Inter-Research Science Publisher
Endangered Species Research
Volume 60:esr01520
Published July 30, 2026
https://doi.org/10.3354/esr01520

OPEN ACCESS

Prediction of climate-driven habitat shifts of the rare and threatened moss *Buxbaumia viridis* in Slovenia

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ABSTRACT: *Buxbaumia viridis* is a peculiar, deadwood-dependent cryptogamous moss characterized by reduced gametophytes and prominent sporophytes that develop directly from the protonema. The species is threatened in many European countries, listed in the EU Habitats Directive (Annex II) and protected under the Bern Convention. We applied ensemble species distribution modelling to project the potential distribution of *B. viridis* under multiple future climate scenarios and to assess its fate by analyzing the main bioclimatic and habitat factors influencing its survival in Slovenia, on the margin of the south-eastern Alps. The analysis was based on 54 occurrence records combined with bioclimatic, elevation and forest-type data using ensemble species distribution modelling. The models indicate that approximately 12% of Slovenia's territory is potentially suitable for the species, primarily in mountainous regions, particularly in northern Slovenia. The highest probability of *B. viridis* occurrence was associated with very low minimum temperatures in the coldest month. Future projections predict a strong reduction in potentially suitable areas, ranging from 67.7 to 100% — depending on the reference period and emission scenario — indicating severe range contraction and a potential loss of suitable habitats. These findings underscore the urgent need for targeted conservation, monitoring and forest management strategies that preserve deadwood-rich forest stands with spruces and firs, to ensure long-term survival of *B. viridis* in Slovenia.

KEY WORDS: Bryophyte · Climate change · Forest · ENM · SDM · Biomod2 · Europe

1. INTRODUCTION

Bryophytes, comprising 3 main lineages — hornworts, mosses and liverworts — are among the earliest representatives of terrestrial flora. Their presence is often overlooked, but despite their small size and biomass, they play pivotal ecological roles in both local and global ecosystems. They contribute to pioneering settlements and soil formation, carbon sequestration, nutrient cycling and water regime regulation (e.g. Glime 2004). As with many other living beings, they are under constant anthropogenic threats that affect bryophyte community changes, function, biotic interactions and species survival. Biodiversity protection programs and conservation initiatives often exclude bryophytes, despite their fundamental role in maintaining ecosystem functionality and services (e.g. Sabovljević et al. 2022).

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The unique ecological and physiological traits of bryophytes can be advantageous for survival in certain environments; however, they may also increase their vulnerability to rapid environmental change and macrohabitat variation. Given that many bryophyte species exhibit strong microhabitat specialization, small changes can cause their local extinction while at the same time signaling the ecosystem changes. Environmental perturbation and ecosystem changes can often be detected quickly through the presence, ecology and physiology of bryophyte species (e.g. Sass-Gyarmati 2025).

Microhabitat changes often go unnoticed, and they are usually linked to changes in general habitat type. This type of macrohabitat alteration almost always results in substantial threats and/or loss of bryophyte diversity due to the destruction of specific microhabitats. Although habitat modification is an important threat to the survival of bryophyte species, there are additional factors that affect species persistence at specific sites, including pollution, urbanization, infrastructure development, habitat fragmentation, reduction of gene flow and genetic erosion. However, the central threat to bryophyte survival is generally considered to be climate change (e.g. Hodgetts et al. 2019a). Climate change represents a multidimensional threat that compounds constant pressure on bryophytes through shifts in temperature, alterations in precipitation patterns and dynamics, extreme weather events and changes in seasonality.

Buxbaumia viridis (Moug. ex Lam. & DC.) Brid. ex Moug. & Nestl. is a distinctive, peculiar and rare moss species, belonging to an isolated group of mosses (Buxbaumiaceae, Buxbaumiales). It has unusual morphology, with reduced gametophytes and asymmetrical sporophytes developing directly on protonema. *B. viridis* prefers old-growth and near-natural montane and boreal forests with deadwood presence in shaded, humid sites with low competition from other cryptogams and tracheophytes (e.g. Dragićević et al. 2012) and is considered a flagship species for deadwood-dependent cryptogam and invertebrate communities (Spitale & Mair 2017). It is sensitive to environmental changes and is an indicator species of well-preserved forest ecosystems. Its relatively large spores limit long-distance dispersal and enhance establishment in stable forest ecosystems.

B. viridis is a strict substrate specialist and it occurs almost exclusively on strongly decayed dead wood and logs of spruce *Picea abies* (L.) H. Karst and rarely other trees like fir *Abies alba* Mill. and beech *Fagus sylvatica* L. (e.g. Sabovljević et al. 1999, Blockeel 2020). In stable conditions, *B. viridis* can also grow on smaller pieces of dead wood lying on damp ground. In Slovenia, it has so far only been found on spruce *P. abies* wood. In the UK, it has been reported to thrive on deadwood of downy birch *Betula pubescens* Ehrh., Scotch pine/red pine *Pinus sylvestris* L., black alder *Alnus glutinosa* (L.) Gaertn., juniper *Juniperus* sp., oak *Quercus* sp., along with several other species, and even directly on the forest floor and anthills (Taylor 2010, 2012). However, this seems to be a rare event that only occurs under specific habitat conditions.

B. viridis is threatened in many European countries, listed in the EU Habitat Directive (Annex II) and protected under the Bern Convention. On the most recent Red List of Slovenian Bryophytes (Martinčič 2024), it is classified as near threatened based on a high number of recent records. In Europe, the overall population is assessed as Least Concern (Hodgetts et al. 2019a), and although Hodgetts et al. (2019b) stated it has not experienced an overall decline in Europe, it has experienced local declines, resulting in it being included on many regional and national red lists. Hodgetts & Lockhart (2020), Ștefănuț et al. (2023), Puglisi et al. (2024), Sabovljević et al. (2024) and Stebel & Żarnowiec (2025) provide national red list assessments for this species across Europe; it is classified as critically endangered in Finland and Montenegro; endangered in Serbia, Greece and Hungary; vulnerable in Romania, Great Britain, Andorra, Spain, Czechia, Slovakia and Estonia; and near threatened in Italy, Norway, Switzerland, Poland and Bulgaria. The species is also listed as threatened under non-IUCN categories in Austria, Germany and Latvia. In other countries, there is insufficient data on its presence and distribution to allow assessment.

