected moss species using all available distribution data collected from published literature references, the Global Biodiversity Information Facility (GBIF), and herbarium specimens.
- Determine the main environmental factors affecting their distribution using species distribution models (SDMs): 19 bioclimatic variables, altitude, and soil types were used.
- Predict possible future distribution patterns under various climate change scenarios and to measure how their range will change over space and time.
- Make conservation suggestions to safeguard investigated rare species, *Entosthodon hungaricus* and *Hennediella heimii*, and its habitas.
- Help develop management plans in order to avert future spreading of the invasive alien species *Campylopus introflexus* and its negative influence on native bryophyte flora.

This study will help to bridge the gap between species distribution modelling and workable biodiversity protection policies, promote conservation efforts, and provide important insight into the ecology of bryophytes in Serbia.

2.2 Research Questions

- What is the potential present distribution of *E. hungaricus, C. introflexus and H. heimii* throughout studied regions?
- What are the key ecological factors influencing the current distribution of the investigated species?
- Which areas provide the highest climate suitability for investigated species?
- How the potential distribution of the investigated species is going to change in the future under different climate pathways?
- Which regions are going to become refugia for the species studied in the future?

2.3 Hypotheses

- The existence and abundance of investigated moss species will be significantly correlated with key environmental factors, namely temperature, precipitation, and soil type.
- Climate change, especially increasing temperatures and changing precipitation patterns, will lead to a reduction in areas with suitable climate for investigated rare moss species, which will consequently lead to a reduction in their distribution and an increase in local extinctions, as well as a shift in their ranges towards more suitable environmental conditions.
- The spread of invasive moss species *C. introflexus* will increase over time due to its ability to colonise environments more efficiently than native species, especially in regions and habitats that are under strong anthropogenic influence and climate change.

The effects of changing climate and global warming on bryophytes are substantial (Turetsky, 2003). Due to their extreme sensitivity to variations in moisture and temperature (Gignac, 2001), change in their range size is one of the major consequences of global warming (Zanatta et al., 2020). In pursuit of appropriate habitats, they may be compelled to relocate to higher latitudes or elevations when temperatures rise and patterns of precipitation change (Steinbauer et al., 2018).

Even though bryophytes are recognised to have a high degree of desiccation resistance, another effect of global warming on them is the modification of their physiology (Proctor, 2007). As shown in one study, they will increase rates of evapotranspiration as temperatures rise, which will reduce the amount of water available and make them more vulnerable to stress from dehydration (Vitt et al., 2014). As a result, bryophytes are extremely susceptible to the effects of changing climate and global warming, which are anticipated to modify their physiology, dispersion methods, and ecological importance.

Species distribution modelling (SDM) can be used for these reasons in order to assess the potential reaction of bryophyte species to future changes in habitat or climate, as well as to examine the predictors that impact their distribution.

However, modelling bryophytes also presents certain difficulties. For instance, bryophyte distribution modelling is challenging due to their scattered distribution and small size, which can make large-scale mapping of their distribution challenging. Furthermore, bryophyte species frequently have an intricate biological needs that can be challenging to record in an SDM, such as certain microhabitats or relationships with particular species of tree. The distribution of bryophytes in many environments has been effectively studied using species distribution models (SDMs) regardless of these (and similar) difficulties.

The association between occurrences of the species and environmental variables is usually modelled by SDMs using statistical or machine learning methods. According to Deneu et al. (2019), input data include environmental variables like climate, topography, land use, soil properties, and species occurrence records.

Major advancement in SDM has been made over the past several decades, and ecological research in this field is still ongoing. Many possible future avenues of SDM exist due to the continuous development of new modelling approaches and the availability of progressively complex data.

SDMs typically provide maps as their primary output, which are useful resources for comprehending and forecasting species distribution. The topic of SDM has had a long existence and has changed significantly in recent years due to the introduction of new techniques and the accessibility of big datasets of species records and ecological factors (Elith et al., 2006). It is anticipated that the spatial pattern and number of taxa is significantly impacted by changing climate. The geographical distribution and habitat suitability of many bryophytes are projected to change as a result of extreme weather events, alterations in temperature, and dynamics in precipitation patterns (Erauskin-Extramiana et al., 2020). For instance, some species can decrease their distribution range or even possibly go extinct, while others might spread out into new regions. Pollination and pest management are two examples of ecosystem-related services that may be negatively impacted by these alterations (Hughes, 2012). According to Zhu et al. (2018), SDM may be used to forecast how species distributions will change in response to various climatic situations.

This can assist in determining regions with high conservation importance, species-risk areas, and potential hotspots for invasive species. Additionally, SDM can help guide conservation strategy and management, including the recognition of hideout for species that might be particularly threatened from changing climate (Zhang et al., 2019). By using characteristics that shape the distribution of species, SDMs are able to separate variability resulting from inaccurate species detection. It has also been used to find cryptic species' appropriate environment (Wilting et al., 2010), particularly for species that spread over wide and/or challenging terrain that makes thorough surveys impossible (McShea et al., 2009).

3. MATERIALS AND METHODS

3.1 Study Area

The study area for *Hennediella heimii* and *Campylopus introflexus* covers the European continent, including the European parts of Russia and Turkey. Europe is characterised by heterogenous topography, spanning from lowland plains and river basins to major mountain systems such as the Alps, Carpathians and Balkan Mountains. Elevation ranges from below sea level in coastal depressions to more than 4000 m in the mountain areas. Beyond the temperate climate zone, Europe spans across several major climate zones, including Arctic, Boreal, Continental, Alpine and Mediterranean. In addition to the influence of latitude and longitude, the climate of Europe is significantly affected by the Gulf Stream and the Mediterranean Sea, which contribute to a milder climate. Moreover, the influence of the Atlantic Ocean decreases from west to east, resulting in an increasingly continental and colder climate. Consequently, mean annual temperature and precipitation vary considerably across the continent (Metzger et al., 2005).

Together, these factors influence microclimatic and ecological heterogeneity, making Europe particularly environmentally rich areas of the world. This high biogeographical diversity is reflected in a range of vegetation types, including tundra, boreal coniferous forests, temperate broadleaf and mixed forests, steppes, Mediterranean woodland and shrubland, wetlands and alpine habitats (Olson et al., 2001). The vegetation cover is primarily determined by climate, topography and elevation. Despite this ecological diversity, much of the European territory has been altered or degraded by human actions, leading to the expansion of urban areas and agricultural land. This environmental diversity makes Europe a great region for investigating species–environment relationships across broad climatic and ecological gradients.

Study area for the species *Entosthodon hungaricus* was territory of Serbia, a country in southeast Europe, situated in the central part of the Balkan Peninsula and the southern part of the Pannonian Plain. The highly variable topography and many impacts from the Carpathians, the Mediterranean coast, and Western Europe all contribute to Serbia's climate's complexity and heterogeneity. In Serbia, the temperate-continental and dry temperate-continental climates are the two main climate types (Stevanović & Stevanović, 1995). Mountainous and high-mountain regions of the country experience the mountain climate because of the pronounced mountain relief. There are notable differences among these fundamental climatic types because of variations in orography, geology, and vegetation cover, and a number of additional variants and transitional forms of climate can be identified.

The climate of the regions in Serbia is classified as moderate-continental. The absence of dry and semi-arid seasons and a comparatively high annual precipitation (720–900 mm) characterise the humid temperate-continental climatic subtype that exists in western Serbia, which is influenced by the humid Atlantic climate (Stevanović & Stevanović, 1995). The eastern continental climate and the southern Mediterranean climate have a bigger impact on Serbia's central and eastern regions. Consequently, the climate in these regions of Serbia is slightly drier than in its western regions, and this climate type is known as a subcontinental subtype.

The continental climate of Serbia is typified by the lowlands of the southern Pannonian plain in the north and the northeastern regions. The occurrence of arid and semi-arid periods in the summer and early autumn, as well as significant temperature extremes and frigid winters, are characteristics of this climatic type. There is 520–590 mm of rainfall on average annualy. However, in contrast to its semi-arid form in Vojvodina, the semi-humid variant in northeastern Serbia is characterised by cooler

winters, relatively drier summers, and more precipitation throughout the winter and spring seasons (Stevanović & Stevanović, 1995).

Reduced average annual temperatures (9–12°C) and precipitation (800–900 mm) are characteristics of the transitional sub-Mediterranean climate found in the southern and southwestern regions of Kosovo and Metohija, as well as in the southeastern region of Serbia (Stevanović & Stevanović, 1995). But because of the penetration through the gorges and canyons, mostly through the Vardar and southern Morava valleys, the Mediterranean's significant influence is visible considerably further inland, north of eastern and southeast Serbia. A comparatively lengthy dry and noticeable semi-arid stage, with 500–600 mm of precipitation annually, is what defines this type of transitional climate. The lengthy, cold winters, high amounts of precipitation in the spring and summer (850–1300 mm annually), and low average annual temperatures (0.5–5°C) are characteristics of the mountain climate type. The central and eastern parts countrywide, which have the continental variation of this climatic type, receive 850–1400 mm of precipitation annually, whereas the mountains in western Serbia experience 1000–2000 mm (Stevanović & Stevanović, 1995).

Serbia has the highest concentration of climate-induced automorphic soils. The features of these naturally formed soils, which vary in degree, are directly influenced by the climate, water regime, vegetation development, and type of geological substrate. This category of soil includes early, underdeveloped soils in the initial stages of formation, such lithosols, as well as well-developed soils with suitable physical and chemical properties and high fertility, such as chernozem and loams (Stevanović & Stevanović, 1995). The development and fertility of azonal, hygromorphic soils vary in degree and are influenced by the nearby watercourses, including flooding, the deposition of river sediments, and the presence of high groundwater levels. Gley soils, such as peat soils in mountain and high mountain regions, developed hygromorphic soils (psudoglay, meadow blackberry), and undeveloped alluvial soils in plains and valleys are all included in this type of soils. Besides climatogenic soils, Serbia also has intrazonal halomorphic, or saline, soils, which occur in the arid Vojvodina regions. According to Vidojević et al. (2016), the soil types that are commonly found in Serbia include Vertisols, Gleysols, Chernozems, Calcisol, Cambisol, Fluvisol, and Solonchak dirts. In the Vojvodina province, Chernozems, Gleysol, and Solonchaks are the most prevailing soils. According to Miljković (2005), solonchaks are the most saline soils, with at least 1% salt content. The predominant salt type in Vojvodina's solonchaks is sodium carbonate (Na_2CO_3), with sulfates (mostly Na_2SO_4) and chlorides (primarily NaCl) present in smaller amounts.

Despite making up only 2% of all European land, Serbia is known for its remarkable plant diversity, including roughly 40% of all plant species in Europe (Šijačić-Nikolić et al., 2020). Serbia was classified biogeographically into five main regions according to the type of habitat: (1) zonobiome of deciduous woodland, (2) steppe zonobiome with a variety of steppe and forest-steppe vegetation, (3) zonobiome of conifer boreal woodlands in mountain areas, and (4) zonobiome of highland “tundra” - alpine rocks and meadows (Radović & Kozomora, 2011). Additionally, numerous extrazonal, intrazonal and azonal ecosystems, such as wetlands, peatlands, saltmarshes and sandy areas, strongly influence the high country’s biodiversity. There is also high vegetation diversity, with estimates ranging from 600 to 1200 plant communities (Lakušić, 2005). The most abundant grasslands types are semi-natural (secondary) grasslands that are created in the forest zone as a result of deforestation, and natural or primary grasslands, which occur as the final stage of vegetation on areas that are not suitable for forest development, such as high-mountainous (above timberline) zones, flooded land in lowland valleys, and xeric steppe and/or saline habitats in the country's northern province of Vojvodina (Dajić Stevanović et al., 2010).

3.2 Species Selection

Three moss species were selected for this dissertation: two rare and threatened species considered facultative halophytes - *Entosthodon hungaricus* and *Hennediella heimii*, as well as one invasive moss species that is spreading further into South-Eastern Europe - *Campylopus introflexus.*

Species were selected for modelling based on their ecological importance, conservation interest and data availability. Two rare species with limited records, *Entosthodon hungaricus* and *Hennediella heimii,* were selected as representatives of sparsely distributed taxa of particular conservation interest**.** Although such species present additional modelling challenges due to reduced sample size, their inclusion enables preliminary insights into potential climate suitability and distributional constraints. Information on species distributions can help in the formulation of conservation policy and support biodiversity management. The third species, *Campylopus introflexus,* known to exhibit invasive characteristics within the study region, was included to assess the environmental conditions that may facilitate its spread and persistence in the country. Protecting native plants and controlling biological invaders need an understanding of present distributions, forecasting future changes, and targeted actions.

3.3 Data Collection

Species occurrence records were compiled from multiple sources. Data on *E. hungaricus* distribution in Serbia were gathered from the bryophyte collection of the Herbarium of University of Belgrade (BEOU) and literature search (Guelmino, 1970, 1972, 1973, 1997; Papp et al., 2016; Sabovljević et al., 2018). The majority of the old records from the literature were verified in the field as still current before being used in this study. In Serbia, the species was reported at 22 localities. Using the biomod2 R package (version 4.2-4) (Thuiller et al., 2023), data were processed to retain sincle occurrence point per environmental grid cell in order to minimise sampling bias. After reducing bias, 16 records were kept for the final modelling. Despite the apparently limited number of species records, previous studies have been confirmed that this type of studies proved rather beneficial and useful (Sillero et al., 2012), especially for species of conservation interest with limited distribution. Most algorithms can perform satisfactorily with this sample size during the modelling process. Furthermore, *E. hungaricus* is a unique species that has a very specific ecological requirements and limited ecological niche, as it is a halophyte species that thrives in saline and alkaline environments.

For the other two selected species, *H. heimii* and *C. introflexus,* there are only a few occurrence records in the country, some of which are quite old and/or doubtful. As these findings were insufficient for the analysis, SDM for *H. heimii* and *C. introflexus* was conducted at the European level. Data on their distribution in Europe were obtained from the GBIF database and supplemented with available records from the literature not included in GBIF. To ensure reliable and accurate results, only records with precise locations (those with coordinates) and only recent records collected after 1990 were used for modelling. To ensure data consistency, only records from the European part of Russia were included in the modelling.

Occurrence records of *H. heimii* in Europe obtained from the GBIF database (2025) were supplemented with additional records from the literature, mainly from continental Europe (Batan et al., 2017; Belkina et al., 2012, 2018; Berg et al., 2015; Bolotov et al., 2018; Callaghan & Ashto, 2008; Ćosić et al., 2022; Fedosov et al., 2025; Ganeva & Yurukova, 2004; Hugonnot et al., 2024; Hugonnot & Ully, 2003; Ivanova et al., 2017; Kerinec & Chardin, 2025; Leushina et al., 2011; Marstaller, 2010; Müller, 2017; Ravera et al., 2021; Sabovljević & Sabovljević, 2009; Thouvenot & Hugonnot, 2019; Tipper, 2007; Weeda, 2011; Zechmeister & Kropik, 2024; Zechmeister et al., 2024).

Regarding the invasive species *C. introflexus*, in addition to its occurrence records obtained from the GBIF database (2025), new findings in Europe not included in the online database, such as its spread in Southeastern Europe and its presence in Serbia, were derived from a thorough assessment of recent literature (Alegro et al., 2018; Blockeel et al., 2007, 2009; Csiky et al., 2017; Ellis et al., 2013, 2017; Górski et al., 2015, 2016; Krajšek et al., 2023; Mikulášková, 2012; Mišíková & Dobiašová, 2014; Priede & Mežaka, 2016; Sabovljević et al., 2020, 2023; Šegota et al., 2021, 2016; Širka et al., 2016, 2018; Szűcs et al., 2014; Szűcs, 2018; Zubel et al, 2009).

The complete occurrence dataset included only presence records. The GBIF data were pre-processed and cleaned using the CoordinateCleaner R package, v3.0.1 (Zizka et al., 2019) before generating the occurrence dataset. Species presence records then were filtered using a grid method with a resolution of 2.5 arc minutes, keeping single record within each grid cell, after which all the cleaned data were combined. This resolution reduces sampling bias and geographical autocorrelation, and is consistent with the ecological predictors used (Boria et al., 2014).

Following the cleaning, combining, and data thinning, a total of 628 occurrences of *H. heimii* and 12,385 occurrence records of *C. introflexus* for the territory of Europe were kept for modelling their possible European range.

3.4 Environmental Variables

For bioclimatic analysis of *E. hungaricus*, 19 bioclimatic variables (Table 1) from CHELSA climate dataset (Climatologies at High Resolution for Earth's Land Surface Areas) were used (Karger et al., 2017; Brun et al., 2022). CHELSA v.2.1 has a 30-arc seconds (~1 km) spatial resolution, that consists of monthly temperature and precipitation data over the 1979– 2013 period.

Table 1. List of 19 bioclimatic variables (according to Brun et al., 2022) used for distribution modelling of *Enthostodon hungaricus*.

Name of the Bioclimatic Variable		Description of the Variable
BIO1	Mean Annual Near-Surface Air Temperature	Mean annual temperature calculated as the average of mean monthly temperatures over the year
BIO2	Mean Diurnal Near-Surface Air Temperature Range	Mean diurnal temperature range computed as the average of monthly (tasmax − tasmin)
BIO3	Isothermality	Isothermality: 100 × (bio02÷bio07); compares day–night variability to annual temperature range
BIO4	Temperature Seasonality	Temperature seasonality given by the standard deviation of mean monthly temperatures
BIO5	Mean Daily Maximum Near-Surface Air Temperature of the Warmest Month	Highest monthly mean of daily maximum temperatures (tasmax) across the year; indicates peak thermal conditions
BIO6	Mean Daily Minimum Near-Surface Air Temperature of the Coldest Month	Lowest monthly mean of daily minimum temperatures (tasmin) across the year; characterises winter cold intensity

BIO7	Annual Daily Mean Near-Surface Air Temperature Range	Annual temperature range calculated as bio05−bio06; measures amplitude between warmest and coldest months
BIO8	Mean Daily Near-Surface Air Temperature of the Wettest Quarter	Average monthly mean temperature over the wettest 3-month period of the year
BIO9	Mean Daily Near-Surface Air Temperature of the Driest Quarter	Average monthly mean temperature over the driest 3-month period of the year
BIO10	Mean Daily Mean Near-Surface Air Temperature of the Warmest Quarter	Average monthly mean temperature over the warmest 3-month period of the year
BIO11	Mean Daily Mean Near-Surface Air Temperature of the Quarter	Average monthly mean temperature over the coldest 3-month period of the year
BIO12	Annual Precipitation	Sum of monthly precipitation totals across the year
BIO13	Precipitation of the Wettest Month	Maximum monthly precipitation total
BIO14	Precipitation of the Driest Month	Minimum monthly precipitation total
BIO15	Precipitation Seasonality	Coefficient of variation (100 × SD ÷ mean) of monthly precipitation totals
BIO16	Mean Monthly Precipitation of the Wettest Quarter	Average monthly precipitation during the wettest 3-month period of the year
BIO17	Mean Monthly Precipitation of the Driest Quarter	Average monthly precipitation during the driest 3-month period of the year
BIO18	Mean Monthly Precipitation of the Warmest Quarter	Average monthly precipitation during the warmest 3-month period of the year
BIO19	Mean Monthly Precipitation of the Coldest Quarter	Average monthly precipitation during the coldest 3-month period of the year

For the other two studied species, *Hennediella heimii* and *Campylopus introflexus*, same 19 bioclimatic variables were obtained from WorldClim v.2.1 dataset (Fick and Hijmans, 2017). WorldClim has a spatial resolution of 2.5 arc minutes and provides 30-year averages of temperature and precipitation for the interval 1970–2000. In general, CHELSA and WorldClim data distinguish in timeframes that they are using; namely CHELSA uses 30year long sequence (2011–2040, 2041–2070, 2071–2100) while WorldClim uses 20year long sequence (2021–2040, 2041–2060, 2061–2080, and 2081–2100). According to Fierke et al. (2024) these two datasets showed different patterns in current and future precipitation and temperature distributions, with CHELSA data indicating higher precipitation levels than WorldClim.

