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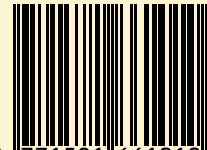
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Front cover photography: After a major storm, the carbonate Nullarbor Plain was flooded due to its impermeable layer of clay (photograph: Matej Lipar).

Fotografija na naslovnici: Po močnejši nevihti je bila sicer karbonatna ravnina Nullarbor poplavljen zaradi nepropustne plasti gline (fotografija: Matej Lipar).

PREDICTING THE POTENTIAL ECOLOGICAL NICHE DISTRIBUTION OF SLOVENIAN FORESTS UNDER CLIMATE CHANGE USING MAXENT MODELLING

Tim Gregorčič, Andrej Rozman, Blaž Repe



TIM GREGORČIČ

The *Hacquetio-Fagetum* forests in the southeastern part of the Mirna Valley.

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Tim Gregorčič¹, Andrej Rozman², Blaž Repe³

Predicting the potential ecological niche distribution of Slovenian forests under climate change using MaxEnt modelling

ABSTRACT: The aim of the article is to assess the potential impacts of climate change on Slovenian forests in the period 2080–2100 based on two climate scenarios: SSP1-2.6 (optimistic) and SSP5-8.5 (pessimistic) using the MaxEnt software. Slovenian forests are divided at the ecological community level into thirteen forest vegetation types. Analyses of changes in ecological niche areas, distances of vectors between centroids of present areas and future ecological niches, and general spatial changes are carried out. In addition, changes in the altitudinal zones of forest vegetation types were investigated. The results indicate significant changes for Thermophilous beech forests and Thermophilous hop-hornbeam, sessile oak, downy oak, Scots pine and black pine forests. The potential changes in the altitudinal zones of forest vegetation types indicate a clear trend of forest vegetation types moving to higher altitudinal zones.

KEY WORDS: phytogeography, ecological niche modelling, shared socio-economic pathways (SSP), forest vegetation types, Slovenia

Ocena možnih vplivov podnebnih sprememb na prostorsko razporeditev ekoloških niš slovenskih gozdov z uporabo metode maksimalne entropije

POVZETEK: Namen raziskave je bil oceniti možne vplive podnebnih sprememb na slovenske gozdove v obdobju 2080–2100 glede na dva podnebna scenarija: SSP1-2.6 (optimistični) in SSP5-8.5 (pesimistični) z metodo maksimalne entropije. Gozdni rastiščni tipi so razdeljeni na trinajst gozdnih vegetacijskih tipov. Opravljeni sta analizi prostorskih sprememb ekoloških niš in razdalj vektorjev med centriodi sedanjih območij in napovedanih ekoloških niš ter sinteza skupnih možnih prostorskih sprememb gozdnih vegetacijskih tipov. Raziskane so tudi možne spremembe sestave vegetacijskih pasov. Rezultati kažejo na možnost znatnih sprememb ekoloških niš. Največje skupne prostorske spremembe so bile ocenjene za termofilna bukvoja in termofilna črnogabrovja, hrastovja, rdečeborovja in črnoborovja. Rezultati analize možnih sprememb vegetacijskih pasov kažejo trend pomikanja v višje nadmorske višine.

KLJUČNE BESEDE: fitogeografija, modeliranje ekoloških niš, smeri skupnega družbenogospodarskega razvoja (SSP), gozdni rastiščni tipi, Slovenija

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1 Introduction

This study uses MaxEnt, one of the ecological niche modelling methods, to assess the potential impacts of climate change on Slovenian forests. Ecological niche modelling has become an important branch of phytogeography as the question of the potential impacts of climate change on species distribution becomes increasingly important. Planet Earth is facing changes in its climate system due to massive anthropogenic greenhouse gas emissions (Masson-Delmotte et al. 2021). The impacts of climate change may significantly alter or damage ecosystems, biodiversity and various plant and wildlife habitats, including the stability of society (Baisero et al. 2020; Brodie et al. 2020; Pörtner et al. 2022).