To develop integrative conservation approaches and address major threats (including habitat degradation, pollution and climate change), novel field and experimental research approaches, together with long-term monitoring, are required. One promising approach is the application of species distribution modelling under various climate change scenarios. Such models enable assessment of the future persistence and conservation needs of the species by identifying the key bioclimatic and habitat factors influencing its survival and distribution. Furthermore, they can facilitate the identification of priority areas for *in situ* conservation in Slovenia and emphasize the need for integrative conservation measures, including physical site protection, the application of biotechnological and biotechnical tools and the adaptation of conservation programs, policies and threatened species management strategies.

2. MATERIALS AND METHODS

2.1. Research area

Slovenia is located in the transition zone between Central and Southeastern Europe, on the margin of the south-eastern Alps. Due to its location at the crossroads of the Mediterranean, Alpine and continental climatic regimes, it experiences large climate variation (Škrk et al. 2021). Despite its relatively small size, the area includes Alpine, pre-Alpine, Dinaric, pre-Dinaric, sub-Pannonian and sub-Mediterranean biogeographical regions, each characterized by distinct climatic conditions and forest community compositions.

Slovenian forests cover almost 60% of the total area of the country (ZGS 2025). Due to its heterogeneous relief, climate and former forest management, Slovenian forests consist of a diverse mosaic of forest types, ranging from lowland floodplain forests to widespread mesic mixed forests dominated by beech at medium altitudes and to mountainous coniferous forests at higher altitudes (Kutnar et al. 2021). In lowland areas that experience periodic flooding, forest stands occur in narrow strips along rivers and streams and are dominated mainly by willow *Salix* sp., alder (*Alnus glutinosa*, *A. incana* (L.) Moench.), ash (*Fraxinus excelsior* L., *F. angustifolia* Vahl) and common oak *Quercus robur* L., with mixtures of various broadleaved trees (e.g. *Carpinus betulus* L., *Acer campestre* L., *Ulmus laevies* Pall.). In the hilly areas above the floodplains, mixed forests of sessile oak *Q. petraea* (Matt.) Liebl. and hornbeam *C. betulus* are the predominant forest types. Most of the mountain areas are covered by forests of European beech *Fagus sylvatica*, with mixtures of various broadleaved trees (e.g. *Acer pseudoplatanus* L., *F. excelsior*, *Ulmus glabra* Huds.) and conifers (*Abies alba* Mill., *Picea abies*). The Dinaric forest of European beech and European silver fir *A. alba* is one of the most extensive forest types in the country, covering more than 10% of the total forest area (Dakskobler 2008, Kutnar et al. 2021). In the Alpine region, various European beech forests mixed with Norway spruce *P. abies*, European silver fir and European larch *Larix decidua* Mill. reach the timberline up to the belt of dwarf mountain pine *Pinus mugo* Turra (Kutnar et al. 2021).

Scots pine *P. sylvestris* forests can be found throughout the interior of the country in nutrient-poor soils. Forest of Austrian pine *P. nigra* J.F. Arnold grow on some extreme slopes in the continental part of the country, where there is a warmer (micro)climate; this tree species was also planted over the greater part of southwestern Slovenia in the Karst region. All over the country, forests and shrubby vegetation of various thermophilic broadleaf species (e.g. *Ostrya carpinifolia* Scop., *F. ornus* L., *Q. pubescens* Willd., *Q. cerris* L., *Sorbus aria* (L.) Crantz) extend mainly on limestone and dolomite rocks on warm, south-facing slopes (Kutnar et al. 2021).

In its natural range, spruce grows more abundantly only in the Alps in the north of the country and to a much lesser extent in cold valleys and karst depressions in the Dinaric region in the southern part of the country. However, in past centuries, spruce was one of the most anthropogenically favoured tree species in Slovenia, as it was intensively introduced and planted in many regions because of its valuable timber and wide ecological adaptability (Kutnar et al. 2021, Kermavnar et al. 2023).

Although principles of management that are close to nature, sustainable and multifunctional have been implemented to a greater degree in Slovenia compared to some other European countries, anthropogenic alterations of forest stands have nevertheless been a common practice. Today's forest status often deviates from that which would have developed without human engagement. The planting of economically profitable but ecologically unsuitable tree species (poorly adapted to local site conditions), such as Norway spruce, remains one of the main problems in Slovenian forestry. In areas outside its natural distribution, spruce is much more sensitive to extreme weather events, and widespread bark beetle infestation is more frequent, especially at lower altitudes (Kutnar & Kobler 2011, 2014, de Groot et al. 2018, 2019, Kutnar et al. 2021, Kermavnar et al. 2023).

The proportion of Norway spruce in the growing stock of Slovenian forests has declined significantly over the last 20 yr, and this decline has been particularly evident in the last 10 yr (Kutnar et al. 2021). Among the tree species in the growing stock of Slovenian forests, European beech (31.9%) and Norway spruce (28.2%) dominate, followed by silver fir (7.9%), sessile oak (5.1%), Scots pine (4.2%), sycamore maple (3.8%) and common hornbeam (2.7%). In total, broadleaves account for 56% of the timber stock, while conifers make up 44% (Pintar et al. 2024).

2.2. Species occurrence data

The earliest record of *Buxbaumia viridis* in Slovenia dates to 1860, from Konjiška Gora in Štajerska (Reichardt 1860). In the 19th and beginning of the 20th century, the species was found in 13 other localities in different parts of Slovenia (Strgulc Krajšek et al. 2025 and references therein). In the second half of the 20th century, several localities from the Kočevje region were published (Martinčič 1976, Hočevar et al. 1980, Hočevar 1985, Strgulc Krajšek et al. 2025 and references therein). Since 2021, when there were systematic searches for the species in different parts of Slovenia with suitable habitats, the number of localities has increased significantly. It has been confirmed to be thriving in some previously known locations, and many new sites have been found (Strgulc Krajšek et al. 2025). Newly discovered locations included Pohorje and several sites in the Koroška region in the northern part of Slovenia. There are some new sites in the Julian Alps, the Krim mountain range and the Kočevje region (Strgulc Krajšek et al. 2025).