Except the 19 bioclimatic variables, the *Entosthodon hungaricus* analysis also incorporated two additional environmental predictors: altitude, which was obtained from SRTM elevation data (WorldClim, 2020), and a soil variable denoting halomorphic soils types (Pavlović et al., 2017). This soil variable was obtained from a binary grid, where 0 indicated the absence of halomorphic soils and 1 indicated their presence. The spatial resolution for both variables is 30 arc seconds (~1 km).

For the species *E. hungaricus*, Pearson correlation coefficients were computed among all environmental variables using the vifcor function in the usdm package in R, to prevent multicollinearity (Naimi et al., 2014). Subsequently, predictors that had correlation coefficients (r) higher than 0.7, were omitted from the further evaluation. For species *E. hungaricus*, the retained variables were altitude (ALT), halomorphic soils (HAL), and following six bioclimatic variables: Precipitation of Wettest Month (BIO13), Precipitation of Driest Month (BIO14), Precipitation Seasonality (BIO15), Mean Daily Temperature Range (BIO2), Isothermality (BIO3), and Mean Temperature of Warmest Quarter (BIO10).

Before developing models for *H. heimii* and *C. introflexus*, variance inflation factors (VIFs) for the variables were calculated using the R package usdm v.2.1.6 for the starting set of 19 bioclimatic variables (Dormann et al., 2012; Naimi et al., 2014). This was done to minimize multicollinearity among the variables. Predictors that showed to have VIF values exceeding 10 were removed from following calculations, because this value is widely recognised as an indicator of a high degree of multicollinearity (Zuur et al., 2009). Regarding *H. heimii*, retained variables were Mean Diurnal Range (BIO2), Isothermality (BIO3), Mean Temperature of Wettest Quarter (BIO8), Mean Temperature of Driest Quarter (BIO9), Mean Temperature of Warmest Quarter BIO10, Precipitation Seasonality (BIO15) and Precipitation of Warmest Quarter (BIO18). For *C. introflexus* the retained variables were Annual Mean Temperature (BIO1), Mean Daily Temperature Range (BIO2), Temperature Seasonality (BIO4), Maximal Temperature of Warmest Month (BIO5), Minimal Temperature of Coldest Month (BIO6), Precipitation Seasonality (BIO15), Precipitation of Wettest Quarter (BIO16), and Precipitation of Warmest Quarter (BIO18).

For the analysis of *Enthostodon hungaricus* four Global Circulation Models (GCMs) from the CMIP6 (Coupled Model Intercomparison Project Phase 6) were selected: GFDL-ESM4, UKESM1-0-LL, MPI-ESM1-2HR, and IPSL-CM6A-LR (Karger et al., 2017). Three time periods were considered: the current climate (1981–2010), and two future projections (2041–2070 and 2071–2100), based on the ISIMIP3b protocol. Furthermore, the posibble effects of changing climate on *E. hungaricus* were predicted using two different Shared Socio-economic Pathways (SSPs): SSP1–2.6 (low-emission pathway, approximately +1.8 °C by 2100) and SSP5–8.5 (high-emission pathway, approximately +4.4°C by 2100) (Blais & Koprowski, 2024; Meinshausen et al., 2000; Tebaldi et al., 2021).

To model distribution of another two species, *H. heimii* and *C. introflexus*, four future time periods were used (2021–2040, 2041–2060, 2061–2080, and 2081–2100) combined with two shared socioeconomic pathways (SSP2-4.5 and SSP5-8.5). The selected shared socioeconomic pathways correspond to forecasts of moderate and high radiative forcing intensity, respectively. The selected scenarios have been obtained from the Max Planck Institute for Meteorology's MPI-ESM1-2-HR global circulation model (Mauritsen et al., 2019).

The SSPs represent different socioeconomic development, emissions, and climate outcomes. In these scenarios, the first digit represents the socioeconomic development pathway, specifically SSP1 - sustainable development, SSP2 - medium pathway, and SSP5 - fossil-fueled development. The following two digits represent the degree of climate change, or intensity of additional radiative forcing caused by man-made greenhouse effects. Thus, SSP1-2.6 is an optimistic climate scenario, sometimes

referred to as Sustainability or Taking the Green Road pathway. It aims to keep global warming below 2°C (approximately +1.8°C) by 2100 by promoting sustainable growth, rapid technological progress, minimal reliance on fossil fuels, and efficient emissions reductions. Therefore, this scenario implies that measures to protect against climate change are being implemented. The intermediate (middle-of-the-road) SSP2-4.5 scenario supposes intermediate economic and population development, causing emissions to peak in the middle of the century and warming of roughly 2–3°C by the end of the century. Finally, the SSP5-8.5 scenario is considered a high-emissions fossil-fuelled pathway, and projects warming of about 4-5°C (approximately +4.4°C) by 2100, based on strong economic expansion and ongoing dependence on conventional energy sources. As a result, SSP5-8.5scenario is related to greater adverse effects, such as increased ecosystem stress, more frequent extreme events, and greater sea level rise.

3.5 Modelling the Species Distribution

In order to estimate possible present range of all investigated species and to project future range dynamics caused by changing climate, ensemble modelling was employed. Ensemble modelling has been demonstrated to improve predicting precision and decrease overfitting, particularly in models of species of conservation interest (Breiner et al., 2015), which is why this strategy was used.

To carry out ensemble modelling of *E. hungaricus* the biomod2 version 4.2-4 package in R was used (Thuiller et al., 2023). The subsequent five models were employed: Random Forest (RF), Maximum Entropy (MAXENT and MAXNET), Generalized Linear Model (GLM), and Generalized Boosted Model (GBM). The algorithms were tested on three pseudo-absence datasets, each including five iterations and 160 randomly chosen points (ten times higher number of original count) for each algorithm. To guarantee a reliable assessment of model performance, cross-validation was carried out 10 times by arbitrarily dividing the dataset into an 80% training set and 20% testing set.

In order to determine the performance of the model, the area bellow the Receiver Operating Characteristic Curve (ROC) (Jiménez-Valverde, 2012) and the True Skill Statistic (TSS) (Allouche et al., 2006) were used. For ensemble modelling solely models with TSS values greater than 0.7 were implemented. The highest ROC and TSS values demonstrated the higher predictive ability of Committee Averaging (EMca) (Mohajane et al., 2021), which led to its selection as the ensemble modelling technique for species *E. hungaricus*. A TSS-based threshold was employed to classify habitats into following two categories: (1) appropriate and (2) unsuitable. This threshold was established by comparing various thresholds and choosing the one that maximises the TSS (Thuiller et al., 2023). Additionally, the biomod2 software was utilised to evaluate how the range of species changed under various climate scenarios.

Species distribution models for *H. heimii* and *C. introflexus* were calibrated using several single algorithms applied in the *biomod2* v.4.2.4 R package, namely GeneralisedLinear Models (GLM), GeneralisedAdditive Models (GAM), GeneralisedBoosted Regression Models (GBM), Random Forest (RF) and Maximum Entropy (MAXNET) (Thuiller et al., 2009). These five different algorithms were used to improve modelling precision, and to take advantage of each of the individual model. Thus, GLM and GAM models are characterised by high interpretability, while other three models (GBM, RF, MAXNET) demonstrate considerable flexibility in modeling more complex non-linear relationships. More specifically, RF enables greater prognostic precision, GLM shows better comprehensibility, while GBM model correspond to an intermediate level. Furthermore, GBM and RF capture interactions among predictors by default, as oposed to GLM, GAM and MAXNET, where such interactions ought to be clearly specified.

In order to avoid subjective selection, no interactions were manually specified during model development. This allowed machine-learning algorithms to account for interactions inherently. Since solely presence-only data were used for the modelling, pseudo-absences were derived using *biomod2* (Thuiller et al., 2009), and each of the algorithms has been trained on three pseudoabsence sets of 20,000 arbitrarily selected points (approximately double the occurrence dataset) for species *C. introflexus* and 1800 randomly selected points for *H. heimii*. All datasets were evaluated using five independent model runs per dataset.

Evaluation of the given model was done based on TSS and AUC values; solely models that surpassed the 0.7 TSS threshold were selected for the ensemble modeling (Allouche et al., 2006; Jiménez-Valverde, 2011).

Ensemble models were created in *biomod2,* employing committee averaging (EMca) and the ensemble median (EMmedian) techniques (Thuiller et al., 2009). In accordance with ROC and TSS values, these methods show superior prognostic ability and therefore their use improves forecast accuracy and stability compared to the single-model strategy (Mohajane et al., 2021; Pantović et al., 2023). Both ensemble techniques were retained to increase model performance, as EMca focuses on consistency among models, while EMmedian provides combined predictions that are not as much influenced by outlying values (Huang et al., 2024; Zhang et al., 2026).

Based on TSS values, model outputs for species *C. introflexus* were categorised into three classes of suitability: (1) consensus-suitable, (2) model-supported suitable, and (3) unsuitable (Thuiller et al., 2009). Consensus-suitable areas are those that have EMca values higher than or equal to the TSS threshold of the EMca ensemble; model-supported suitable areas are those that have EMmedian values in between the TSS thresholds of the EMca and EMmedian ensemble models; and finally, unsuitable areas are those that have EMmedian values lower than the EMmedian TSS threshold.

According to the EMedian ensemble model's predictions and the TSS threshold applied for the species *H. heimii*, model outputs were categorised into four classes of suitability, namely: (1) Unsuitable, (2) Low/marginal suitability, (3) Moderate/model-supported suitability, and (4) High suitability.

Distinctions in suitability scores and variations in the percent of area coverage among the three classes of suitability, as ell as across all estimated projected climate pathways, were assesed in R using the Kruskal–Wallis test followed by the Dunn’s post hoc test (R Core Team, 2024).

4. RESULTS

4.1 Distribution modelling of *Entosthodon hungaricus*

The existence of *E. hungaricus* in Northern Serbia (Vojvodina province) was accurately predicted by every algorithm employed in this investigation. Other regions of Serbia were excluded from further tests due to a lack of appropriate substrates. Performance of algorithms that is the mean ROC and TSS scores for all single-algorithm models were 0.981 ± 0.041 and 0.958 ± 0.080, in the order given. Random Forest (RF) outperformed other models in terms of ROC and TSS scores, succeeded by GBM, GLM, MAXNET, and MAXENT (Figure 10).

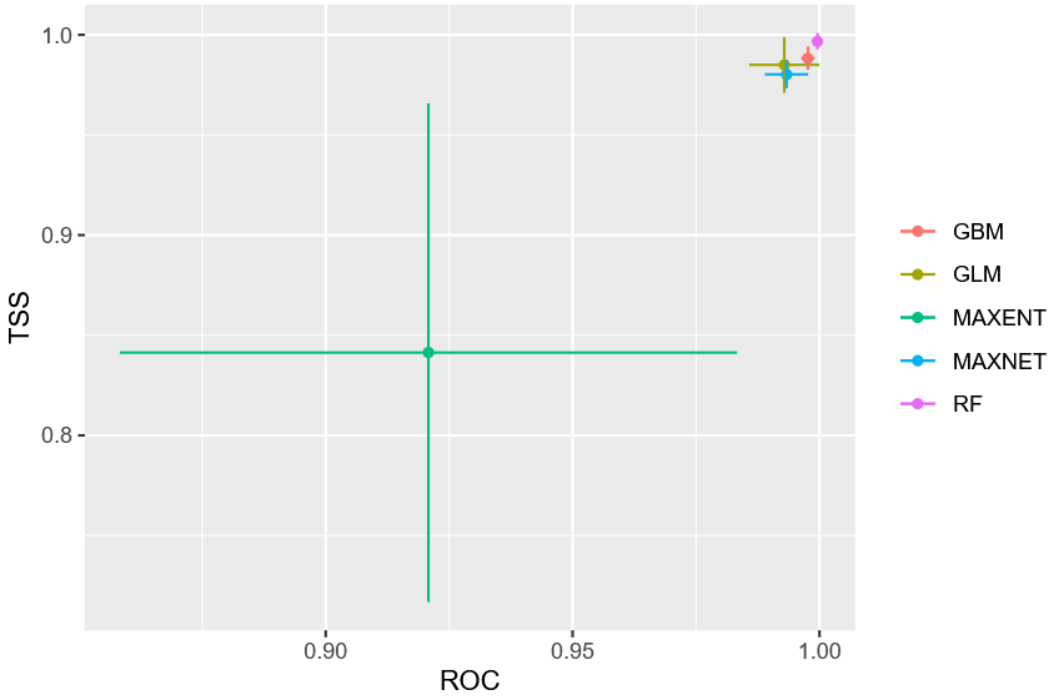

Figure 10. Single-algorithm performace. Mean ROC and TSS values of all single-algorithm models used for modelling distribution of *Entosthodon hungaricus*, summarizing overall predictive performance. Points represent median algorithm performance, lines represent ranges.

Nine GLM, eleven GBM, nine MAXENT, twelve MAXNET, and nine RF models were included in the ensemble model, which was developed using single-model approaches with a TSS greater than 0.7. Compared to the single-model approaches, the ensemble's ROC and TSS for the committee averaging model (EMca) were 0.997 and 0.99, correspondingly, demonstrating a superior predictive accuracy (Figure 11).

The ensemble model estimated that 1285 km^2 (approximately 1.7% of the country's territory) would be a suitable area for *E. hungaricus* under current climate conditions (1981–2010) (Figure 12). This climate suitability is marginally higher than the present known distribution of the investigated species. As *E. hungaricus* is a halophyte species, distribution models are not greatly impacted by halomorphic soil type (HAL) in the time span. Certain climatic variables above the current saline areas, under different climate scenarios and altitudes, showed little or no influence on the species' occurrence.

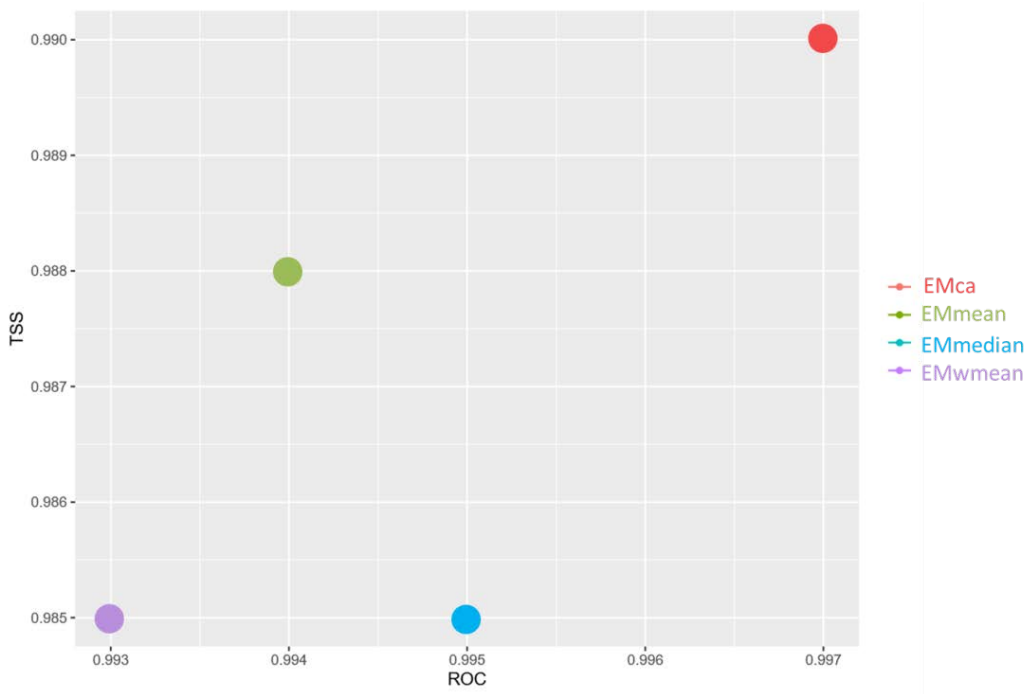

Figure 11. Ensemble model performace. Mean ROC and TSS values of four tested ensemble models, summarizing overall predictive performance of each technique. As EMca showed superior predictive performance, it was selected for modelling distribution of *Entosthodon hungaricus*.