A total of 54 points were obtained after spatial bias reduction (1 sample per raster cell ≈ 1 km^2 at the equator), comprising 11 records from the 19th century, 11 from the 20th century, and 32 from the 21st century, which were used for modelling.

2.3. Predictor variables

Bioclimatic (current and future) data, together with elevation and forest type data, were used for species distribution modelling and future projections. Current bioclimatic and elevation data were obtained from the WorldClim 2.1 database (Fick & Hijmans 2017) at a spatial resolution of 30 arc-seconds. Future climate data were acquired from the same source, at the same spatial resolution, using different climate models for 2 reference periods of 2050 (2041–2060) and 2090 (2081–2100). Two shared socioeconomic pathways (SSPs) were considered: SSP2-4.5 (intermediate emission scenario) and SSP5-8.5 (very high emission scenario) (Pörtner et al. 2022). The selected future climate models for these reference periods and SSPs were MIROC6 (Shiogama et al. 2019) and GISS-E2-1-G (Kelley et al. 2020).

In addition to the bioclimatic data, vegetation data on the forest area in Slovenia were used. These data were obtained from the Vegetation Map of Forest Communities of Slovenia at a scale of 1:400 000 (Čarni et al. 2002, Marinček & Čarni 2002). Forest type vector data were rasterized to match the spatial extent and resolution of the bioclimatic layers (30 arc-seconds) using QGIS (v.3.44.4) (Dawson et al. 2025).

All variables were subjected to collinearity reduction, implementing the variance inflation factor (VIF) procedure with a VIF threshold of 10, using the vifstep function in the 'usdm' R package (Naimi et al. 2014).

The selected bioclimatic predictors included bio3 (isothermality), representing the ratio of the mean diurnal temperature range to the annual temperature range, expressed as a percentage (%); bio4 (temperature seasonality), representing the standard deviation of monthly mean temperatures multiplied by 100 (SD × 100); bio6 (minimum temperature of the coldest month), representing the minimum temperature (°C) recorded during the coldest month of the year; bio8 (mean temperature of the wettest quarter), representing the mean temperature (°C) during the wettest consecutive 3 mo period; bio15 (precipitation seasonality), representing the coefficient of variation of monthly precipitation totals, expressed as a percentage (%); and vegetation, comprising the classification of forest communities.

Classification of forest communities from 1 to 60 does not follow a specific gradient, given that communities are classified according to various factors, such as altitude, tree composition, geological substrate and ecological and site conditions. Consequently, forest communities are classified on a nominal scale, and their order does not reflect an obvious climate-related gradient. However, the numbering scheme reflects some underlying grouping, where similar forest types (e.g. oak-dominated, beech forests, spruce forests) are clustered within adjacent value ranges rather than being randomly assigned. Therefore, in this study, this variable was treated as a pseudo-numeric predictor to preserve this partial ecological structure. We acknowledge that this approach does not imply equal distances between classes, but allows the models to capture broad transitions among related vegetation types. Given the structure of the data set and the modelling framework, this representation was considered a pragmatic compromise between fully categorical encoding and loss of ecological ordering.

2.4. Species distribution modelling

Ensemble modelling was implemented in R (v.4.3.2; R Core Team 2023) using the 'biomod2' R package (v.4.3-4; Guéguen et al. 2025). A total of 5 sets of 200 pseudo-absences were generated using a random sampling strategy. This ratio (between presences and pseudo-abscences) reflects the size of the research area and was selected in order to maximize predictive accuracy, as a large imbalance between presence and absence data can lead to biased model coefficients and a decrease in sensitivity for certain types of algorithms (Barbet-Massin et al. 2012). In total, 600 individual models were computed (5 sets of pseudo-absences × 10 cross-validation replicates × 12 modelling algorithms) and evaluated using receiver operating characteristic (ROC) and true skill statistic (TSS) metrics (Allouche et al. 2006, Jiménez-Valverde 2012). The modelling algorithms included artificial neural network (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model (GBM), generalized linear model (GLM), multivariate adaptive regression splines (MARS), maximum entropy (MAXENT), random forest (RF), surface range envelope (SRE) and extreme gradient boosting (XGBOOST).

Only models with ROC > 0.9 and TSS > 0.7 (i.e. models with excellent predictive power; Allouche et al. 2006, Okeh & Okoro 2012) were retained for ensemble model construction. The committee averaging approach was used for ensemble model creation due to its superior predictive performance. Model cross-validation was performed by splitting the data into training (80%) and testing (20%) subsets, with each model replicated 10 times. Selected variable importance of the ensemble model was computed, alongside species response curves and loss, gain and range change percentages. Model projections (current and future) were generated for different climate models, reference periods and emission scenarios.

3. RESULTS

3.1. Ensemble model of the current distribution in Slovenia

Out of 600 individual models, only those demonstrating excellent predictive performance (ROC > 0.9) were included in the final ensemble model. The best-performing ensemble approach was committee averaging, achieving a ROC value of 0.977 and a TSS of 0.858, reflecting outstanding predictive accuracy. The projection of this ensemble model, representing the predicted current distribution of *Buxbaumia viridis* (Fig. 1A), reveals that around 12% of the territory of Slovenia is potentially suitable for the species (suitability higher than 0.5). Most suitable areas are concentrated in mountainous regions, particularly in northern Slovenia, encompassing the Julian and Kamnik—Savinja Alps and the Pohorje mountain range. Additionally, highly suitable areas were identified in the southern parts of the country, including the area between Loški Potok and Draga, and Snežnik Mountain, the Kočevski Rog karst plateau and Krim Mountain. Many occurrence points from the 19th and 20th centuries are located outside the predicted suitable habitats or in areas of low suitability, illustrating the long-term effects of climate change on the species distribution, as well as land use change through time (Fig. 1A).

Among the selected predictors (chosen based on VIF analysis), the highest variable importance was recorded for bio6 (minimum temperature of the coldest month; mean ± SD: 0.54 ± 0.016), followed by bio3 (isothermality), vegetation (forest community type), bio4 (temperature seasonality) and bio8 (mean temperature of the wettest quarter) (Fig. 1B).

3.2. Ecological requirements and response curves

The highest probability of *B. viridis* occurrence was associated with very low minimum temperatures in the coldest month (bio6), specifically between −7.5

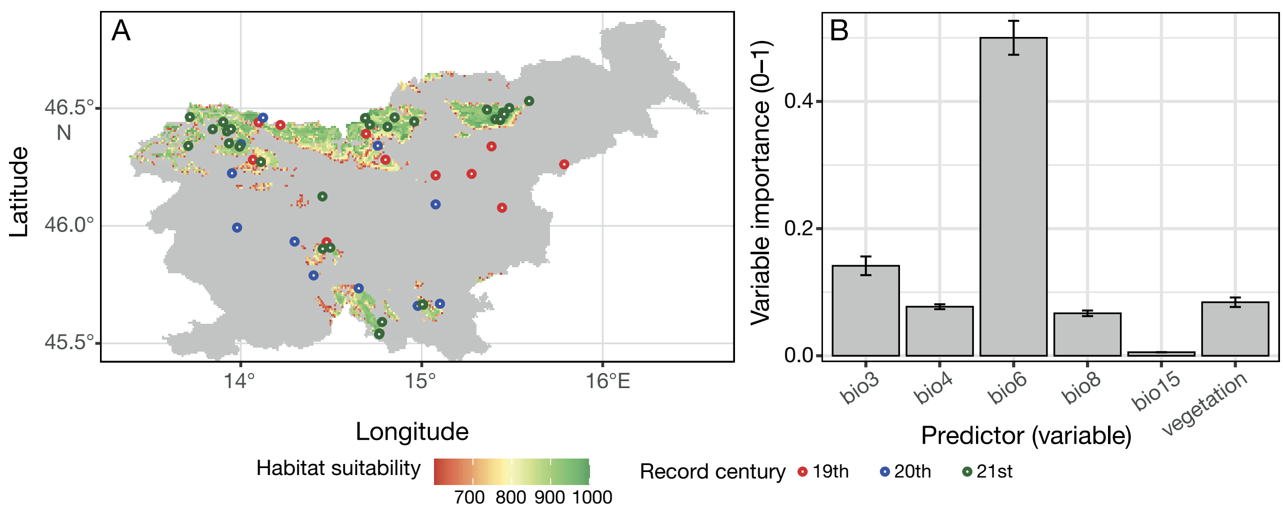

Fig. 1. (A) Predicted current distribution of *Buxbaumia viridis* in Slovenia showing species occurrence records from different time periods and (B) the relative importance of variables in the ensemble model, presented as mean ± SD. Bio3 (isothermality): ratio of the mean diurnal temperature range to the annual temperature range (%); bio4 (temperature seasonality): SD of monthly mean temperatures multiplied by 100; bio6 (minimum temperature of the coldest month): minimum temperature (°C) recorded during the coldest month of the year; bio8 (mean temperature of the wettest quarter): mean temperature (°C) during the wettest consecutive 3 mo period; bio15 (precipitation seasonality): coefficient of variation of monthly precipitation totals (%); vegetation: classification of forest communities

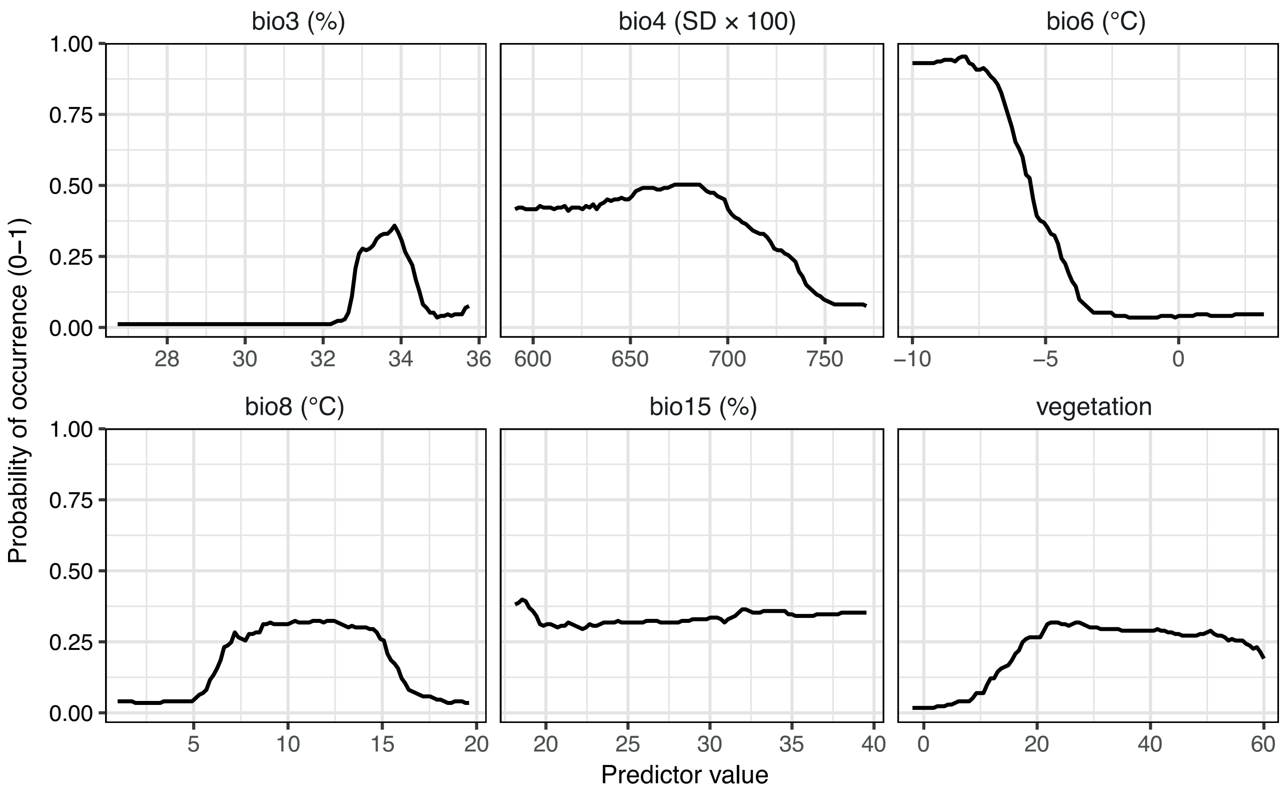

Fig. 2. Response curves illustrating the predicted probability of *Buxbaumia viridis* occurrence for all selected variables included in the ensemble model. See Fig. 2 for definitions of the variables