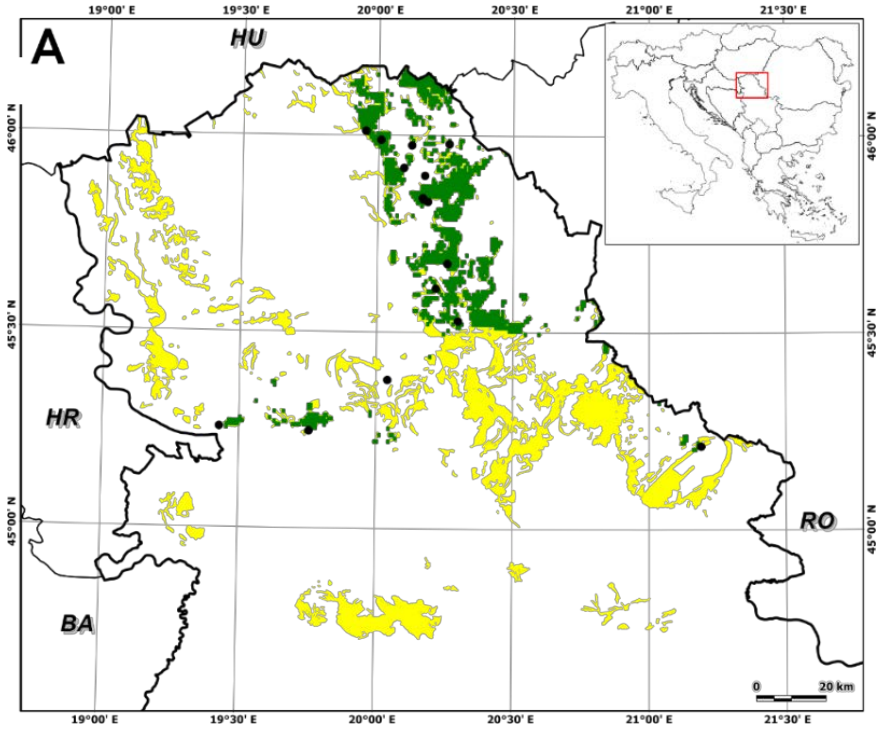

Figure 12. Current potential distribution of *Entosthodon hungaricus* in Serbia, with the location of Vojvodina in SE Europe and Serbia. Yellow indicates suitable substrate areas, while green represents optimal requirements for the current distribution of this species. Points indicate recent ocurrence records used for modelling (BA-Bosnia and Herzegovina, HU-Hungary, HR-Croatia, RO-Romania).

Based on the Pearson's correlation coefficients, a total of eight variables that had correlation coefficients (r) lower than 0.7 have been selected for modelling: six climatic, one topographic and one soil-related factor. Among all analysed predictor variables, a soil substrate (halomorphic soils) was identified as the key predictor of the investigatedspecies' distribution. Among the analysed bioclimatic predictors, the one with the greatest impact on species distribution was the precipitation of the driest month (bio14) that exhibited mean relative importance of 0.024 ± 0.007, succeeded by altitude (ALT) with 0.003 ± 0.000, mean diurnal temperature range (bio2) with 0.003 ± 0.100, the precipitation seasonality (bio15) with 0.002 ± 0.00, the mean daily air temperature of the warmest quarter (bio10) with 0.001 ± 0.000, the precipitation amount of the wettest month (bio13) with 0.001 ± 0.000, and the isothermality (bio3) with 0.001 ± 0.000 (Table 2, Figure 13). The response curve for these variables, indicates that the occurrence probability of *E. hungaricus* increases with the soil salinity (Figure 14).

Table 2. Contribution of predictor variables to model performance of *Entosthodon hungaricus*.

Variable	Mean	Min	Max	SD	SE	Median
ALT	0.002864	0.002732	0.002993	0.000130	7.535914	0.002867
HAL	0.948065	0.890649	0.977734	0.049733	0.028713	0.975812
BIO10	0.001405	0.001209	0.001705	0.000264	0.000152	0.001302
BIO13	0.001249	0.000871	0.001544	0.000344	0.000199	0.001334
BIO14	0.024207	0.019393	0.032463	0.007183	0.004147	0.020765
BIO15	0.002032	0.001689	0.002268	0.000304	0.000175	0.002138
BIO2	0.002825	0.002524	0.003138	0.000307	0.000177	0.002812
BIO3	0.000504	0.000374	0.000597	0.000116	6.698009	0.000541

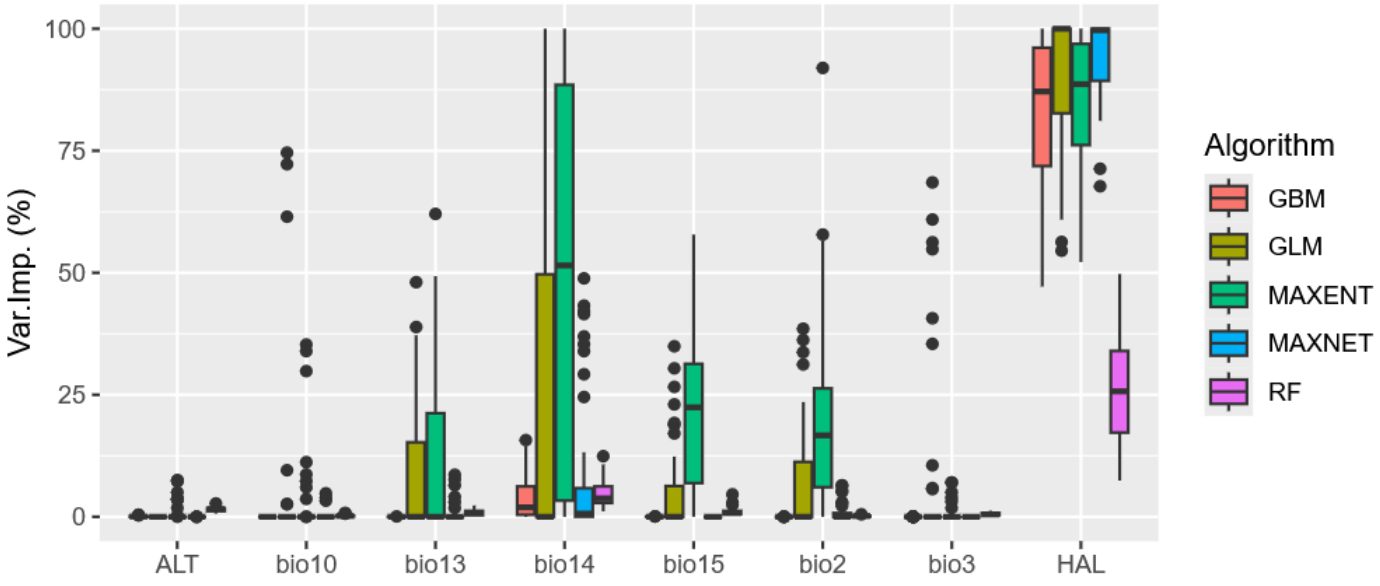

Figure 13. Relative contributions (%) of eight selected environmental variables to all single-algorithm distribution models developed for *Entosthodon hungaricus.*

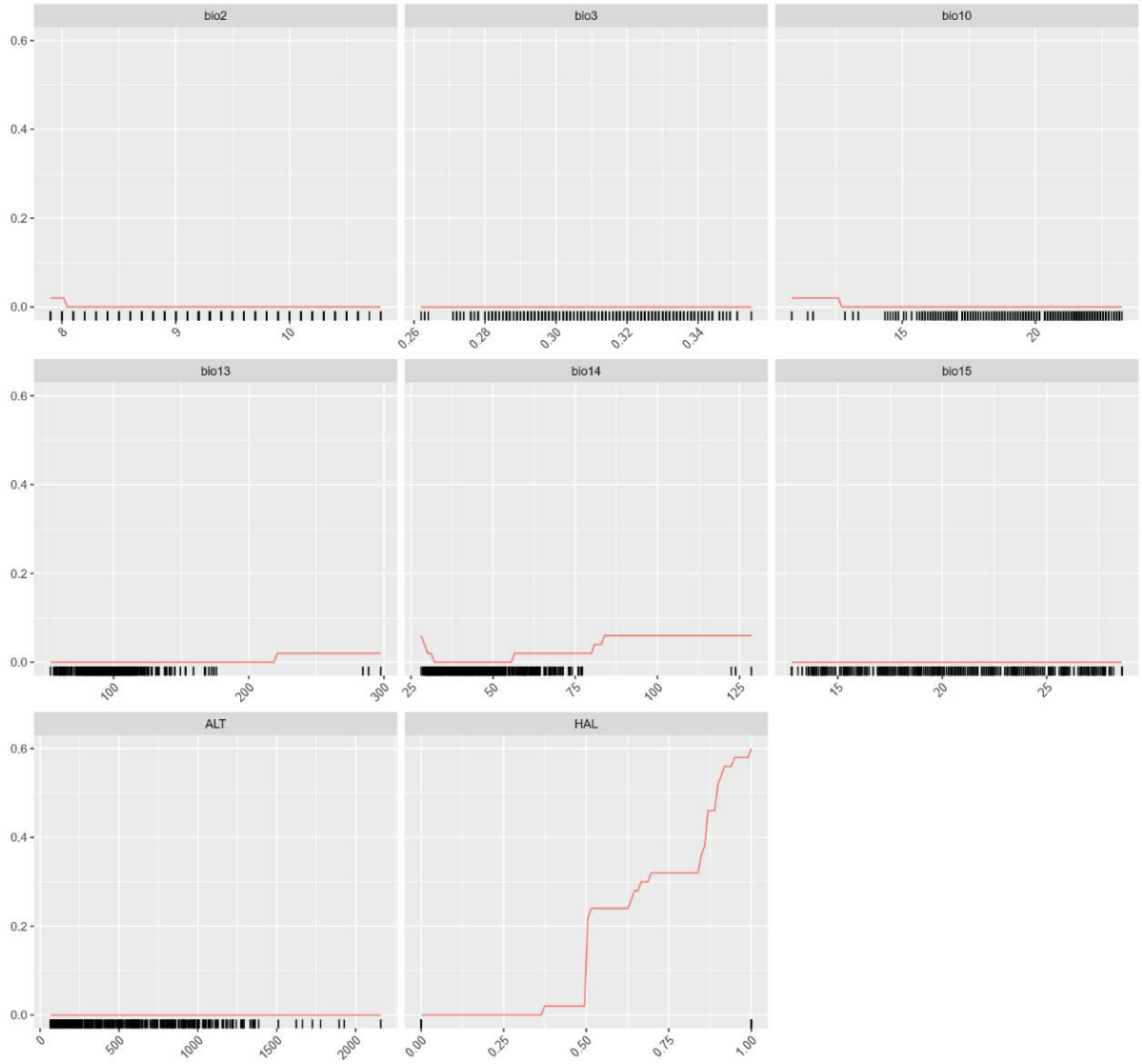

Figure 14. Response curves of *Entosthodon hungaricus* for the following variables: (A) BIO2 (B) BIO3 (C) BIO10 (D) BIO13 (E) BIO14 (F) BIO15, (G) Altitude and (H) soil type. Line indicates fitted values estimated from a Emca model.

Specifically, it is anticipated that suitable habitat for *E. hungaricus* will decline by 75.0 ± 27.5% (SSP1–2.6, 2041–2070), 74.0 ± 42.7% (SSP1–2.6, 2071–2100), 72.9 ± 21.9% (SSP5–8.5, 2041–2070), and 92.0 ± 15.8% (SSP5–8.5, 2071–2100) (Table 3, Figures 15–18).

Table 3. Projected decline of suitable areas (%) based on SDM under two climate change scenarios

SSP Scenario	Period	Mean	Min	Max	SD	SE
ssp126	2055	-70.31125	-100	-29.883	33.035895	16.517947
ssp126	2085	-71.51725	-99.377	-0.233	47.712818	23.856409
ssp585	2055	-55.75850	-100	4.125	44.463414	22.231707
ssp585	2085	-86.20625	-100	-45.058	27.432387	13.716193

According to data obtained under future climate scenarios, the mid-term models' forecast range decreased under the low-emission scenario, with average decreases that spanned from −70.3 ± 33.0% in SSP1–2.6 scenario for 2041–2070 (Figure 15) to −71.52 ± 47.7% in SSP1–2.6 scenario for 2071–2100 (Figure 16).

Based on the findings of range shifts in the case of the pessimistic pathway, *E. hungaricus* is expected to undergo substantial decrease of range under projected climate scenarios, with average decreases spanning from −55.8 ± 44.4% in the SSP5–8.5 scenario for the 2041–2070 interval (Figure 17) to −86.28 ± 27.4% in the SSP5–8.5 scenario for the 2071–2100 interval (Figure 18). Under projected climate pathways, the loss of favorable ecosystems is likely the main cause of these changes.

On the other hand, it is expected that under future climate circumstances, some areas that are at present unsuitable for the species will transform into favourable, with a range extension of 4.7 ± 5.6% (SSP1–2.6, 2041–2070), 2.5 ± 5.1% (SSP1–2.6, 2071–2100), 17.1 ± 23.8% (SSP5–8.5, 2041–2070), and 5.8 ± 11.7% (SSP5–8.5, 2071–2100) (Figure 19).

In terms of future habitat appropriateness, the various global circulation models (GCMs) provided differing forecasts of changes, including both declines and increases in suitable areas. The biggest reduction in suitable habitat area was recorded for UKESM1-0-LL model across both timeframes and climate pathways, whereas the greatest gain, also across both timeframes and climate pathways, was detected for the IPSL-CM6A-LR model (Figure 15–19).

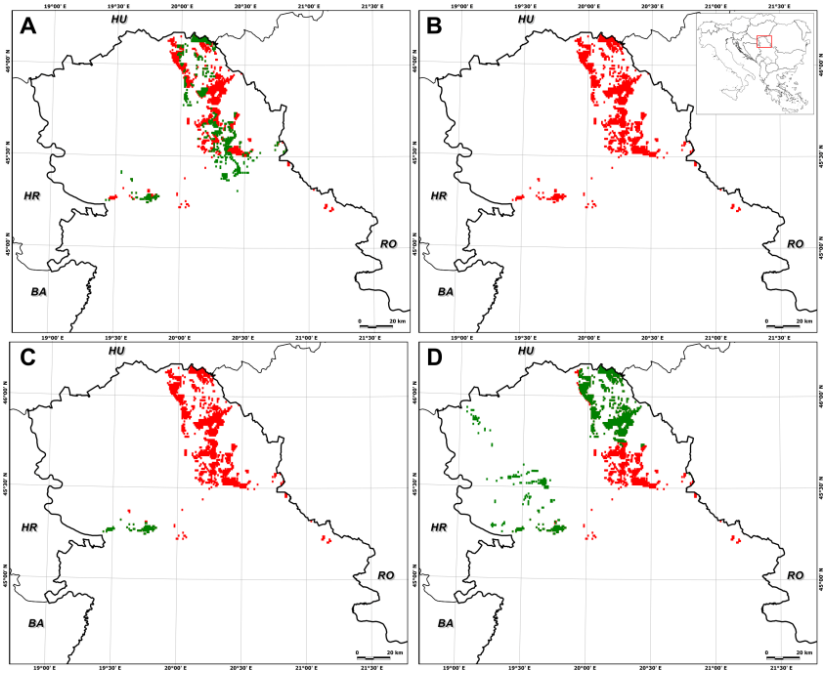

Figure 15. Projected mid-term distribution of *Entosthodon hungaricus* in Serbia for **2041-2070** under a **low-emission** climate change scenario. Projections were generated using four global circulation models: **(A)** GFDL-ESM4; **(B)** UKESM1-0-LL; (**C**) MPI-ESM1-2HR; (**D**) IPSL-CM6A-LR. Red denotes areas expected to lose climatic suitability, whereas green represents areas projected to retain suitable conditions for the species.

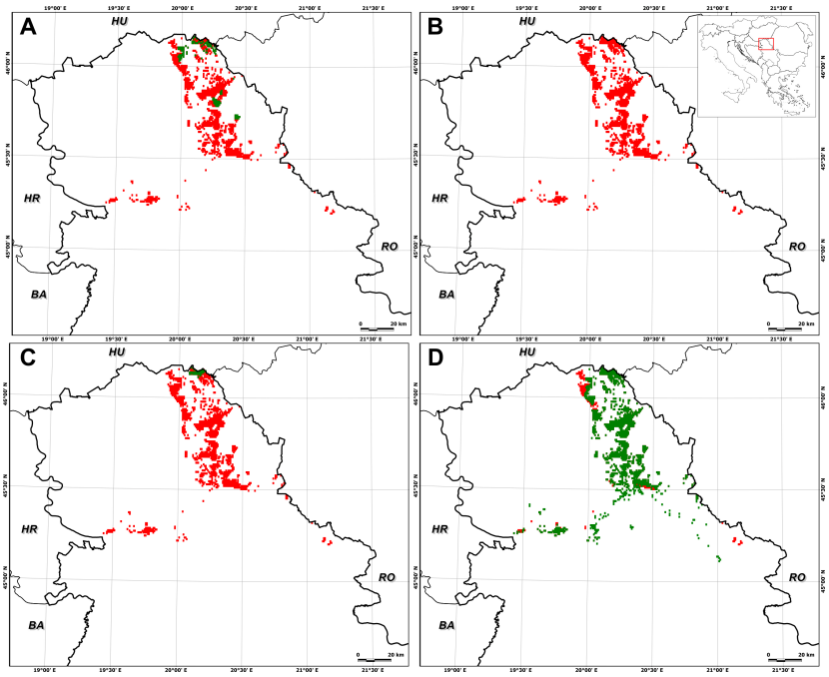

Figure 16. Projected long-term distribution of *Entosthodon hungaricus* in Serbia for **2071-2100** under a **low-emission** climate change scenario. Projections were generated using four global circulation models: **(A)** GFDL-ESM4; **(B)** UKESM1-0-LL; (**C**) MPI-ESM1-2HR; (**D**) IPSL-CM6A-LR. Red denotes areas expected to lose climatic suitability, whereas green represents areas projected to retain suitable conditions for the species.

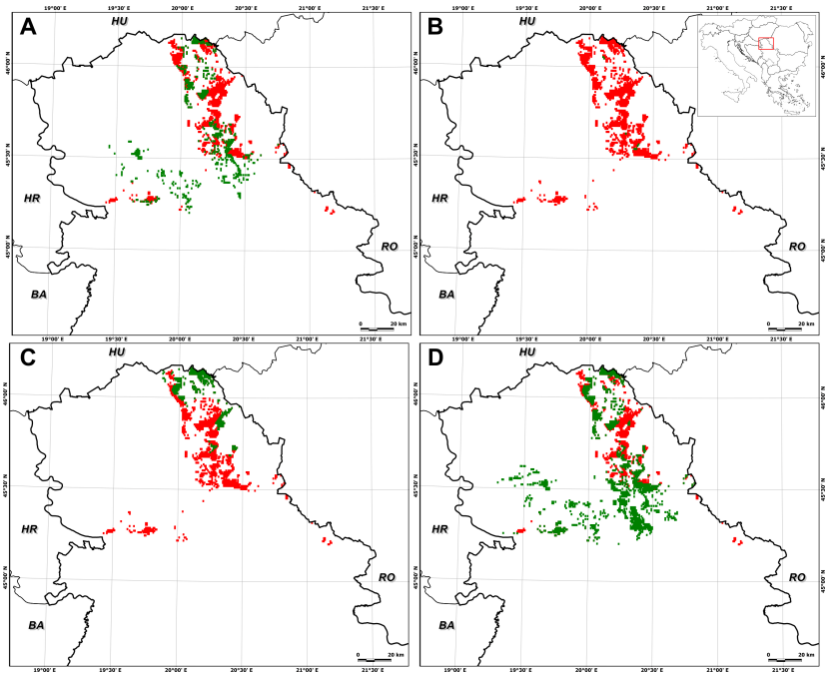

Figure 17. Projected mid-term distribution of *Entosthodon hungaricus* in Serbia for **2041–2070** under a **high-emission** climate change scenario. Projections were generated using four global circulation models: **(A)** GFDL-ESM4; **(B)** UKESM1-0-LL; (**C**) MPI-ESM1-2HR; (**D**) IPSL-CM6A-LR. Red denotes areas expected to lose climatic suitability, whereas green represents areas projected to retain suitable conditions for the species.

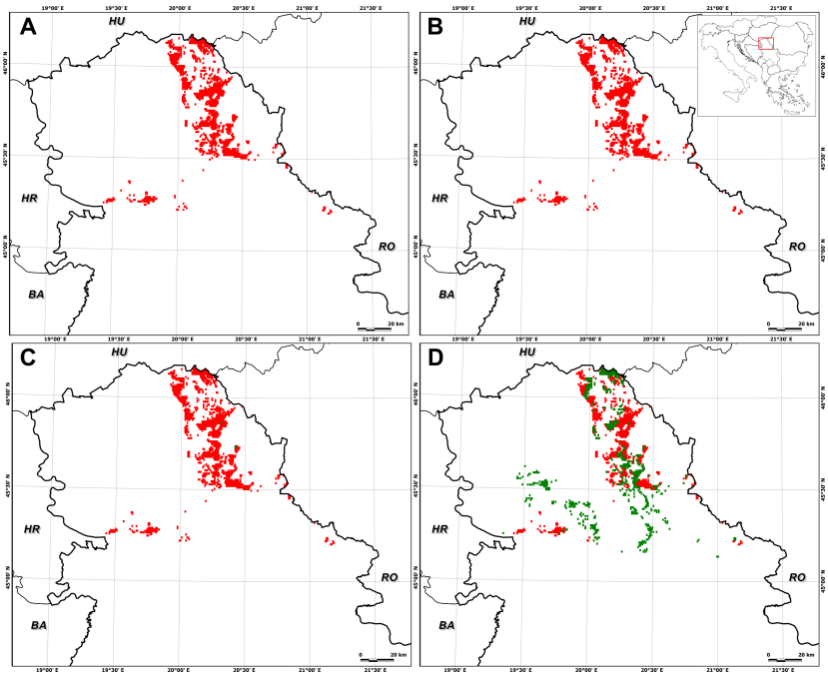

Figure 18. Projected long-term distribution of *Entosthodon hungaricus* in Serbia for **2071–2100** under a **high-emission** climate change scenario. Projections were generated using four global circulation models: **(A)** GFDL-ESM4; **(B)** UKESM1-0-LL; (**C**) MPI-ESM1-2HR; (**D**) IPSL-CM6A-LR. Red denotes areas expected to lose climatic suitability, whereas green represents areas projected to retain suitable conditions for the species.

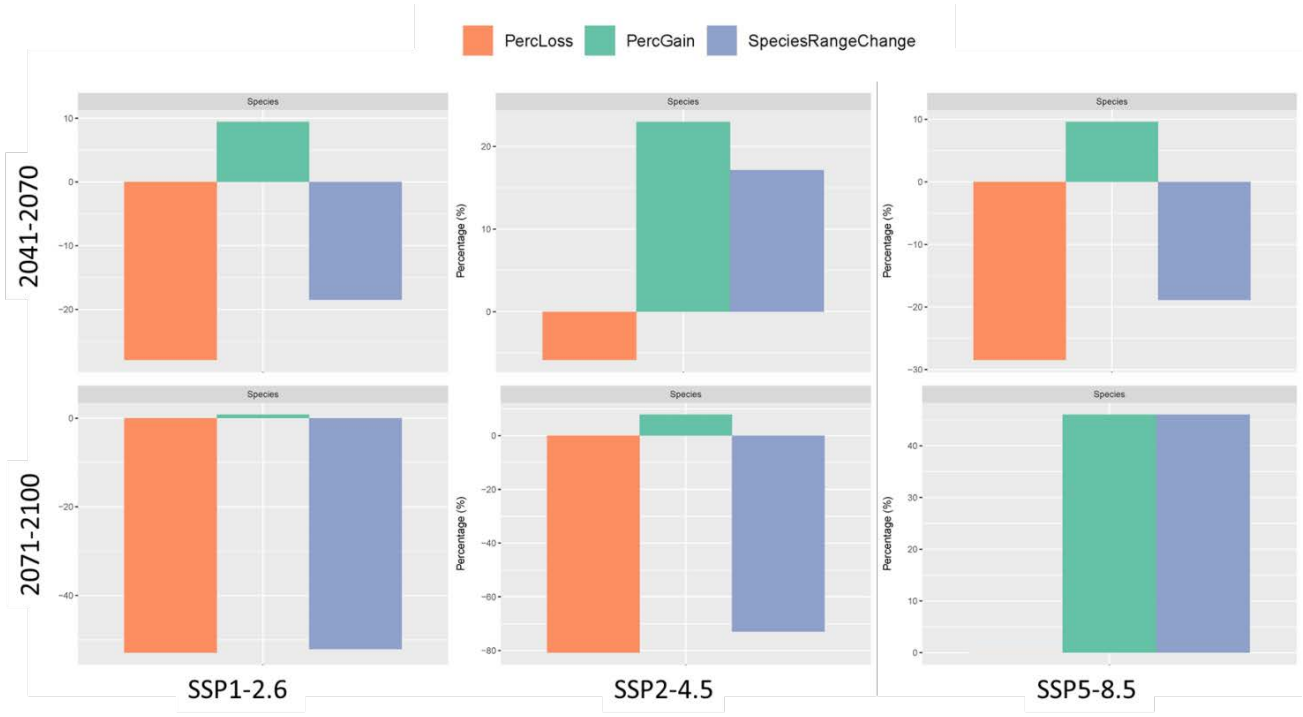

Figure 19. Prediction of lost and gained suitable area and total range change (%) for the species *Enthostodon hungaricus* in three different climate change pathways (SSP1-2.6, SSP2-4.5 and SSP5-8.5) during two timeframes (2041-2070 and 2071-2100) using EMmedian ensemble model.

4.2. Distribution modelling of *Hennediella heimii*

Following data cleaning, merging, and thinning, a total of n = 628 European occurrences of *H. heimii* have been kept to model the species' posibble range. With comparatively similar ROC and TSS values, all algorithms that have been used in this investigation successfully predicted the occurrence of *H. heimii* in Europe. The mean ROC and TSS scores in single-model approaches were 0.982 ± 0.0001 and 0.899 ± 0.006, in the order given (Figure 20). The models with the highest ROC and TSS scores were Random Forest (RF), succeeded by Generalized Boosted Regression (GBM), Generalized Additive Model (GAM), MAXNET and Generalized Linear Model (GLM).

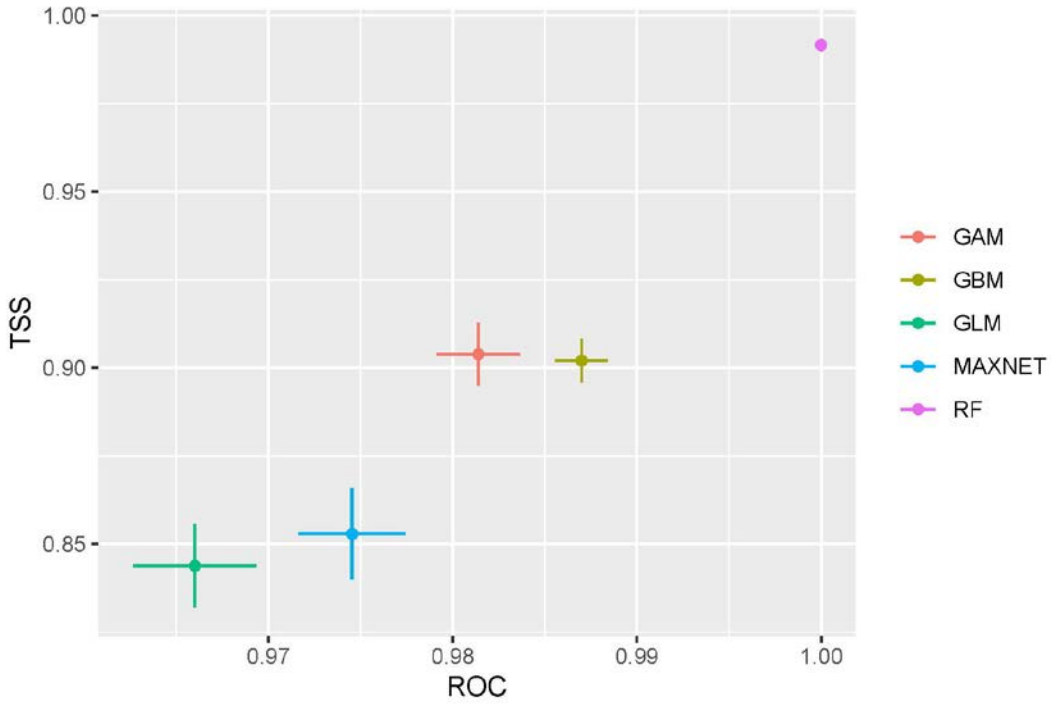

Figure 20. Single-algorithm performace. Mean ROC and TSS scores of all single- model approaches employed for modelling distribution of *Hennediella heimii*, summarizing overall predictive performance. Points represent median algorithm performance, lines represent ranges.

Since each individual model's TSS was higher than 0.7, all of them have been used in the ensemble modelling. The ensemble model using median had the highest ROC and TSS scores among all ensemble models of 0.982 and 0.917, respectively (Figure 21). This suggests that ensemble models have greater predictive potential than individual models. TSS value of the ensemble model using median was used to create maps of species habitat suitability.

According to the EMedian ensemble model's predictions and the TSS threshold applied to the current climate (1970–2000), the highly suitable habitat area for *H. heimii* was 48,708.8 km² (0.52% of the total area). The EMmedian values between the TSS threshold of the EMmedian ensembles and its 95th percentile indicated that the moderate/model-supported suitable area was 538,224.3 km² (5.71% of the total area). Based on the EMmedian values between the 95th and 75th percentiles of the EMmedian ensembles, the low/marginally suitable area spanned 2,081,463.2 km² (22.07% of the total area), whereas unsuitable areas comprised 6,763,064.4km² (71.70% of the total area) (Figure 22).

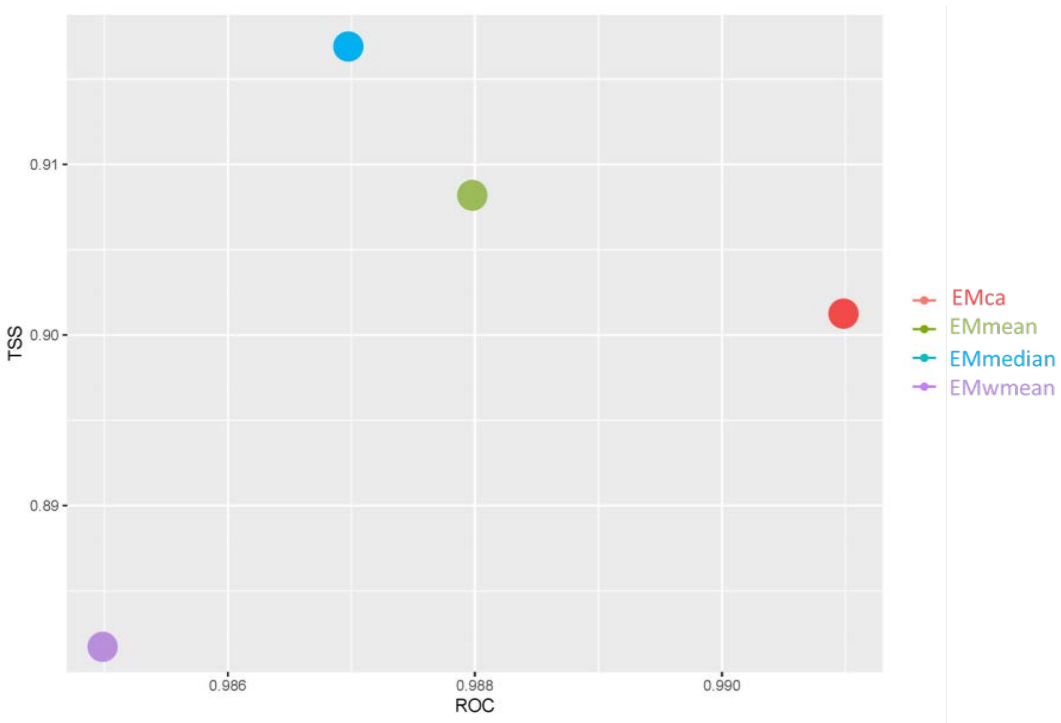

Figure 21. Ensemble model performace. Mean ROC and TSS values of four tested ensemble models, summarizing overall predictive performance of each technique. As EMedian showed superior predictive performance, it was selected for modelling distribution of *Hennediella heimii*.

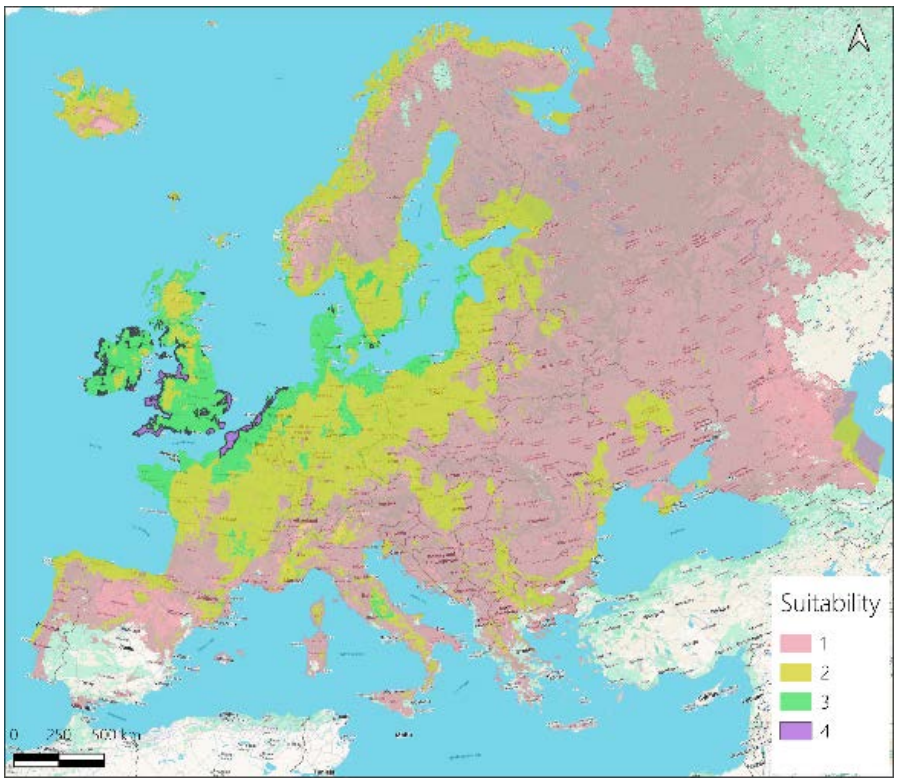

Figure 22. Map of Europe showing projected current suitable habitat area for *Hennediella heimii* (1970–2000). Suitability classes: 1–Unsuitable, 2–Low/ marginal suitability, 3–Moderate / model-supported suitability and 4-High suitable.

Regarding the contribution of bioclimatic variables, mean diurnal range (BIO2) was the most significant predictor influencing the possible distribution of the examined species among the seven predictor variables, with a mean relative importance of 0.376 ± 0.011, succeeded by 0.220 ± 0.006 for isothermality (BIO3), 0.193 ± 0.0003 for mean temperature of driest quarter (BIO9), 0.094 ± 0.004 for mean temperature of warmest quarter (BIO10), 0.061 ± 0.001 for precipitation of the warmest quarter (BIO18), 0.059 ± 0.001 for mean temperature of wettest quarter (BIO8), and 0.021 ± 0.002 for precipitation seasonality (BIO15), respectively (Figure 23, Table 4).

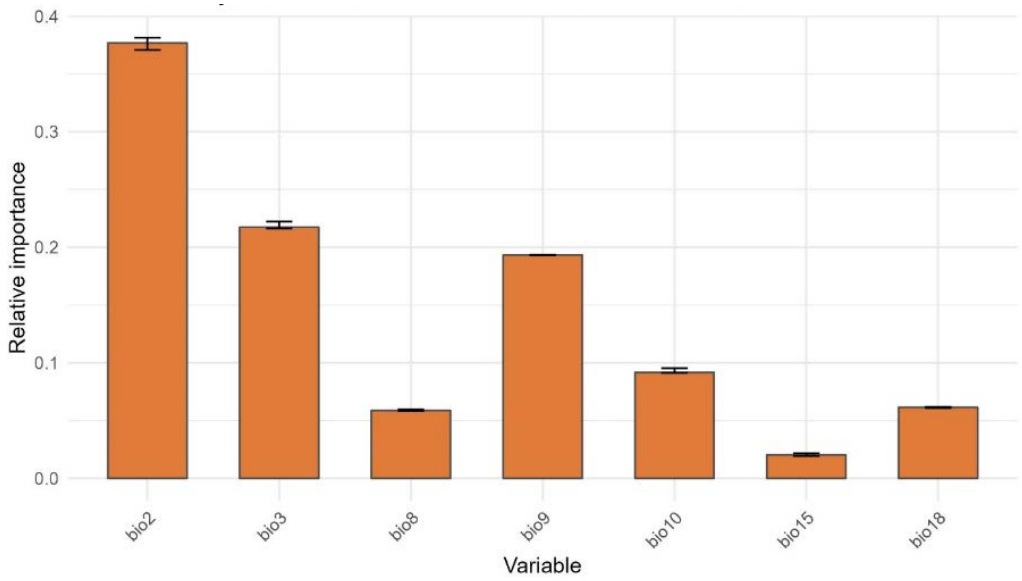

Figure 23. Relative contributions of bioclimatic variables that determine the posibble distribution of *Hennediella heimii* in Europe. Abbreviations: BIO2 – Mean Diurnal Range; BIO3 – isothermality; BIO9 – mean temperature of driest quarter; BIO10- mean temperature of warmest quarter; BIO18 – Precipitation of Warmest Quarter; BIO8 – mean temperature of wettest quarter, BIO15 – Precipitation Seasonality.

Table 4. Contribution of predictor variables to model performance of *Hennediella heimii*.