and −10°C (Fig. 2). In addition, the species showed preference for environments with relatively high isothermality (bio3), indicating rather low daily temperature fluctuations in relation to annual variation, and relatively low temperature seasonality (bio4), reflecting more thermally stable conditions throughout the year (Fig. 2). During the wettest quarter, the highest probability of occurrence was predicted at mean temperatures between 7 and 15°C, as inferred from bio8 values (Fig. 2). With respect to forest community, the highest habitat suitability was associated with forest types corresponding to *Fagetum* sensu lato, followed by *Picetum* sensu lato associations (Fig. 2). The maximums of probability of occurence were recorded for *Omphalodo–Fagetum* and *Ranunculo platanifoliae–Fagetum* associations (Fig. 2).

3.3. Predicted distribution in Slovenia

3.3.1. Prediction of future distribution under SSP2-4.5

Most currently suitable habitats are projected to be lost by 2050, with even greater reductions expected by 2090 according to the MIROC6 model under the SSP2-4.5 greenhouse gas emission scenario (Fig. 3A,B). This model predicts that suitable habitats will persist mainly within the northern mountain ranges, including the Julian Alps, Kamnik–Savinja Alps and the Pohorje region by 2050, while the latter is expected to disappear by 2090. Furthermore, the MIROC6 model indicates that most newly gained suitable areas will occur within the Julian Alps (Fig. 3A,B). Overall, habitat losses are estimated at 73.1 and 86.3% for 2050 and 2090, respectively, with only minor gains of 5.4 and 3.4%, resulting in total range contractions of 67.7 and 82.9% (Fig. 4A,B).

The GISS-E2-1-G climate model produced even more restrictive projections under the same emission scenario (SSP2-4.5), indicating a greater loss of suitable habitats. According to this model, suitable areas are expected to persist only within the Kamnik–Savinja Alps by 2050, followed by an almost complete disappearance of suitable conditions by 2090 (Fig. 3C,D). No range gains were predicted under this model and scenario, resulting in a total projected range contraction of 97.9 and 100% for 2050 and 2090, respectively (Fig. 4C,D).