Expl.var	Mean	Min	Max	SD	SE	Median
BIO2	0.375708	0.364365	0.385859	0.010796	0.006233	0.376900
BIO3	0.219966	0.215305	0.227270	0.006405	0.003698	0.217324
BIO8	0.059008	0.057947	0.060334	0.001215	0.000702	0.058744
BIO9	0.193297	0.192985	0.193590	0.000303	0.000175	0.193317
BIO10	0.093815	0.090782	0.098938	0.004461	0.002576	0.091726
BIO15	0.020609	0.018487	0.023124	0.002343	0.001353	0.020215
BIO18	0.061330	0.060260	0.062350	0.001046	0.000604	0.061379

In all projected climate pathways, highly suitable regions accounted on average for 0.22 ± 0.0.9% of the overall area, moderate/model-supported suitable regions for 5.94 ± 0.46%, the low/marginally suitable regions for 25.06 ± 3.78%, and unsuitable regions for 68.78±3.84% of the total area. The Kruskal-Wallis test showed substantial disparities in future suitability levels between classes ($H = 22.5$, $df = 3$, $p < 0.001$). The outcomes of the post hoc Dunn test showed that the unsuitable class showed great differences from both the highly suitable class ($Z = 2.35$, $p < 0.05$) and the low/marginally suitable moderate/model-supported suitable ($Z = -2.24$, $p < 0.05$), whereas no

statistically significant difference was detected between unsuitable and the moderate/model-supported suitable classes (Z = −0.96, p > 0.05). Statistically significant differences were also noted between low/marginally suitable and highly suitable class (Z = 4.58, p < 0.0001) and moderate/model-supported suitable and highly suitable classes (Z = 3.30, p < 0.0001).

In all examined future scenarios, there was a general decrease in *H. heimii* highly suitable, moderate/model-supported suitable and unsuitable habitats, while low/marginally suitable habitats expanded. Figure 24 presents detailed changes across the individual climate scenarios. More precisely, in comparison to the present climate conditions, highly suitable areas decreased by −61.62 ± 16.84% on average, moderate/model-supported suitable e areas by −55.67 ± 18.5%, and unsuitable areas by −16.33 ± 9.84%, while low/marginal suitable increased by 0.009± 9.34%. Regarding differences among future scenarios, post hoc Dunn testing indicated that the unsuitable class differed considerably from both the highly suitable class (Z = 5.12, p < 0.0001) and the moderate/model-supported suitable (Z = 3.41, p < 0.001), whereas no statistically significant difference was detected across unsuitable and the low/marginally suitable classes (Z = 1.71, p > 0.05). Statistically significant differences were also noted between low/marginally suitable and highly suitable classes (Z = 3.41, p < 0.0001).

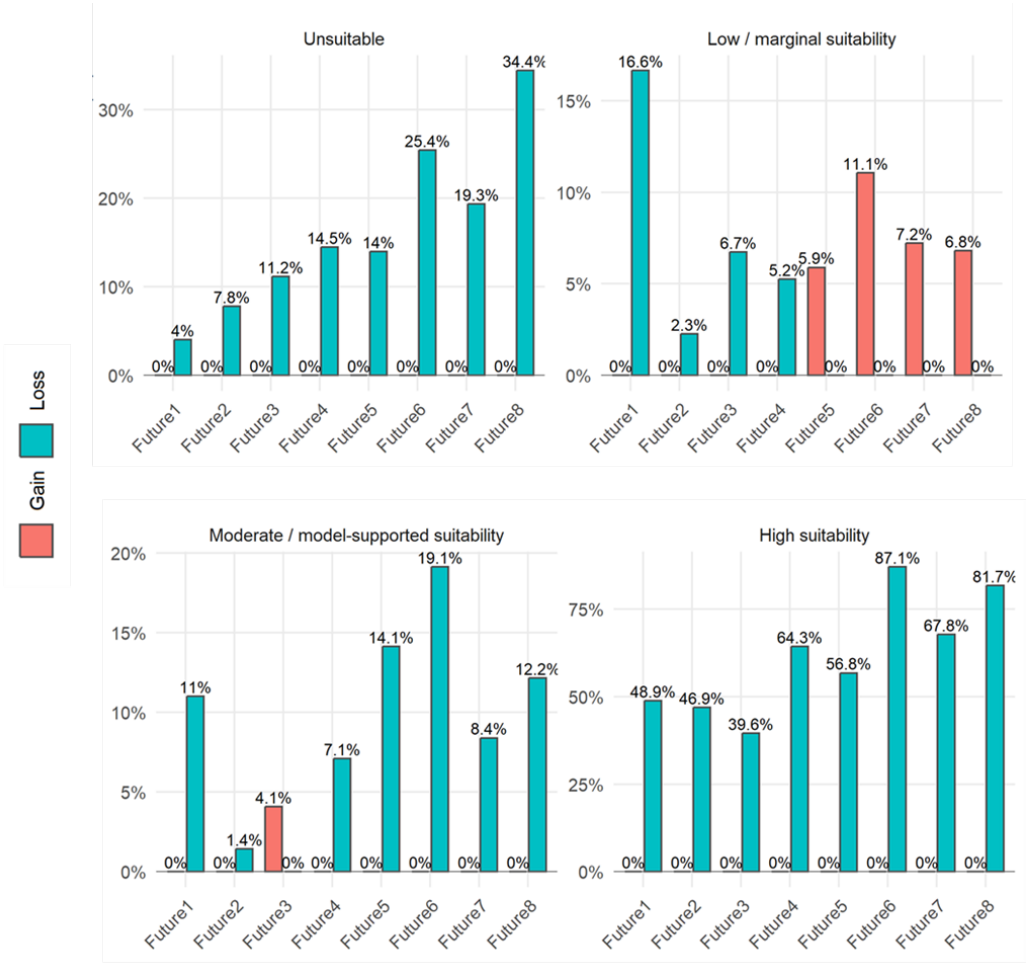

Figure 24. Changes in suitable habitats of *Hennediella heimii* under projected climate change pathways relative to present climatic conditions, expressed as percentages of habitat gain and loss. Abbreviations: Future1 – SSP2–4.5(21-40); Future2 – SSP5–8.5(21-40); Future3 – SSP2–4.5(41-60); Future4 – SSP5–8.5(41-60); Future5 – SSP2–4.5(61-80); Future6 – SSP5–8.5(61-80); Future7 – SSP2– 4.5(81–100); Future8 – SSP5–8.5(81–100).

There were no statistically supported variations in the percentage variation throughout the examined projected climatic pathways, according to the Kruskal-Wallis test for every suitability class (high suitable: H = 7, df = 7, p = 0.429; moderate/model-supported suitable: H = 7, df = 7, p = 0.429; low/marginal suitable: H = 7, df = 7, p = 0.429) and unsuitable: H = 7, df = 7, p = 0.429).

According to the Kruskal-Wallis test for each suitability class (high suitability: H = 7, df = 7, p = 0.429; moderate/model-supported suitability: H = 7, df = 7, p = 0.429; low/marginal suitability: H = 7, df = 7, p = 0.429) and unsuitable: H = 7, df = 7, p = 0.429), there were no statistically supported variations in the percentage variation throughout the examined climatic pathways.

The assessment of changes in species range showed a major reduction in highly suitable habitats (Figure 25). Under the medium-emission pathway (SSP2–4.5), the highly suitable range exhibited average downward trend of −48.85% for 2021–2040 (Figure 25: A1), −39.56% for 2041–2060 (Figure 25: A2), −56.77% for 2061–2080 (Figure 25: A3), and −67.78% for 2081–2100 (Figure 25: A4). Under the high-emission pathway (SSP5–8.5) for the same periods, a decline in the average area of highly suitable habitats was noted, from −46.93% in 2021–2040 (Figure 25: B1), −64.32% in 2041–2060 (Figure 25: B2), −87.08% in 2061–2080 (Figure 25: B3), and −81.69% by 2081–2100 (Figure 25: B4).

A downward trend in moderate/model-supported suitable areas was also observed in the assessment of changes of species' range in all but one scenario. The reduction in area for moderate/model-supported suitable regions was smaller than for highly suitable habitat. Under the medium-emission scenario (SSP2–4.5), the prediction range for moderate/model-supported suitable areas showed average declines of −11.00% for 2021–2040 (Figure 25: A1), −14.14% for 2061–2080 (Figure 25: A3), and −8.96% for 2081–2100 (Figure 25: A4), while there was an increase of 4.09 % for 2041–2060 (Figure 25: A2). Under the high-emission pathway (SSP5–8.5) for the same timeframes, a decrease in the average area of suitable habitats was noted, from −1.44% in 2021–2040 (Figure 25: B1), −7.10% in 2041–2060 (Figure 25: B2), −19.13% in 2061–2080 (Figure 25: B3), to −12.15% by 2081–2100 (Figure 25: B4).

For low/marginally suitable regions, the assessment of changes in species range indicated a decline for 2021–2040 and 2041–2060 periods under both the medium-emission (SSP2–4.5) and high-emission pathways (SSP5–8.5), while both scenarios exhibited an expansion in area during the 2061–2080 and 2081–2100 periods. Under the medium-emission pathway (SSP2–4.5), the prediction range for low/marginally suitable area showed average reduction of −16.64% for 2021–2040 (Figure 25: A1) and of −6.74% for 2041–2060 (Figure 25: A2), while there was an increase of 5.89% for 2061–2080 (Figure 25: A3) and 7.21% for 2081–2100 (Figure 25: A4). Under the high-emission pathway (SSP5–8.5) for the same timeframe, a decline in the average area of suitable habitats was noted, from −2.27% in 2021–2040 (Figure 25: B1), −5.25% in 2041–2060 (Figure 24: B2), while there was an increase of 11.06% in 2061–2080 (Figure 25: B3), to 6.81% by 2081–2100 (Figure 25: B4).

Unsuitable areas also decreased across all periods and both scenarios. Under the medium-emission pathway (SSP2–4.5), the unsuitable prediction range showed average downward trend of −4.03% for 2021–2040 (Figure 25: A1), −11.16% for 2041–2060 (Figure 25: A2), −13.99% for 2061–2080 (Figure 25: A3), and −19.34% for 2081–2100 (Figure 25: A4). Under the high-emission pathway (SSP5–8.5) for the same timeframes, a reduction in the average area of unsuitable habitats was noted, from −7.81% in 2021–2040 (Figure 25: B1), −14.47% in 2041–2060 (Figure 25: B2), −25.41% in 2061–2080 (Figure 25: B3), and −34.42% by 2081–2100 (Figure 25: B4).

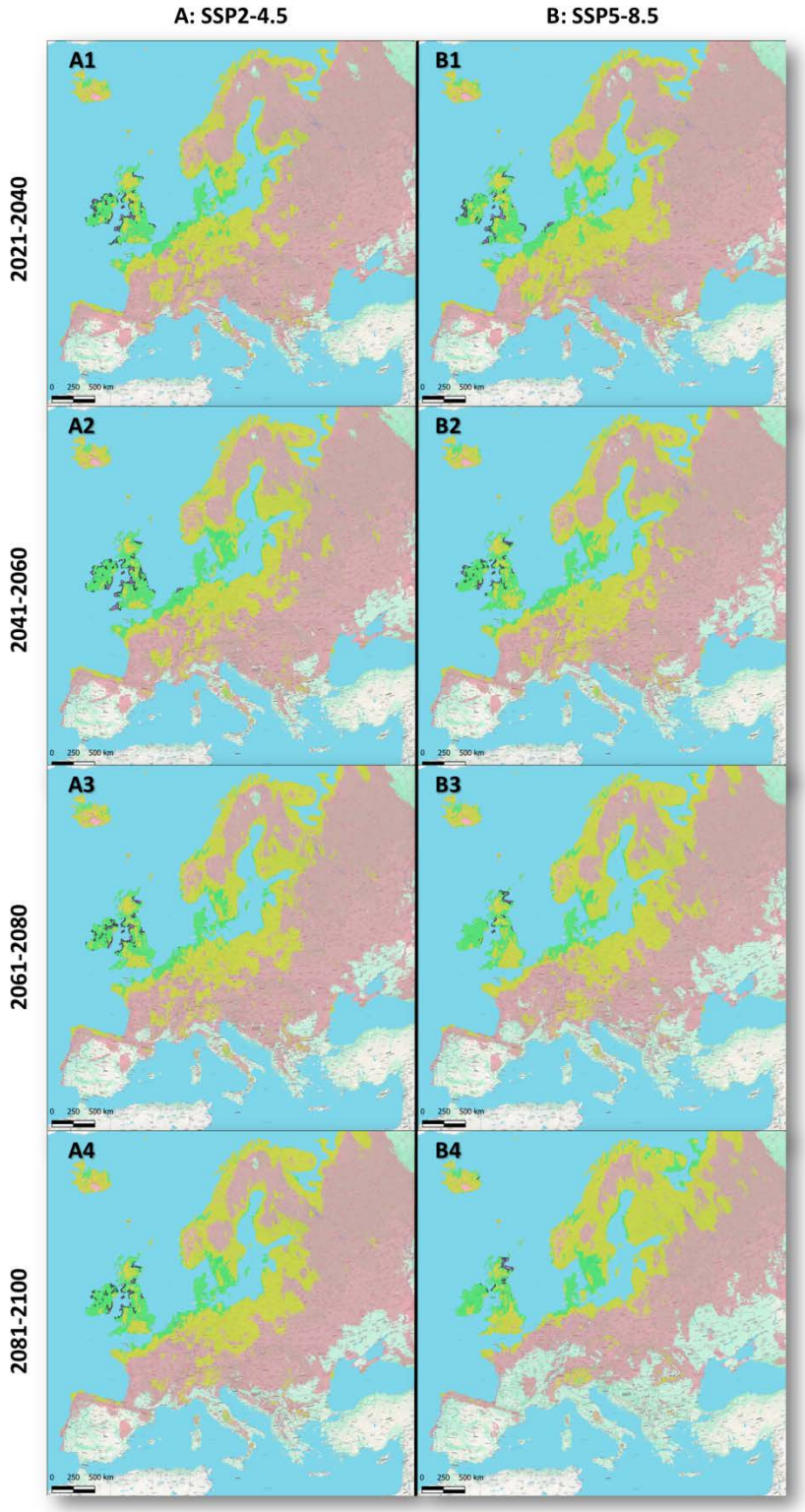

Figure 25. Projected shifts in the European distribution of *Hennediella heimii* under two climate-change pathways: a moderate-emission pathway **(A)** and high-emission pathway **(B)** for four timeframes (1: 2021–2040; 2: 2041–2060; 3: 2061–2080 and 4: 2081–2100). Habitat suitability is classified as: 1 – Unsuitable, 2–Low / marginal suitability, 3–Moderate / model-supported suitability and 4-High suitability.

4.3. Distribution modelling of *Campylopus introflexus*

Following data cleaning, merging, and thinning, a total of n = 12,385 European occurrence records of *C. introflexus* were kept to model the species' posibble range. With comparatively similar ROC and TSS scores, all models used in this investigation successfully predicted the existence of *C. introflexus* in Europe. The mean ROC and TSS scores across single-models approaches were 0.979 ± 0.003 and 0.896 ± 0.009, in the order given. The models with the highest ROC and TSS values were Random Forest (RF), succeeded by Generalized Boosted Regression (GBM), Generalized Additive Model (GAM), Generalized Linear Model (GLM), and MAXNET (Figure 26).

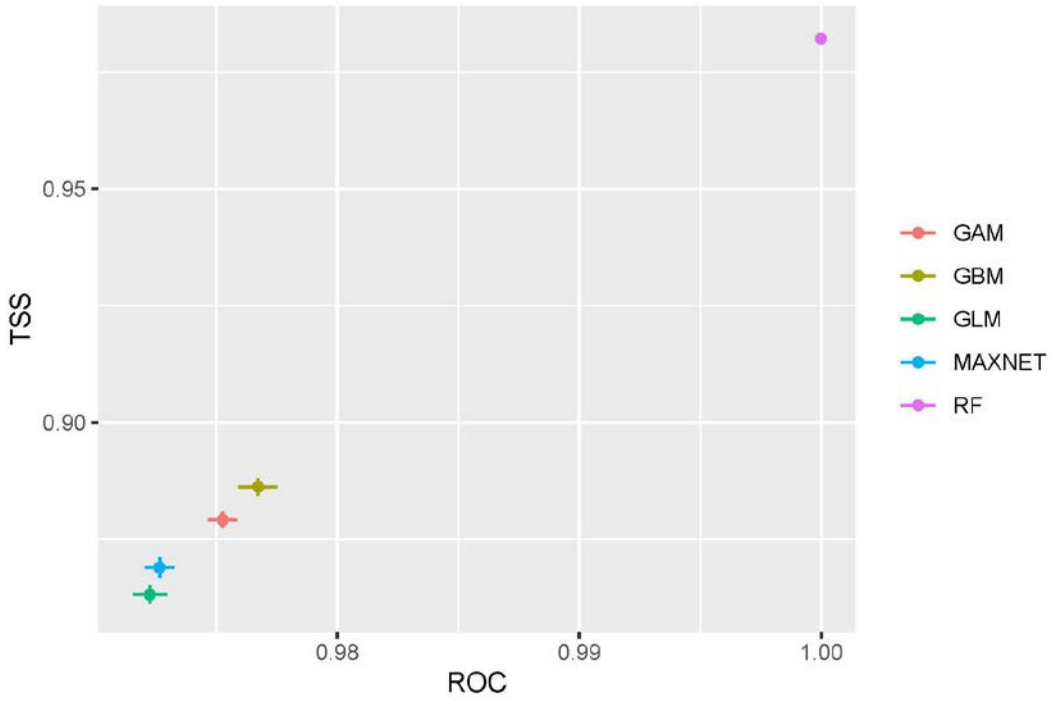

Figure 26. Single-algorithm performace. Mean ROC and TSS scores of all single- model approaches employed modelling distribution of *Campylopus introflexus*, summarizing overall predictive performance. Points represent median algorithm performance, lines represent ranges.

Since each individual model's TSS was higher than 0.7, all of them have been used for the ensemble modelling. The ensemble model using committee averaging had ROC and TSS scores of 0.991 and 0.917, while the ensemble model using the median had ROC and TSS scores of 0.983 and 0.892, in the order given (Figure 27). This suggests that ensemble models have greater predictive potential than individual models.

According to the EMca ensemble model's predictions and the TSS threshold applied to the current climate (1970–2000), the consensus-suitable area for *C. introflexus* was 403,954.9 km² (7.39% of the overall area). The EMmedian scores in between the TSS thresholds of the EMca and EMmedian ensemble models indicated that the model's supported suitable area, was 77,459.1 km² (1.42% of the total area), whereas unsuitable areas comprise 4,982,851.1 km² (91.19% of the overall area) (Figure 28).