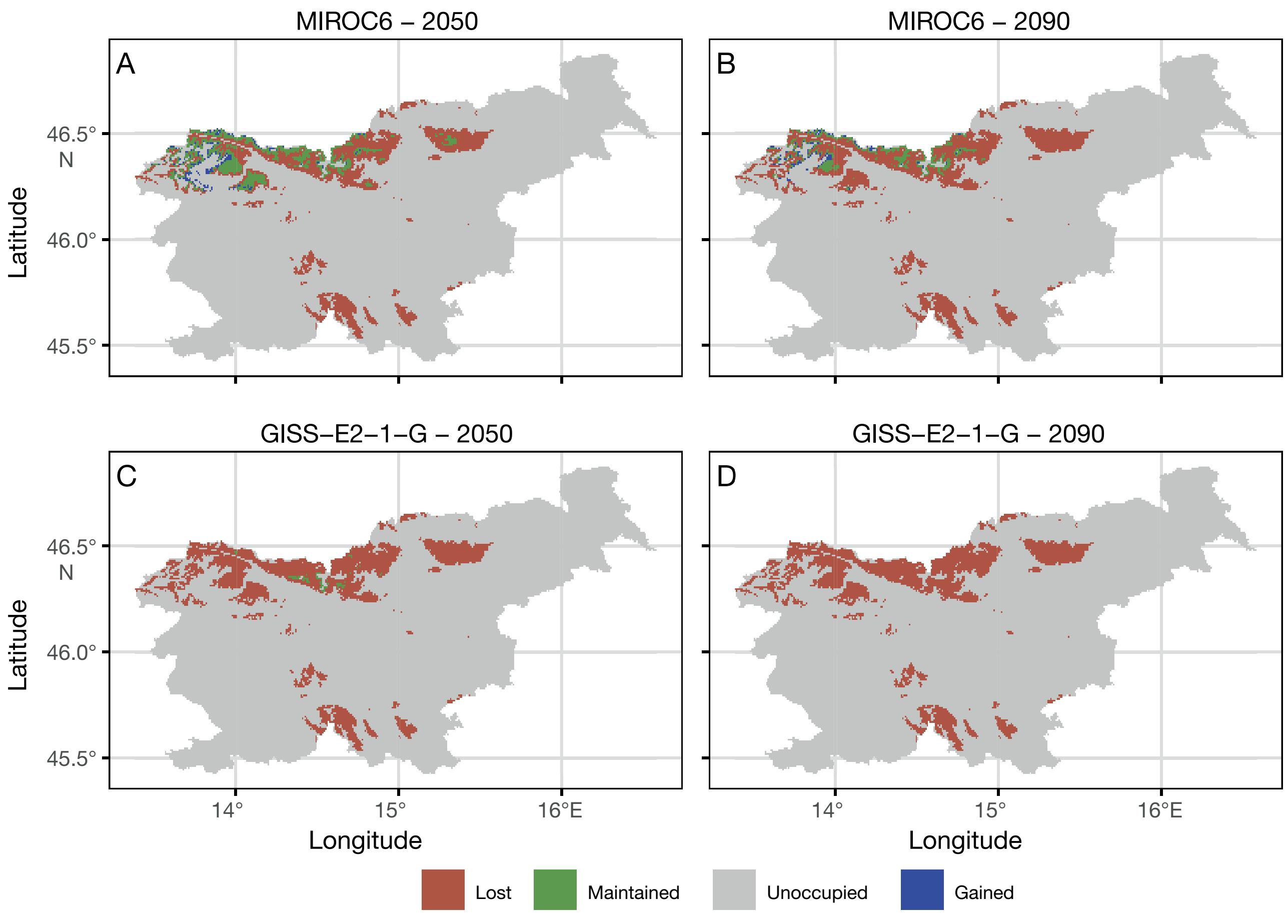

Fig. 3. Projected distribution of *Buxbaumia viridis* in Slovenia under the SSP2-4.5 scenario for different climate models and time periods. (A) MIROC6 2050; (B) MIROC6 2090; (C) GISS-E2-1-G 2050; (D) GISS-E2-1-G 2090

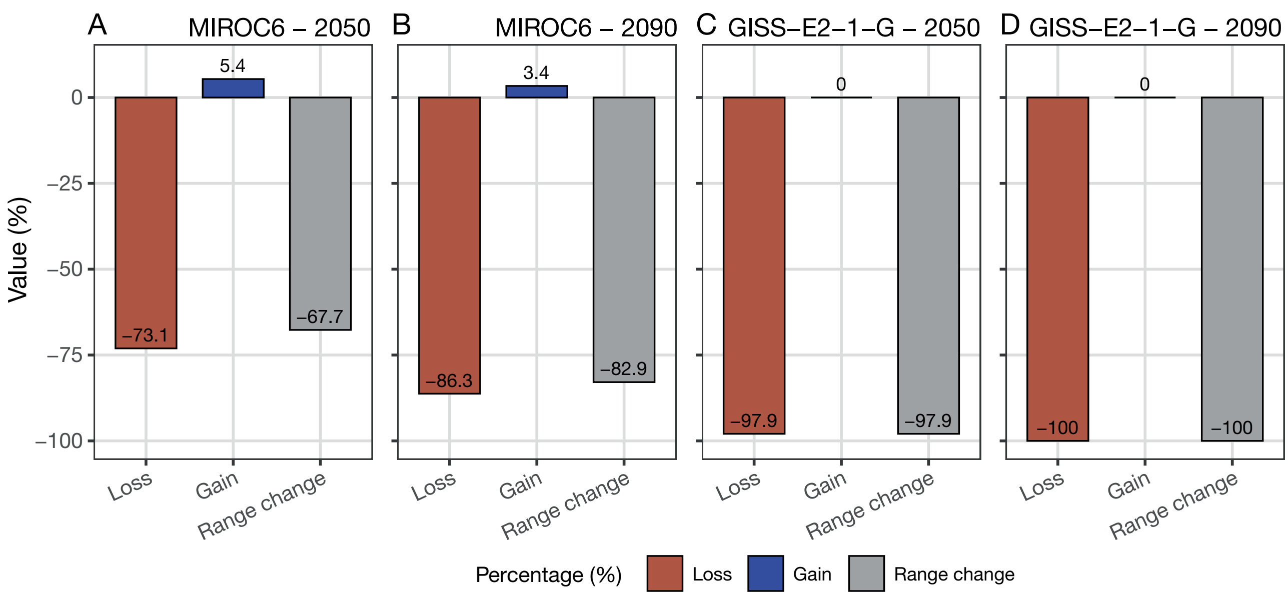

Fig. 4. Predicted habitat loss, gain, and overall range change of *Buxbaumia viridis* under the SSP2-4.5 scenario for different climate models and time periods. (A) MIROC6 2050; (B) MIROC6 2090; (C) GISS-E2-1-G 2050; (D) GISS-E2-1-G 2090

3.3.2. Prediction of future distribution under SSP5-8.5

Under the more severe emission scenario (SSP5-8.5), the MIROC6 model predicts a slightly more restricted distribution for the year 2050 compared to SSP2-4.5 (Fig. 5A). Similar to SSP2-4.5, the majority of the predicted range is located in the Julian Alps and the Kamnik–Savinja Alps, with even stronger reductions in the Pohorje region. By 2090, the predicted suitable range is fully reduced (Fig. 5B). Predicted species habitat range loss varies between 73.8 and 100% for the MIROC6 model in 2050 and 2090, respectively (Fig. 6A,B), with small predicted gains observed only for 2050 (Fig. 6A).

A complete loss of suitable area for the species within Slovenia is predicted by the GISS-E2-1-G model for both reference periods (2050 and 2090) (Fig. 5C,D), with predicted range reductions between 99.9 and 100% (Fig. 6C,D).

4. DISCUSSION

Habitat loss for *Buxbaumia viridis* in Slovenia is projected under all tested climate scenarios. Under the high-emission CO_2 scenario (SSP5-8.5) for the year 2090, models predict a complete loss of climatically suitable habitat. Comparable projections have been reported for other parts of South-eastern Europe, including Serbia (Pantović et al. 2023) and Romania (Ștefănuț et al. 2023), indicating a consistent regional pattern of range contraction. Although intensified survey efforts have increased the number of known occurrences and led to lower threat assessments in some countries (Natcheva et al. 2024), the convergence of modelling results across studies highlights the urgent need for enhanced long-term monitoring and proactive conservation actions.