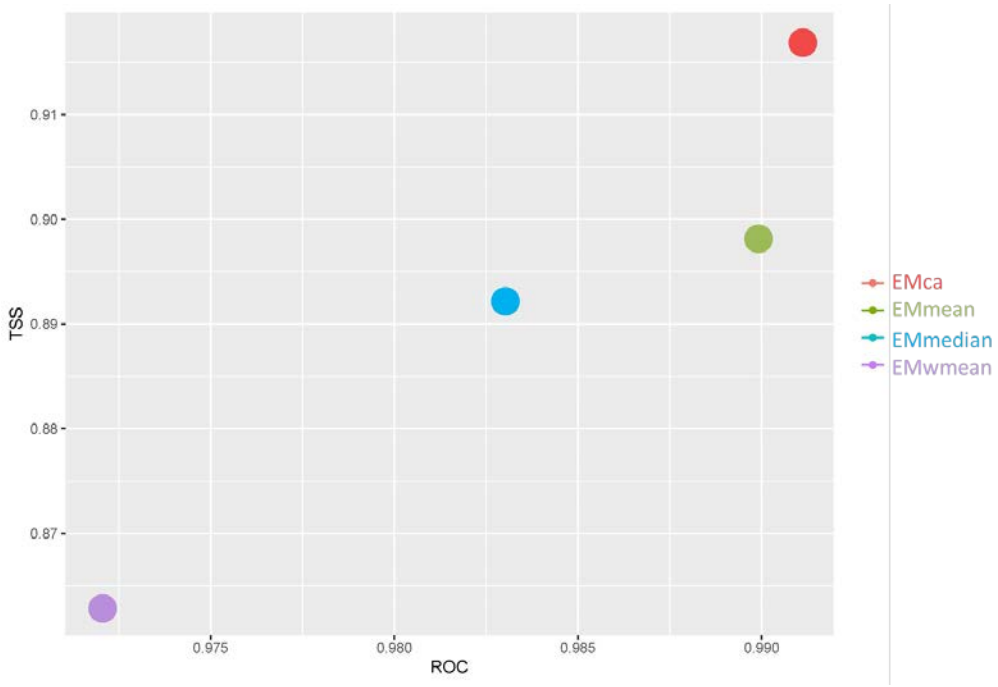

Figure 27. Ensemble model performace. Mean ROC and TSS values of four tested ensemble models, summarizing overall predictive performance of each technique. As EMca showed superior predictive performance, it was selected for modelling distribution of *Campylopus introflexus*.

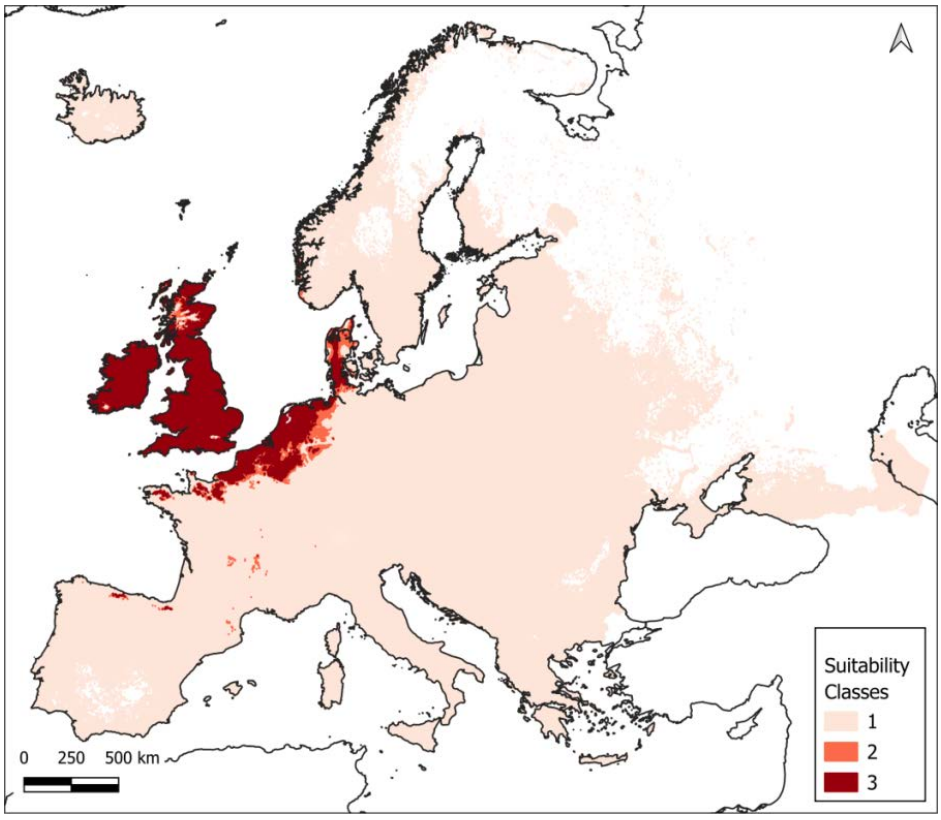

Figure 28. Map of Europe showing suitable habitat area for *Campylopus introflexus* as projected under present climate (1970–2000). Suitability classes: 1–Unsuitable, 2–Model supported suitable, and 3–Consensus suitable.

When both ensemble methodologies are taken into accoun, temperature seasonality (BIO4) distinguished as a key predictor influencing the possible distribution of the examined moss among the eight predictor variables, with a mean relative importance of 0.651 ± 0.002 for EMca and 0.542 ± 0.002 for EMmedian (Figure 29, Table 5). Precipitation was practically insignificant in comparison to remaining temperature-related variables. In particular, the relative significance of the predictor factors in the EMca and EMmedian ensemble models was 0.157 ± 0.001 and 0.133 ± 0.001 for annual mean temperature (BIO1), 0.107 ± 0.001 and 0.058 ± 0.001 for mean diurnal range (BIO2), 0.088 ± 0.001 and 0.085 ± 0.0003 for maximum temperature of the warmest month (BIO5), 0.113 ± 0.001 and 0.063 ± 0.0001 for minimum temperature of the coldest month (BIO6), 0.008 ± 0.0001 and 0.003 ± 0.00003 for precipitation seasonality (BIO15), 0.012 ± 0.0002 and 0.006 ± 0.00007 for precipitation of the wettest quarter (BIO16), and 0.028 ± 0.0001 and 0.021 ± 0.001 for precipitation of the warmest quarter (BIO18), in the order given.

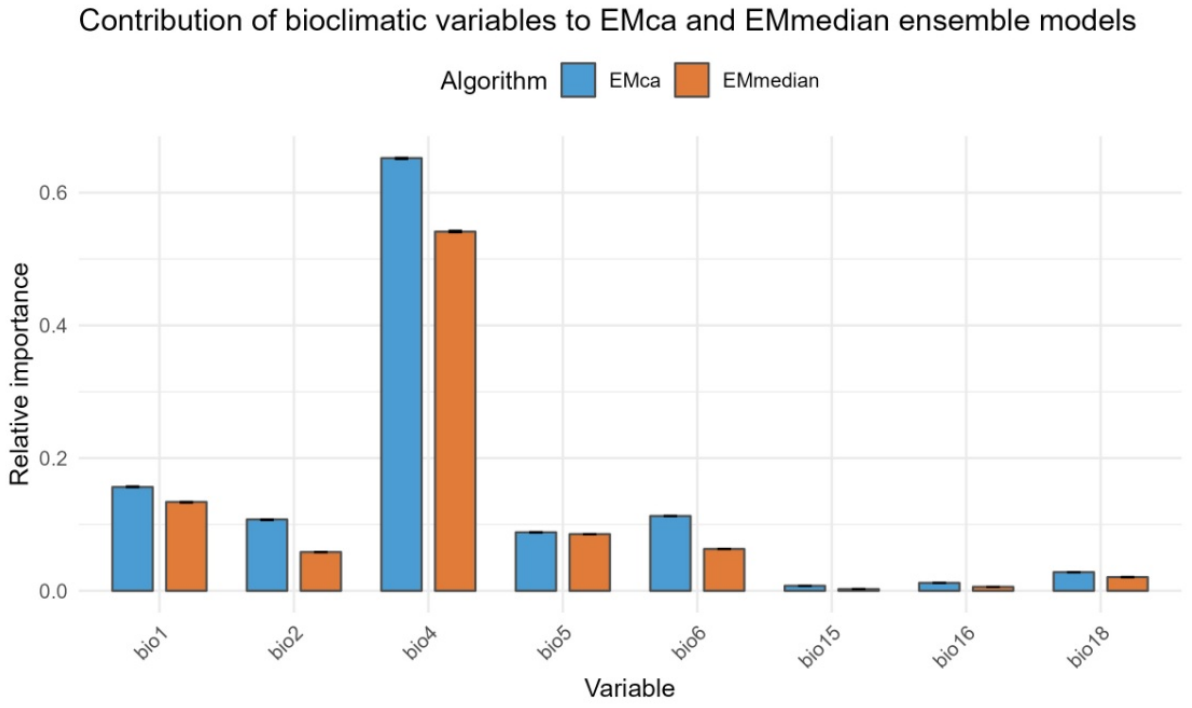

Figure 29. Relative importance of bioclimatic variables that determine the possible European distribution of *Campylopus introflexus*. Abbreviations: BIO1 – Annual Mean Temperature; BIO2 – Mean Diurnal Range; BIO4 – Temperature Seasonality; BIO5-Maximum Temperature of Warmest Month; BIO6 – Minimum Temperature of Coldest Month; BIO15 – Precipitation Seasonality; BIO16 – Precipitation of Wettest Quarter; BIO18 – Precipitation of Warmest Quarter.

On average, across all future climatic pathways, consensus-suitable areas comprised for 2.70 ± 1.22% of the overall area, model-supported suitable areas for 0.80 ± 0.13%, and unsuitable areas for 96.51±1.29% of the overall area analyzed. The Kruskal-Wallis test showed substantial disparities in p suitability levels between classes ($H = 19.0$, $df = 2$, $p < 0.001$). Post hoc Dunn testing indicated that the unsuitable class showed great differences from both the consensus-suitable class ($Z = 2.44$, $p < 0.05$) and the model-supported class ($Z = 4.34$, $p < 0.001$), while there was no statistically supported difference between the latter two classes ($Z = -1.91$, $p > 0.05$).

Table 5. Contribution of predictor variables to model performance of *Campylopus introflexus*.

Alg.	Expl.var	Mean	Min	Max	SD	SE	Median
EMca	**BIO1**	0.156870	0.156016	0.158174	0.001147	0.000662	0.156420
	BIO15	0.007605	0.007496	0.007716	0.000110	6.35E-05	0.007602
	BIO16	0.012156	0.011991	0.012469	0.000271	0.000156	0.012009
	BIO18	0.028113	0.027981	0.028192	0.000115	6.63E-05	0.028165
	BIO2	0.106946	0.105511	0.107722	0.001244	0.000718	0.107604
	BIO4	0.651484	0.649468	0.652895	0.001792	0.001035	0.652090
	BIO5	0.088106	0.087433	0.088710	0.000641	0.00037	0.088176
	BIO6	0.112811	0.112273	0.113360	0.000544	0.000314	0.112800
EMmedian	**BIO1**	0.133303	0.132	0.133978	0.001129	0.000652	0.133931
	BIO15	0.002598	0.002569	0.002623	2.72E-05	1.57E-05	0.002601
	BIO16	0.006021	0.005943	0.006085	7.21E-05	4.16E-05	0.006036
	BIO18	0.020598	0.020069	0.021072	0.000504	0.000291	0.020653
	BIO2	0.058279	0.057666	0.058697	0.000542	0.000313	0.058474
	BIO4	0.541544	0.539436	0.543959	0.002277	0.001315	0.541236
	BIO5	0.085401	0.085087	0.085637	0.000283	0.000163	0.085479
	BIO6	0.063168	0.063048	0.063335	0.000149	8.60E-05	0.063122

In all examined future scenarios, there was a general decrease in *C. introflexus* compatible regions, comprising the two consensus-suitable and model-supported suitable areas, while unsuitable habitats expanded (Figure 30). More precisely, in comparison to the present climatic conditions, consensus-suitable areas declined by −31.19 ± 11.5%, model-supported suitable areas by −55.67 ± 18.5%, and unsuitable areas expanded by 31.00 ± 8.5%. As with projected suitability levels, the Kruskal-Wallis test findings revealed statistically supported dissimilarities in the percentage variations in suitability among classes ($H = 18.2$, $df = 2$, $p < 0.001$). The results of the Dunn test were similar: the unsuitable class differed significantly from both the consensus-suitable ($Z = 4.26$, $p < 0.001$) and model-supported classes ($Z = 2.55$, $p < 0.05$), while there was no statistically supported dissimilarity between the two remaining classes ($Z = 1.70$, $p > 0.05$).

According to the Kruskal-Wallis test for each suitability class (Consensus suitable: $H = 7$, $df = 7$, $p = 0.429$; model-supported suitable: $H = 7$, $df = 7$, $p = 0.429$; unsuitable: $H = 7$, $df = 7$, $p = 0.429$), there were no statistically supported dissimilarities in percentage variation across the examined future climatic pathways.

The assessment of species range change showed a major decline in consensus-suitable areas, that is, highly suitable habitats. In the case of medium-emission pathway (SSP2–4.5), the consensus-suitable projected range exhibited average reduction of −36.02% for 2021–2040 (Figure 31: A1), −41.75% for 2041–2060 (Figure 31: A2), −58.55% for 2061–2080 (Figure 31: A3), and −56.30% for 2081–2100 (Figure 31: A4). In the case of pessimistic climate scenario (SSP5–8.5) for the same timeframes, a ongoing reduction in the mean area of suitable habitats was detected, from −35.33% in 2021–2040 (Figure 31: B1), −54.50% in 2041–2060 (Figure 31: B2), −75.27% in 2061–2080 (Figure 31: B3), to −87.60% by 2081–2100 (Figure 31: B4).

A decrease in model-supported suitable areas (moderately suitable habitats) was also detected in the assessment of species range changes. The decline in area for model-supported suitable areas was slightly smaller in comparison to consensus-suitable areas. In the case of moderate-emission scenario (SSP2–4.5), the consensus-supported suitable area projected range exhibited average reduction of −23.08% for 2021–2040 (Figure 31: A1), −28.48% for 2041–2060 (Figure 31: A2), −49.21% for 2061–2080 (Figure 31: A3), and −21.68% for 2081–2100 (Figure 31: A4). In the case of most pessimistic climate scenario (SSP5–8.5) for the exact timeframes, an ongoing reduction in the average area of suitable habitats was detected, from −22.83% in 2021–2040 (Figure 31: B1), −44.89% in 2041–2060 (Figure 31: B2), −38.98% in 2061–2080 (Figure 31: B3), to −20.36% by 2081–2100 (Figure 31: B4).

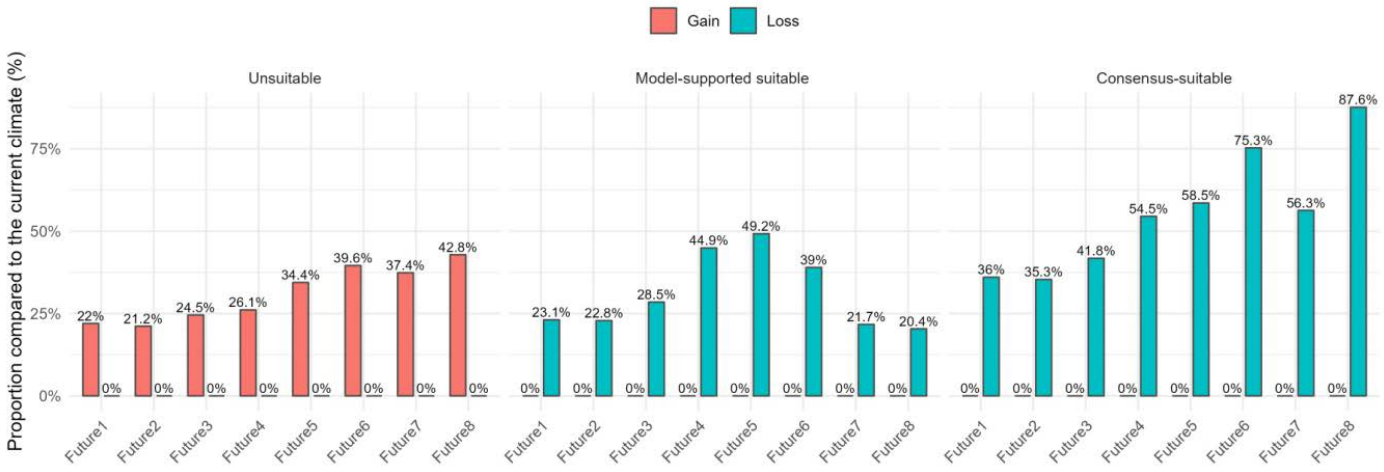

Figure 30. Changes in suitable habitats of *Campylopus introflexus* under projected climate change pathways relative to present climatic conditions, expressed as percentages of habitat gain and loss. Abbreviations: Future1 – SSP2–4.5(21-40); Future2 – SSP5–8.5(21-40); Future3 – SSP2–4.5(41-60); Future4 – SSP5–8.5(41-60); Future5 – SSP2–4.5(61-80); Future6 – SSP5–8.5(61-80); Future7 – SSP2– 4.5(81–100); Future8 – SSP5–8.5(81–100).