Additionally, recent findings on protonemal gemmae production in *B. viridis* (Guillet et al. 2021) may reflect suboptimal developmental conditions in some

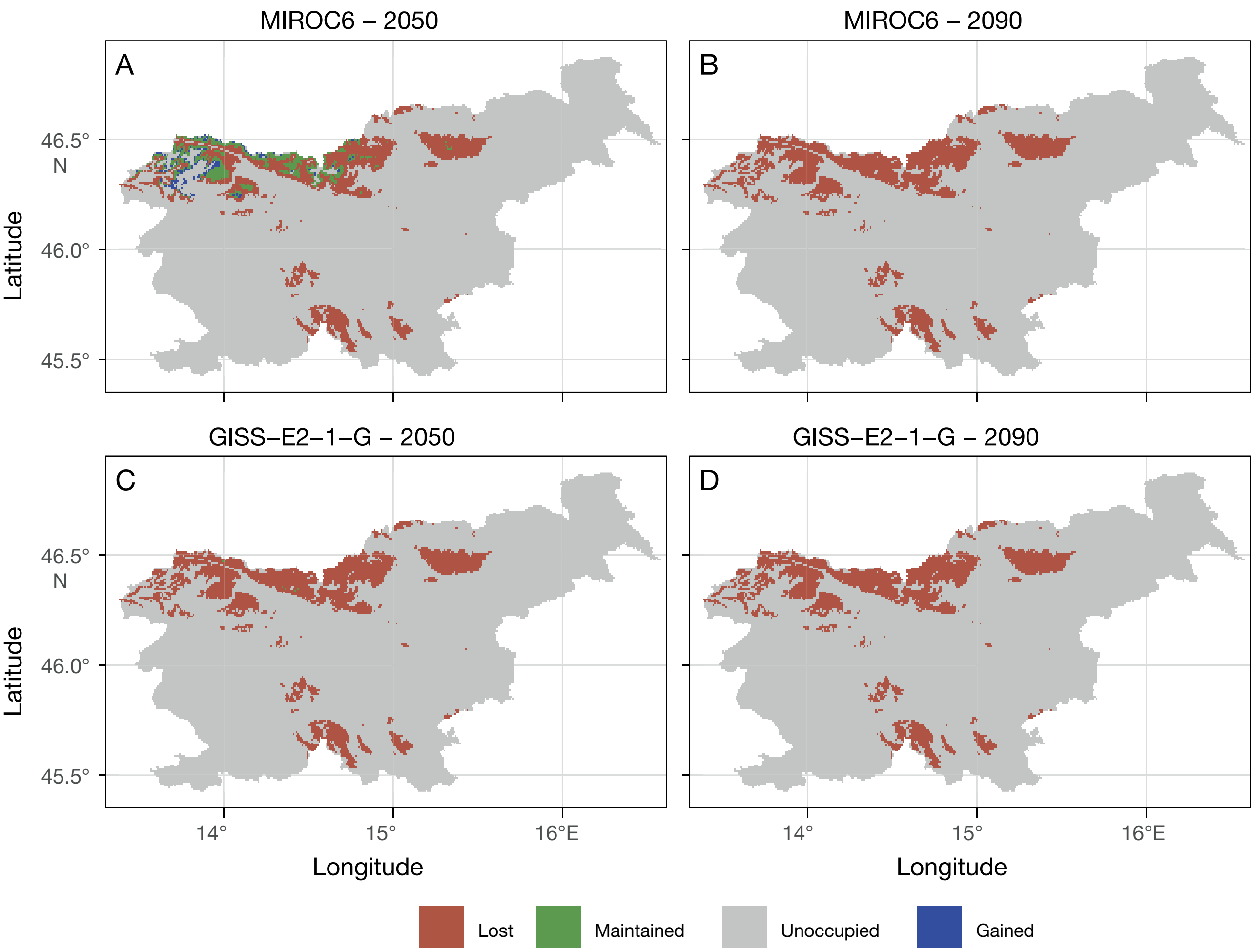

Fig. 5. Projected distribution of *Buxbaumia viridis* in Slovenia under the SSP5-8.5 scenario for different climate models and time periods. (A) MIROC6 2050; (B) MIROC6 2090; (C) GISS-E2-1-G 2050; (D) GISS-E2-1-G 2090

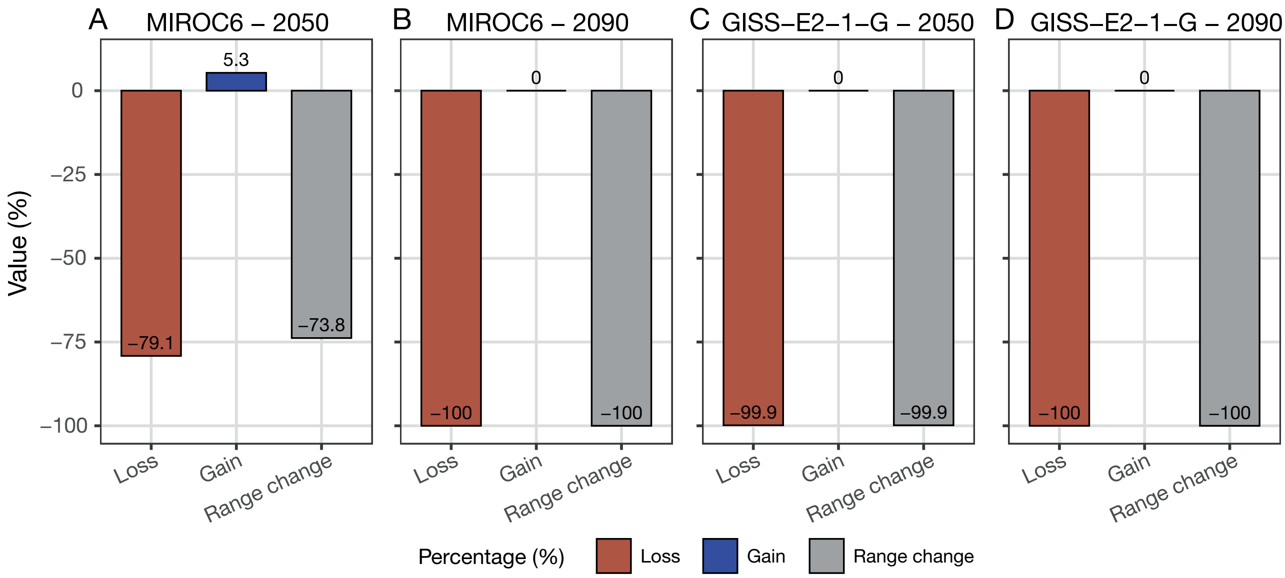

Fig. 6. Predicted habitat loss, gain, and overall range change of *Buxbaumia viridis* under the SSP5-8.5 scenario for different climate models and time periods. (A) MIROC6 2050; (B) MIROC6 2090; (C) GISS-E2-1-G 2050; (D) GISS-E2-1-G 2090

regions, where stress at the protonemal stage limits reproductive effort and suppresses sporophyte induction and development. Deme & Csiky (2021) demonstrated that a higher occurrence of protonemal gemmae can positively affect species survival, likely by promoting vegetative spread under unfavourable conditions. However, this strategy may come at the cost of reduced genetic diversity due to clonal propagation.