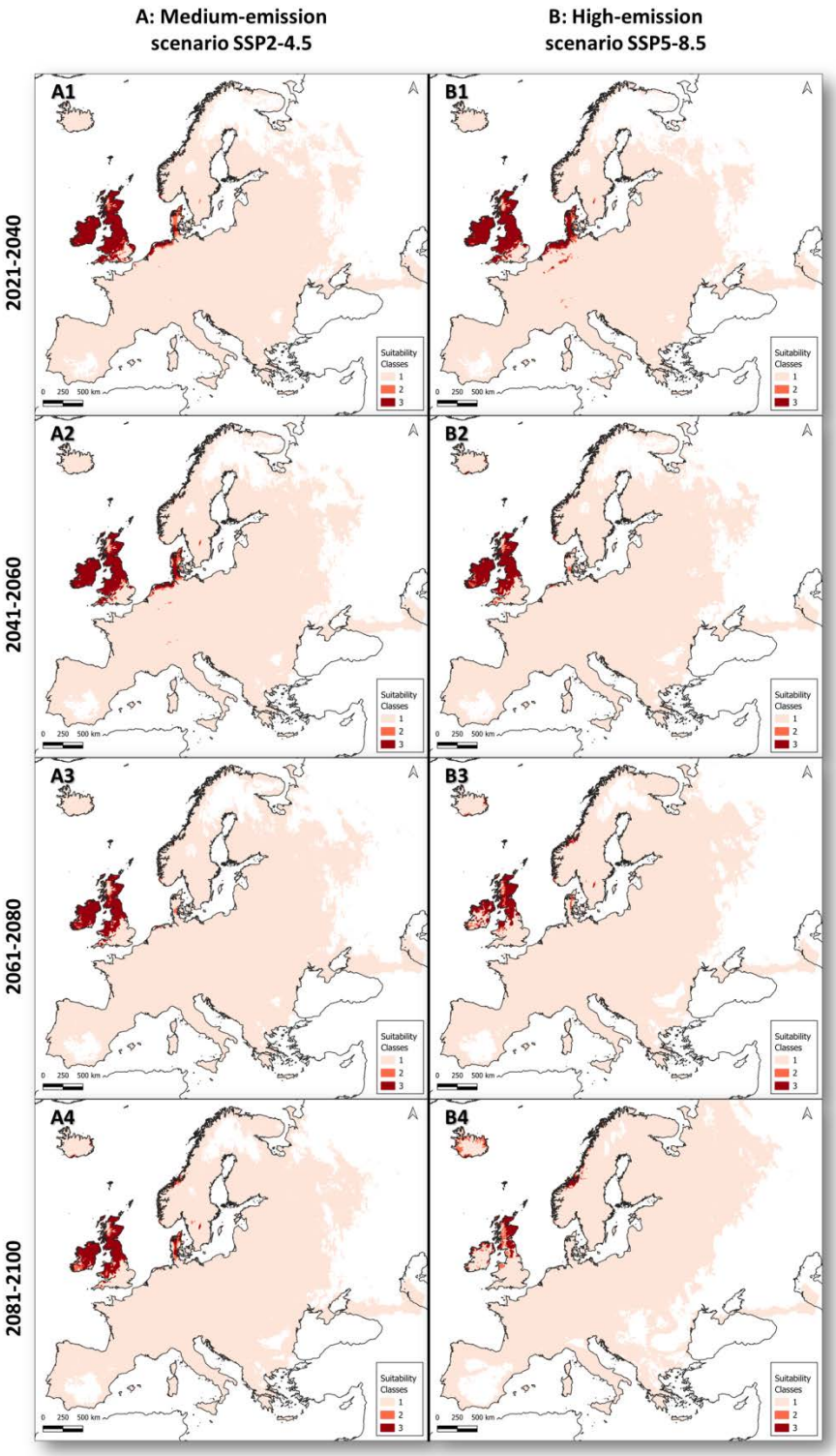

Figure 31. Predicted shifts in the European distribution of *Campylopus introflexus* under two climate pathways: a moderate-emission pathway **(A)** and high-emission pathway **(B)** for four timeframes (1: 2021–2040; 2: 2041–2060; 3: 2061–2080 and 4: 2081–2100) based on species distribution modelling. Suitability classes: 1 – Unsuitable, 2 – Model-supported suitable, 3 – Consensus suitable.

5. DISCUSSION

In this study SDM was used to evaluate the current and future distribution of three mosses that have limited occurrence data. Several different single models, as well as an ensemble modelling were used to evaluate patterns and spatiotemporal dynamics of species ranges. Additionally, the importance of environmental factors determining species' distribution was assessed and suitable areas were identified, both current and future conditions. The results indicate general decline of all investigated species in the future, as well as changes in habitat suitability. These findings provide valuable data on the ecological niches of the species and their vulnerability to climate change.

Although all species showed to be vulnerable to the expected changes in climate, subtle differences in their responses to climate change were observed. Among the three investigated species, *E. hungaricus* appeared to be the most susceptible to the changing climate, exhibiting the highest reduction in suitable habitat and the greatest contraction of its future distribution range. This indicates that this species could be at a higher risk of population decline compared to other two investigated species. The observed slight differences among species likely reflect their distinct ecological requirements, habitat specificity, and adaptive capacity to changing environment.

5.1. *Entosthodon hungaricus*

5.1.1. Ecological drivers and patterns of species distribution

In this study, we analysed the relative contributions of eight selected environmental variables (six climatic, one topographic, and one soil-related) to the distribution models. The findings indicate that the salt substrate (halomorphic soil) is essential for the survival of *E. hungaricus*. Among investigated bioclimatic factors at a macro scale, the precipitation of the driest month, precipitation seasonality, and mean diurnal temperature range showed to be the most important climatic factors affecting the distribution of this species in the country. These are all important climatic variables that determine water availability during stressful periods (drought). These results suggest that soil and humidity-related factors are primary determinants of *E. hungaricus* distribution.

For halophyte mosses such as *E. hungaricus*, the impact of climate change is highly complex. Due to its dependence on saline substrates (Sabovljević et al., 2012), even if the climate is favourable, the species' successful dispersal is limited by soil characteristics. Edaphic variables such as salinity can limit colonisation of the species, playing a major role in its distribution at the microhabitat scale. Compared to species with a wider ecological niche, specialised species such as *E. hungaricus* are even more affected by the effects of rising temperatures and changing climate in general.

Precipitation seasonality describes how precipitation varies and is distributed throughout the year. Regions with high precipitation seasonality are characterised by drought-tolerant species that remain dormant, or by ephemeral species that complete their life cycle before the prolonged summer drought, such as *E. hungaricus.* Precipitation seasonality is particularly important for the reproduction of these species, as sporophyte development is synchronized with the rainy season. Moreover, very low values of precipitation of the driest month may limit the distribution of some species. The mean diurnal temperature range can considerably influence the timing of different developmental phases, such as spore germination or the development of sex organs.

Similarly, severe fluctuations in winter precipitation can have an important impact on the development and reproduction of the species. *Enthostodon hungaricus* in Serbia develops during the rainy seasons, which is in the late winter and early spring. However, in some years, relatively high

temperatures and dry springs caused a decline in the occurrence of this short-lived species (Sabovljević et al., 2018). Thanks to the presence of a spore bank, seasonal variation had no noticeable impact on development in the following year. However, spring climate deviations in the subsequent year led to a decline in the occurrence of some site populations during the next suitable development season (Sabovljević et al., 2018). Thus, if unfavorable periods occur frequently due to the effects of climate change, this can weaken the species' fitness in the long term, and eventually lead to the local extinction of populations.

An area that has proven particularly important for *E. hungaricus* in Serbia is the Banat region, especially its northern and central parts, which, in addition to the presence of saline soils, are characterised by favorable climatic conditions. Majority of known records of this species in the literature come from this region. The importance of specific saline habitats in Banat is further demonstrated by the presence of many protected areas, such as the Special Nature Reserves "Selevenjske pustare" and "Pašnjaci velike droplje", the Region of Exceptional Characteristics "Kanjiški jaraši" and the Nature Park "Slatine u dolini Zlatice". These protected areas are therefore crucial for the *in situ* protection and survival of this moss species in the country.

However, many other areas characterised by saline soils in the Vojvodina province, such as Bačka, Srem, and southern Banat, according to the projected current distribution, do not have suitable climatic factors and lack records of this species. Although the Banat and Bačka regions appear climatically very similar, they differ slightly in aridity (Hrnjak et al., 2014). These subtle differences between them can influence habitat climatic suitability, and may be important for the species modelling. However, many other factors not considered could influence the areas' microclimate, such as the effects of large rivers (e.g. Tisa and Danube), winds, soil types, and land use.

Finally, differences in climatic suitability may be result from sampling bias. According to Pantović (2018), almost twice as many bryophyte records were documented in Banat compared to Srem, while Bačka is considered one of the least researched regions of Serbia, with a very small total number of bryophyte records. Banat is regarded as the best bryofloristically studied part of the Vojvodina province, and therefore the possible influence of sampling bias on the projected distribution of the species should not be excluded. Targeted field investigations in these areas in future could confirm the accuracy of the models.

5.1.2. Future distribution and climate change impact

Ensemble modelling was used in this study to evaluate range dynamics of the species in different scenarios of the climate change. According to all prediction models, by the end of the century, suitable habitat for *E. hungaricus* is projected to decrease significantly under all investigated pathways, with range losses greater than 75%. The most severe environmental changes (SSP5-8.5 pathway) will cause a major decline of 92% in the Serbian population of *Entosthodon hungaricus* by the end of this century.

According to the predictions, some currently unsuitable areas will become climatically favourable, extending species range from 2.5% to 17.1%, depending on the investigated time period and climate scenario. However, the total range of *E. hungaricus* will not expand because the eastern regions will be too arid for the investigated species to survive (Abubakar et al., 2024).

This further indicates that the species' survival in the country will be questionable in the future and it should influence conservation strategies. The populations may move from the at present drier

northern Banat situated in the east of country's Vojvodina province to the at present slightly more humid Bačka region which is situated in the western Vojvodina (Abubakar et al., 2024).

The sustainability of global ecosystems is threatened by the global temperature increase, which is affecting biodiversity in all areas (Dawson et al., 2011; Purves & Dushoff, 2005). Species are moving to higher latitudes and altitudes as a result of rising temperatures and climate that is rapidly changing (Chen et al., 2011; He et al., 2019; Parmesan & Yohe, 2003). Additionally, rare and endangered species that have small populations, narrow geographic ranges, or peculiar habitats are at greater risk of extinction due to migration to higher altitudes and decrease in their ranges (Jump & Peuelas, 2005; Pauli et al., 2012; Daskalova et al., 2020).

5.1.3. Model reliability and limitations

The IPSL-CM6A-LR model should be used with caution, even though it seems to be the most optimistic of the three models examined. It has been demonstrated that this model's very poor spatial resolution makes it unsuitable for species with specific ecological requirements, such as *E. hungaricus* (Boucher et al., 2020). Consequently, the probability for the future survival and dispersal of this species is low.

For ephemeral species that are challenging to identify or are easily omitted in the field, SDM models can be very important (Sérgio et al., 2007). This study confirms that these models are also appropriate for ephemeral mosses that have narrow niches, as demonstrated for the moss *E. hungaricus*. As a result, these models help identify the probable present distribution in the investigated area as well as favourable habitats. The factors that influence the emergence and distribution of *E. hungaricus* in nature have not yet been studied. The ability to forecast the species' future range, which is essential for its conservation, is another reason why these studies are significant. The scenario of the losing most of the currently suitable habitats of this species in the future is extremely feasible, as evidenced by the previously documented trend of rising temperatures in Serbian territory combined with decreased precipitation and/or uneven annual distribution (Dimkić, 2019).

This species is classified as vulnerable (VU) in Serbia (Sabovljević et al., 2024). Until recently, *E. hungaricus* was also considered vulnerable (VU) at the European level. However, in the most recent threat assessment, its European extinction risk has been changed to least concern (LC), due to the high reproduction capacity and number of spores this species shows (Sabovljević et al., 2019; Hodgetts et al., 2019). However, the effects of climate that is rapidly changing and the degradation of salty grasslands, often considered as areas of low economic values, were not considered in earlier assessments. These findings indicate that there are still significant challenges to the survival of the species.

5.1.4. Implications for management and recommendations for future research

The results of the species distribution modelling provide an important basis for developing conservation strategies for the moss *E. hungaricus.* Areas identified as highly suitable represent key areas that should be prioritized in future monitoring programmes, habitat management and conservation assessment. Given the fragmented distribution and soil preference of this species, conserving suitable microhabitat may be essential for its long-term persistence.

Rare inland saline habitats are among the main factors contributing to the rarity of this species. Due to their uniqueness and importance for biodiversity, saline terrestrial habitats in Europe, such as Pannonic saline meadows (EUNIS code E6.212) and Saline pustza (EUNIS code E6.211), have been

identified as priority habitats, and are protected through various international agreements, European directives, and national laws. Despite this, the number of saline grasslands has decreased significantly over the past century (Zlatković, 2021). These habitats are often regarded as having low economic value, and are therefore subject to strong anthropogenic pressures. The expansion of agriculture, urbanisation, drainage, and reduction in the groundwater level have the greatest negative impact. For example, in Serbia, saline meadows are often used as landfills, construction deposits, or are overgrazed by cattle.

Further field research in poorly investigated areas identified as suitable is needed in order to better understand the ecological preferences of the species, to reduce sampling bias, and validate predicted suitable areas. Additionally, continuous monitoring is needed to evaluate long-term population trends and the influence of changing environment on survival of the investigated species.

The projected distribution emphasises the potential vulnerability of suitable habitats to ongoing environmental and climatic changes. As bryophytes are particularly susceptible to modifications in moisture regime, temperature, and habitat disturbance (Proctor et al., 2007; He et al., 2016), even relatively small environmental changes may severely affect their distribution dynamics. Thus, management strategies are crucial for maintaining suitable conditions for the species, including controlled grazing, maintaining the hydrological regime, and removing invasive species.

As it is projected that range of this rare moss species is going to decline considerably in the future under changing climate, conservation efforts should focus on protecting existing populations and maintaining the specific microhabitat conditions required for their survival. Management actions may include the following conservation of sites:

1. Maintaining natural water regime of saline habitas,
2. Restricting conversion of saline habitats into agricultural land,
3. Limiting mecanical disturbance of soil surface,
4. Control vegetation succesion or overgrazing (maintain open habitat)
5. Establish monitoring of populations or rare halophilous species

Ultimately, the long-term survival of *E. hungaricus* depends strongly on effective conservation and active restoration of its habitats.

5.2. *Hennediella heimii*

5.2.1. Ecological drivers and patterns of species distribution

Among the investigated climate variables, three were identified as the most significant predictors that influence species distribution: bio2 (Mean Diurnal Range), bio3 (Isothermality), and bio9 (Mean Temperature of Driest Quarter). This suggests that the investigated species is highly influenced by temperature stability, specifically temperature variability both within a day and across seasons. Thus, regions with relatively stable thermal regimes and lower day-night temperature variation appear to provide the most suitable habitats. Additionally, bio9 explains how species distribution is influenced by seasonal drought periods when water availability is lowest. For example, moderate temperatures during the driest quarter may allow species to survive even in relatively dry environments. However, if temperatures are too high during dry summer months, evapotranspiration and physiological stress can increase significantly, making the species more sensitive to high temperatures and reduce its habitat suitability.

The projected distribution map reveals variation in species suitability across Europe, shaped by a combination of different climatic factors. Areas determined as highly suitable are concentrated in narrow parts of the western coastal regions of Europe, particularly around the British Isles and parts of northwestern Europe, where mild temperatures, high humidity, and stable precipitation regimes create favorable environmental conditions. Moderate suitability extends to these areas, as well across mountainous areas further into south-east Europe: central parts of the Massif Central in France, Alps and central part of Apennine Mts. These regions provide partially climatically suitable habitats but may be constrained by other factors. In the Balkan Peninsula only areas with marginal suitability are present, namely the mountainous areas of the Carpathians and the Peloponnese. However, all these areas in continental Europe are highly fragmented.

Coastal habitats are important not only because of species halophytic nature. Oceanic conditions reduce thermal extremes and increase atmospheric moisture, creating more stable conditions for this species, especially during summer droughts. In contrast, inland continental regions are characterised by greater temperature fluctuations and lower moisture availability, thus increasing drought stress. This explains the high suitability observed in oceanic and coastal Western Europe.

In contrast, large areas of eastern and southeastern Europe, where daily temperature variation is more pronounced, are projected to be unsuitable or only marginally suitable in terms of favourable climate for the investigated species.

These results suggest a west–east gradient in climate suitability, emphasizing the importance of temperature and precipitation as primary ecological determinants of the distribution of *H. heimii* in Europe. Coastal and oceanic regions of Europe appear to be the most suitable, while continental regions remain less favorable.

As *H. heimii* is also a (facultative) halophyte species (Ćosić et al., 2022), its distribution is strongly influenced by soil type. Relying only on climatic factors to predict its range, as was done in this study, can overestimate its potential distribution area. Including both edaphic and climatic factors in species distribution modelling is crucial to enhance model accuracy, especially for rare and endangered specialist species such as *H. heimii*. Thus, one of the key aspects of future research of this rare species should be the inclusion of soil type as an environmental predictor in modelling its distribution.

5.2.2. Future distribution and climate change impact

The projected distribution of *H. heimii* under two different climate scenarios by 2100 indicates a significant decrease in suitable areas for the investigated species across Europe. Specifically, the model suggests a reduction in areas with suitable climate in parts of the Central and Eastern Europe, while areas with favourable climatic conditions will remain in western and northwestern coastal regions. Increasing temperature extremes and reduced moisture availability in continental Europe are expected to contribute to climatic stress, thus limiting the species' regional survival and altering its European distribution.

The results show a gradient in suitability from the western to the eastern parts of Europe. Western Europe, influenced by the Atlantic Ocean, is predicted to remain more climatically stable. In these areas thermal variability is lower and moisture availability higher, which aligns with the importance of mean diurnal range, isothermality, and mean temperature of the driest quarter as key ecological variables influencing species distribution. In contrast, the Eastern Europe becomes increasingly unsuitable under future climate conditions, likely due to stronger continentality, higher temperature extremes, and intensified summer droughts.

A decline in suitable areas is observed under both modelled climate scenarios when comparing the current distribution to projections for 2100. Although the extent of reduction differs between scenarios, the general trend remains - a progressive decrease in areas with suitable climate over time, along with fragmentation of the remaining habitats. This indicates that climate change strongly influences the distribution and local survival of the species, with higher-emission scenarios intensifying the extent of loss.

Mountain regions such as the Alps, Carpathians, and parts of Scandinavia can be important refugia despite unfavourable climate conditions in the surrounding continental lowlands. However, suitability in these areas is highly fragmented. Consequently, future populations are expected to become more isolated, increasing the risk oflocal extinctions.

These changes may increase the risk of local extinction in southern and inland populations. Climate change can therefore cause a decrease in the range size of *H. heimii*, as well as a range shift towards coastal and oceanic parts of Europe. At the same time, limited northward and westward expansion may occur where newly suitable climatic conditions arise.

The projected distribution highlights the possible negative effects of changing climate on future range dynamics of *H. heimii* and emphasises the importance of monitoring habitats and climate trends for management planning and conservation of species. Additionally, strong adverse anthropogenic influence, including urbanisation and agricultural intensification, may limit the establishment of the species and its further spread in climatically favourable regions.

5.2.3. Model reliability and limitations

Although the SDM is very useful for assessing potential future climate suitability under the climate change scenarios, there are several model limitations that should be considered when interpreting results.