Given that *B. viridis* is dioecious, with male and female sexes developing on separate protonemata, it is also plausible that sex-specific differences in developmental or stress responses exist. Such differences remain poorly understood and cannot be excluded at present. The presence of *B. viridis* protonemal gemmae is indicated, but is still too uncertain to be reliably included in species distribution modelling. Consequently, our projections may represent a conservative scenario, potentially overestimating the rate of local extinction at fine spatial scales by not accounting for this vegetative (i.e. gemmae presence and dispersal) survival strategy. Addressing this knowledge gap will require the development of reliable molecular tools, including species barcoding applicable to non-sporophytic developmental stages and molecular sex markers, as recently proposed by Božović et al. (2024).

All analyses consistently indicate pronounced future range dynamics characterized by a substantial reduction of suitable areas on a national level. The mean temperature of the wettest quarter (bio8), isothermality (bio3) and precipitation seasonality (bio15) emerged as common bioclimatic drivers of *B. viridis* distribution in both Slovenia and Serbia (Pantović et al. 2023). In Slovenia, the minimum temperature of the coldest month (bio6) and temperature seasonality (bio4) appear to be particularly influential in shaping the current and projected distribution of the species. By contrast, in Serbia, due to its different geographic position and climatic regime, additional key predictors include the annual temperature range (bio7) and the mean temperature of the driest quarter (bio9). Collectively, these variables indicate that *B. viridis* is highly sensitive to drought stress and elevated temperatures, while favouring thermally stable climatic conditions. Such climatic stability likely acts synergistically with other ecological factors, notably moisture availability and forest structure, to enhance habitat suitability. This pattern aligns well with the known ecological requirements of the species, which can be broadly characterized as a preference for stable, cool and moist forest stands. Accordingly, *Fagetum* sensu lato, followed by *Picetum* sensu lato forest associations, represent key forest communities supporting the persistence and spread of *B. viridis*, as they provide the microclimatic buffering and deadwood availability essential for its survival.

Fagetum sensu lato is not entirely the most suitable forest community for the habitat of *B. viridis*. However, this is expected given that many beech forests have a higher proportion of spruce (and fir) due to forest management, and some mountain beech forests have a higher natural admixture of conifers (including spruce); for example, *Luzulo–Fagetum* or *Abieti–Fagetum* sensu lato (including *Omphalodo–Fagetum*). Further models might provide a higher resolution and be more reliable if they incorporate real vegetation or forest stand maps showing the proportion of tree species.

The available evidence suggests that a long-term trend of range contraction has already been underway in Slovenia over the past few centuries. Historical occurrence records from the 19th and 20th centuries are largely outside areas currently predicted as suitable or fall within zones of low habitat suitability, illustrating the prolonged and ongoing influence of climate change and global warming on the distribution of *B. viridis*, as well as a lack of novel investigation and land usage changes through time. Distribution dynamics predicted by the models suggest a further pronounced decline and potential loss of suitable habitats for *B. viridis* in Slovenia. In addition, with the spruce forest decrease in Slovenia due to climate changes and disturbances as documented by Kutnar & Kobler (2011, 2014) and Kutnar et al. (2021), the species will be of high conservation interest and require constant monitoring.

Modelling the distribution and habitat suitability of bryophyte target species not only improves our understanding of past and future ranges, but also allows us to (try to) prevent and plan for changes that occur in the natural environment. Such models provide valuable tools to determine the effects of invasive species, mitigate infrastructure development, assist in monitoring and management of natural spaces, assess potential genetic diversity loss and aid in biodiversity conservation and/or high-priority investment in habitat protection. The importance of these tools is emphasized by the limited number of studies that currently address the fate, survival and distribution of bryophytes under changing environmental conditions (e.g. Mallen-Cooper et al. 2023, Abubakar et al. 2024, Abay & Gül 2025a,b, Bacilliere et al. 2025).

5. CONCLUSIONS

Our findings indicate that *Buxbaumia viridis* is strongly constrained by cold-climate conditions. The species is associated with relatively high isothermality and low temperature seasonality, favouring thermally stable environments. Its occurrence is also closely linked to the availability of deadwood-rich forest microhabitats, particularly those originating from conifers (in particular, spruce). These dependencies make *B. viridis* especially sensitive to ongoing climate warming, forest structural simplification and forest management practices that do not support sufficient deadwood accumulation. The projected loss of suitable habitats suggests that future persistence of *B. viridis* in Slovenia will increasingly rely on climatically buffered forest refugia, characterized by stable, relatively cool and humid microclimates and a continuous supply of decaying wood and woody debris. The protection and management of such refugial habitats (including primeval and other well-preserved forest reserves), particularly within montane forests with predominant spruce, together with long-term monitoring, will be essential to mitigate the combined effects of climate change and habitat degradation.

Acknowledgements. The study was financially supported by the Slovenian Research Agency (grant no. P1–0212), the Ministry of Environment and Spatial Planning (document no. N2550–18–0037), project LIFE17 IPE/SI/000011–LIFEIP NATURA.SI, which is co-funded by the European Union under the LIFE Programme, the Ministry of Natural Resources and Spatial Planning and partners, and by the Serbian Ministry of Science, Technological Development and Innovations, contract nos. 451-03-34/2026-03/200178 and 451-03-33/2026-03/200178. We thank all field botanists who contributed data.

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Editorial responsibility: Brendan Godley, University of Exeter, Cornwall Campus, UK
Reviewed by: G. Gecheva and 2 anonymous referees
Submitted: March 23, 2026; Accepted: May 11, 2026
Proofs received from author(s): July 24, 2026