One important limitation is that the model is primarily based on climatic variables and didn't include other ecological factors that influence species survival and distribution. For example, soil type and characteristics weren't included in this research, which is particularly important given that *H. heimii* is a halophyte species. This means that the percentage of occupied habitats in areas that are

climatically suitable is likely considerably smaller than modelled. Similarly, other variables, such as land-use change, habitat quality, dispersal barriers, biotic interactions, and anthropogenic disturbances, can strongly affect establishment success and population survival but are difficult to incorporate into models. As a result, some areas projected as suitable may not be occupied in reality.

Model uncertainty is also associated with the assumption that the current interaction between species occurrence and environmental conditions remains stable over time, without considering the possibility of evolutionary adaptation or ecological response.

Another important potential source of uncertainty is the quality and spatial distribution of occurrence records used for modelling. Sampling bias, uneven geographic coverage and limited occurrence data can influence model performance and prediction accuracy. However, for ephemerous mosses that are likely omitted in the field, or under-recorded, SDM models can be very important in ecological studies.

Despite all limitations, the model provides a useful framework for identifying large-scale species trends, potential climatic refugia, and regions vulnerable to future habitat loss. Therefore, the projections should be considered as probabilistic estimates that support conservation planning of *H. heimii* and basis for future ecological research rather than exact predictions of future species distribution.

5.2.4. Implications for management and recommendations for future research

The projected habitat suitability under the climate change scenario indicates a considerable decrease and redistribution of climatically suitable areas across Europe, with highly suitable areas confined to western coastal and oceanic regions, particularly the British Isles and northwestern Europe.

From a management perspective, these results emphasize the need to prioritise conservation efforts in regions predicted to remain suitable in the long term. Coastal and ocean-influenced areas are likely to function as key refugia, making them critical for the persistence of populations under climate change. Maintaining and restoring habitat connectivity between these suitable areas will be essential to support dispersal and enable potential range shifts. At the same time, reducing anthropogenic pressures such as habitat fragmentation, agricultural intensification, and urban expansion could enhance ecosystem resilience, particularly in marginal habitats where populations may persist under suboptimal conditions.

Future research should aim to enhance the precision of species distribution models by including more additional ecological factors, such as soil properties and land-use change. Long-term field monitoring is also essential to validate modelled range shifts and observe early changes (e.g. decline) in species distributions.

5.3. *Campylopus introflexus*

5.3.1. Ecological drivers and patterns of species distribution

The results from this study suggest that two climatic factors that have the biggest influence on the distribution of *C. introflexus* are temperature seasonality and the minimal temperature of the coldest month.

Campylopus introflexus is a suboceanic temperate species occurring in temperate regions of Europe that are influenced by the proximity of the ocean, that is maritime climate (Hassel & Söderström 2005). Such areas are represented by moderate winters and cold summers, with high precipitation and moisture levels. Thus, they have relatively low temperature seasonality compared to other, continental parts of the European continent. These suboceanic temperate species are therefore highly vulnerable to long lasting drought periods or very cold and long winter periods. Because of that, they depend on favorable milder conditions typical of areas with low temperature seasonality. As obtained in this study, only small percent of the investigated territory is suitable for the current spread of the alien species *C. introflexus*. Consequently, suitable habitats for *C. introflexus* are predominantly distributed along the coastal, northwestern regions of Europe. Even small increase in temperature seasonality with latitude or distance from the coast may limit species occurrence, making it an important factor limiting its distribution. Current European distribution and eastern range limit of investigated species *C. introflexus* thus could be explained by the temperature seasonality.

Bryophytes are typically highly susceptible to variations in air temperature and humidity levels (Proctor et al., 2007). For example, the naturalization of alien bryophytes can be significantly predicted by climatic factors such as Annual Mean Precipitation (Essl et al., 2014a). Despite the fact that most bryophytes' poikilohydric adaptation enables them to endure brief to severe droughts (Proctor et al., 2007), the external environment remains crucial for their survival and reproduction. As they can rapidly dry out completely whith the increase in temperatures and decrease of humidity, many species are highly susceptible to high temperatures. Consequently, photosynthesis in many bryophyte species is severely restricted by high temperatures, which further limits their metabolic activity and considerably reduces the survival of the species (He et al., 2016). This is particularly important for *C. introflexus*, a species that thrives in both moderately moist and dry environments and in full light (h photophyte) (Dierßen, 2001; Blockeel et al., 2014).

Niche shift wasn’t observed in this research, as the modelled distribution range does not differ significantly in temperature and precipitation regimes. These results are consistent with the previous study of Mateo et al. (2014), which showed that the invasion of *C. introflexus* is associated with a climate that is similar to the climate in its native range, and that the species did not exhibit niche increase in the occupied regions.

Although the increased number of records of *C. introflexus* in the region may to some extent be explained by the intensified bryological research, recent findings simultaneously provide evidence of its ongoing eastward spread in Southeast Europe. However, to better understand its invasiveness and spread, various environmental factors need to be considered in further research.

5.3.2. Future distribution and climate change impact

The obtained results showed considerable decline in range size and suitable habitats of the investigated invasive species across Europe under future climate conditions. Namely, *C. introflexus* will significantly decline following the initial phase of spread in Europe. This further implies that the

range of *C. introflexus* in Europe may be reduced in areas with unfavorable climate, which appears to represent a major portion of the species' range. The loss of suitable habitats may lead to reduced genetic diversity and increased population fragmentation. However, according to the tested models, its natural and complete disappearance from Europe is not expected. This aligns with research conducted by Désamoré et al. (2012), that showed that temperate bryophytes may expand their ranges in response to changing climate, they will eventually lose suitable ares in south of Europe.

Changes in bryophyte distribution patterns is one of the most important recognized effects of climate change, particularly rising temperatures (Zanatta et al., 2020). In order to find adequate habitats, many species will shift their ranges towards higher latitudes and elevations. Similarly, due to the great decrease of suitable areas under predicted climate scenarios, species *C. introflexus* will undergo a shift in its distribution range (Abubakar et al., 2026). Namely, the species will move to higher latitudes in Europe that are influenced by Atlantic climatic conditions.

One of the main discoveries of this research is that *C. introflexus* will not expand its range in the future in the investigated area. Researchers have demonstrated that some plants, especially invasive species in non-competitive habitats, are likely to benefit from climate change, including rising temperatures and CO_2 levels (Dukes, 2000; Meyerson & Mooney, 2007). However, findings from one meta-study indicate that while high temperatures, elevated atmospheric CO_2 concentrations, and nitrogen deposition may encourage invasion, drought may prevent invasive alien plant species from spreading (Liu et al., 2017). These conclusions are consistent with the results obtained, especially considering that this is an oceanic species.

Nevertheless, changing climate may exhibit unfavourable influence on native bryophytes that are inhabiting same habitats (e.g. Pantović et al., 2023; Abay & Gül, 2025), which in the prolonged period can influence (local) extinctions. Once already disturbed habitats, with low competition may be suitable for the spread of invasive species despite limiting climatic factors, especially when the species those with great phenotypic plasticity and tolerance to environmental change. Invasive species are inherently dynamic and thus it can occasionally be challenging to predict their invasion strategies (Srivastava et al., 2019). Especially knowing that it has already been demonstrated that alien species can invade areas larger than expected, including those that have different climates compared to their native ranges (Cordier et al., 2020).

Competition and changes to the structure of autochthonous taxa and alliances have been identified as the two most significant adverse consequences of invasion by alien bryophytes (Essl et al., 2014a). It is difficult to eliminate an invasive species once it has become established and naturalized. For instance, *C. introflexus* can create dense, homogeneous cusions that are hard to treat and prevent the restoration of the native environment. Even the use of herbicides and mechanical soil removal failed in a restoration project in the Netherlands. A few years later, this species again become dominant.

Invasion success depends on the ecological properties of the species, such as genetic plasticity and consequently its competitiveness, in addition to the features of the occupied territory and the chronology of introduction (Pyšek & Richardson 2007; Williamson et al., 2009). According to Hassel & Söderström (2005), the invasive moss *C. introflexus* has disseminated quickly across Europen continent due to its very diminutive spores (12–14 μm), which are primarily carried by the wind. It can take up to ten years for this species to form sporophytes, produce spores, and reproduce sexually. But once established, it spreads and multiplies swiftly asexually by leaf fragmentation (Glime, 2017). Asexual propagules appear to be produced and dispersed quickly in bryophyte species with a high potential for invasion.

5.3.3. Model reliability and limitations

The factors that determinedistribution of the species, as well as their colonization and further dispersion are complicated. Species distribution models primarily rely on correlations between species occurrence and habitat predictors, but typically do not consider other factors such as biotic interactions, spread limitations, habitat disturbance, and species' adaptibility. These can have significant impact on the colonization success and range dynamics, particularly in the unstable environment.

Most SDMs assume that species distribution is mainly determined by environmental suitability and abiotic factors such as climate. However, areas identified as suitable may in reality remain unoccupied due to biotic factors such as competition, which could strongly influence the establishment of invasive species in new habitats (Essl et al., 2014b). Unfortunately, interactions that could favour the spread or contract of this invasive species regionally remain unsufficientlly researched (Abubakar et al., 2026).

Such models are also limited by data bias, as uneven sampling or spatial gaps in occurrence records can lead to inaccurate predictions of a species' true range. Although extremely valuable, GBIF records of bryophytes are often spatially biased towards countries with a long history of field research. This can result in uneven records across Europe, with the majority from Western and Northern Europe, and comparatively few from Central and Eastern Europe - regions that could be considered under-recorded in terms of bryophyte flora.

There are also some limitations related to choice of model, environmental factors, and climate pathways. All this can cause realized geographic distribution to differ from modelled predictions.

5.3.4. Implications for management and recommendations for future research

Considering all limitations of SDMs, these findings should only be used as a foundation for further studies of species' ecology, its negative effects on native species and ecosystems, tracking any additional spread or range dynamics, and developing management plans. Even though changing climate can have severe influence on its future range, more explorationof species' present range, potential further spread and invasiveness, as well as its possible detrimental effects.

It is not surprising that little research has been done in the past on the effects of invasive bryophytes on autohtonous species and communities and the economy, considering the very small percent of invasive mosses worldwide. Considering the limited research on their harmful impact on native species and communities (Schirmel et al., 2011; Bourgeois et al., 2012; Schirmel & Buchholz, 2013; Pehle & Schirmel, 2015), many aspects remain unclear.

There are very few, if any, proactive measures being taken to prevent spread of *C. introflexus* and restore invaded habitats. Therefore, it's essential to comprehend the distribution of *C. introflexus*, and its possible effects, particularly in the region where it is currently spreading. Furthermore, negative effects on biological diversity and the socio-economy are frequently observed long after the introduction of the alien invasive species, as demonstrated by Essl et al. (2013, 2014). Since prevention, along with early detection and rapid response is the best measure to conserve natural environments, monitoring of regional spread is essential for the future. Thus, identifying and mapping risk areas should be priority for management and prevention efforts.

The obtained results of this research emphasize the significance of integrating SDMs into management strategies for the investigated invasive moss species, particularly in newly invaded

regions. Areas identified as highly suitable should be prioritized for targeted monitoring and early detection efforts to enable timely management interventions. Although climate change projections do not indicate increased long-term climatic suitability for further spread of this species, continued monitoring remains necessary, as anthropogenic disturbances, habitat changes, and dispersal through human activities may contribute to its establishment and further expansion. Management actions should therefore focus on reducing potential dispersal, protecting native communities, and implementing site-specific control measures where necessary. Enduring monitoring is essential to observe future distribution patterns and improve the effectiveness of invasive species management under changing environmental conditions.

6. CONCLUSIONS

It is essential to understand how species with limited occurrence data, particularly rare and threatened taxa, respond to climate change to assess biodiversity concerns and develop conservation strategies. The tested models allow for the identification of new adequate microhabitats and subpopulations of rare and threatened species within the country. Improved management and maintenance are also required for their habitats, which, in addition to being rare, are often degraded and subject to high anthropogenic impact. In order to prevent species decline and local extinctions, additional attention must be given to the development of monitoring programmes and conservation strategies, such as *in vitro* propagation with the aim of population strengthening and (re)introduction to suitable habitats. Similarly, SDM is very useful for investigating biological invasions and alien species. It helps to better understand their potential distribution and spread in unoccupied areas, their ecological impact, and possible responses to changing climate, thus supporting more efficient monitoring and management approaches.

The following main conclusions were obtained in the research on modelling species distribution of selected moss species:

6.1. Species distribution modelling

1. SDMs deliver valuable data of probable distribution of the species, even those with limited occurrence data.
2. Model performance and spatial predictions vary considerably among algorithms, confirming that ensemble approaches reduce uncertainty providing more accurate estimates of the species distribution compared to individual models, as shown in the case of all three investigated species.
3. Future climate projections suggest high vulnerability of rare and threatened species to climate change, including range dynamics, i.e. range decrease, shifts in suitability, or fragmentation of suitable areas.
4. SDMs provide data which threatened species are of highest priority for active and integrative conservation measures.
5. SDMs can also be an efficient tool for identifying key areas for future field studies and conservation, thus supporting improvement of conservation management, including the protection of priority areas, and implementation of species reintroduction programmes.
6. Future research should focus on incorporating other variables, such as soil type and characteristics, vegetation type, dispersal limitations, and land-use dynamics, to increase the predictive power of SDMs.
7. Such projections need to be explained with caution due to certain limitations, and support active conservation of the species in the future.

6.2. *Entosthodon hungaricus*

8. Among the investigated moss species, *E. hungaricus* showed to be most vulnerable to climate change, with projected greatest loss of suitable habitats and largest decrease in range size.

9. Under current climate conditions, only 1.7% of the country's teritorry is considered suitable in terms of climate for *E. hungaricus*.
10. All distribution models for *E. hungaricus* in Serbia indicate negative trends, suggesting declines of 75–92% in suitable climate based on the study period and climate pathway.
11. While IPSL-CM6A-LR showed as the most favourable among the all tested model, its results need to be interpreted carefully due to certain limitations.
12. Future projections suggest a potential shift of populations from the eastern to the western parts of Vojvodina towards slightly wetter conditions, without an overall range increase.
13. The species *E. hungaricus* faces an increased risk of local extinction, especially under the most pessimistic climate pathway over the longer term.
14. The suitable substrate is one of the key variables that affect the distribution of the moss *E. hungaricus* and its survival under future climate change.
15. Among the climatic factors, precipitation (specifically Precipitation of the Driest Month, Precipitation Seasonality and Mean Diurnal Temperature Range) represent the greatest limiting factor for the species distribution.
16. Previously undiscovered microhabitats and potential subpopulations, identified based on model projections, should be prioritized for additional targeted field studies, particularly in parts of eastern Bačka, northern Srem, and southern Banat.
17. Conservation strategies need to be improved, specifically in the selection of suitable microhabitats for *ex situ* conservation of the species.
18. The urgent development and implementation of monitoring and conservation measures are necessary to prevent local extinction of native at-risk species *E. hungaricus*.
19. Species' habitat types, primarily saline grasslands, are highly sensitive ecosystems that require improved management and maintenance in order to prevent further habitat degradation and ensure the survival of the species.

6.3. *Hennediella heimii*

20. Ensemble models showed greater predictive potential than individual models for modelling the distribution of *H. heimii*.
21. Under current climate conditions, only 0.52% of the European territory is considered highly suitable in terms of climate for the occurrence of the rare species *H. heimii*, while 71.7% of the territory is considered as climatically unsuitable area.
22. Mean Diurnal Range, along with Isothermality and Mean Temperature of Driest Quarter, were the most important climate factors influencing *H. heimii* distribution across Europe.
23. Long-term projections for the survival of the species *H. heimii* in Europe are unfavourable, as a substantial reduction in range size is estimated.
24. A general decrease in areas with highly suitable, moderately suitable, and unsuitable habitats in terms of climate is observed in the majority of future scenarios investigated, while low or marginally suitable habitats expanded, depending on the emission scenario and time period.

25. The highest loss of −87.08% is observed in highly suitable areas in terms of climate under the high emission scenario for the period 2061–2080.
26. An increase of up to 11.1% in suitable areas is observed only for low or marginally suitable areas in both emission scenarios during the periods 2061–2080 and 2081–2100.
27. The European range of the species is expected to shift towards north-western coastal regions - climatically stable refugial zones characterised by moderate thermal variability, reduced temperature extremes, and higher moisture availability.
28. Central and Eastern Europe are expected to experience a significant decline in suitability and possible local population extinction under future climate conditions.
29. The habitats that this species occupies in continental Europe, primarily saline grasslands and the shores of saline lakes, are highly sensitive ecosystems already under strong anthropogenic influence and therefore require improved management and conservation to prevent further habitat degradation and local species extinctions.
30. Future research should incorporate soil type into modelling to enhance model accuracy and conservation of the investigated species.

6.4. *Campylopus introflexus*

31. Ensemble models showed greater predictive potential than individual models for modelling the distribution of *C. introflexus*.
32. Under current climate conditions, only 7.39% of the investigated teritorry is considered suitable in terms of climate for the alien species *C. introflexus*.
33. A substantial decrease in areas with suitable climate is observed in all examined future scenarios, with average declines of up to 87.60%, depending on the model used, scenario, and time period.
34. Projected climate changes for Europe do not indicate an expansion of the investigated *C. introflexus* in the future.
35. Species distribution models for *C. introflexus* indicate a long-term decline in range size across Europe, accompanied by a shift in its suitable climatic areas.
36. Temperature Seasonality showed as the main climate predictor that affects species distribution and determines current range limit of the species.
37. Range dynamics of the species should stay in the focus of future field investigations in order to confirm the model predictions, enable management of the species and reduce its impact on the native habitats and species.

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Isyaku Abubakar was born on April 2, 1985, in Kankara, Katsina State, Nigeria, and finished elementary and high schools in Kankara. He completed his basic academic studies at the Department of Biological Sciences at Bayero University, Kano, Nigeria, majoring in Applied Biology, in 2010. He completed his master's academic studies in 2020 at Umaru Musa Yar’adua University, Katsina, Nigeria. He enrolled in doctoral studies at the Faculty of Biology of the University of Belgrade (study program Ecology, module Conservation Ecology and Environmental Protection) in the 2021/2022 year. He passed all exams for his doctoral studies within the deadline with an average grade of 9.83. Isyaku Abubakar was a doctoral student under a bilateral agreement scholarship between the Nigerian Ministry of Education and the Serbian Ministry of Education. He has been a research staff in Nigeria since 2015 at the Biotechnology Advanced Research Center of Sheda Science and Technology Complex, Abuja, Nigeria.

He has co-authored twelve (12) papers published in reputable journals (two (2) are from his PhD research work), and he is the first author of five (5) of them. He has also attended several conferences in Nigeria and one (1) in Serbia, and he has published abstracts in nine (9) of those conferences.

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