Martinez Del Castillo et al. (2022) predicted growth declines of European beech forests by 2090 for the CMIP6 climate scenarios SSP1-2.6 and SSP5-8.5. They predicted the most significant productivity losses towards the southern distribution limit of *Fagus sylvatica*. A reduction in areas suitable as habitat for most tree species, with higher elevation areas is expected in Greece in SSP1-2.6 and SSP5-8.5 experiencing greater potential habitat shrinkage (Fyllas et al. 2022). Buras and Menzel (2019) projected a decline in tree species richness in Mediterranean and Central European lowlands based on the CMIP5 climate scenarios RCP4.5 and RCP8.5, while Scandinavian and Central European high mountain forests are expected to experience an increase in diversity over the period 2061–2090. Another European study by Dyderski et al. (2018) shows different response patterns of tree species to projected climate change in RCP2.6 and RCP4.5 scenarios, although the species studied would face a significant decrease in suitable habitat area.

With about 61.5% of the country's land area, Slovenia is the country with the third largest forest area in relation to the total area in the EU-28, according to Eurostat. The diverse ecological conditions have enabled the development of a relatively high forest species richness on a small area (Kutnar, Kobler and Bergant 2009). Kutnar, Kobler and Bergant (2009) showed that global warming could have a significant impact on the redistribution of Slovenian forest vegetation types (FVTs).

A later study by Kutnar and Kobler (2011) predicted a decline in beech forests and an increase of thermophilous forests by 2100 for both optimistic and pessimistic climate scenarios. It was also predicted that a large proportion of coniferous forests would be transformed to deciduous forests. According to Kutnar and Kobler (2014), the abundance of three of the most important tree species in Slovenian forests – *Picea abies*, *Fagus sylvatica* and *Abies Alba* – is likely to decrease significantly by the end of the 21st century. In the pessimistic scenario, the population of these tree species could decline by 97%, 82% and 97%, respectively. They predicted the spread of thermophilous, drought-tolerant species and vegetation types (e.g. *Ostrya carpinifolia*, *Fraxinus ornus*, *Quercus pubescens*), the largest potential increase was predicted for *Robinia pseudoacacia*.

The aim of this study is to assess the potential impacts in the period 2080–2100 based on the two CMIP 6 climate scenarios: SSP1-2.6 (optimistic) and SSP5-8.5 (pessimistic). The optimistic scenario predicts an increase in global average temperature of 2.0 °C (with a 5–95% range of 1.3–2.8 °C) in the period 2081–2100 compared to the period 1850–1900. In contrast, the pessimistic scenario, characterised by high GHG emissions and limited mitigation action, predicts a stronger increase in global average temperature of 4.8 °C (with a 5–95% range of 3.6–6.5 °C) during the same period compared to the period 1850–1900 (Lee et al. 2021).

2 Methods

2.1 Data

The 78 most important Slovenian forest communities were grouped into 13 FVTs at the ecological community level based on their common preferences for site conditions following the approach from Kutnar, Kobler and Bergant (2009) and Kutnar and Kobler (2011) (Table 1).

The FVT sampling data were taken from the Slovenian Forest Vegetation Map at a scale of 1:100,000 (Košir et al. 1974; Košir et al. 2003; Košir et al. 2007). The map covers the entire territory of Slovenia. Part of the FVT08 (Table 1) located on the Karst plateau and in the coastal region) was manually added to the FVT10, as we were guided by the latest forestry vegetation data from 2021 (Bončina et al. 2021), which were not available in GIS. For the presence data, 200 points were created randomly for each FVT, except for FVT09, FVT11 and FVT13. For these FVTs, 130 points were created randomly, as their area is relatively small compared to the grid cell size of the environmental data (500 m).

Table 1: The 13 Slovenian forest vegetation types.

Forest vegetation type	Representative forest communities
Acidophilous beech forests (FVT01)	<i>Blechno–Fagetum</i> , <i>Castaneo–Fagetum</i> , <i>Hieracio rotundati–Fagetum</i> , <i>Luzulo–Fagetum</i>
Acidophilous Scots pine forests (FVT02)	<i>Vaccinio myrtilli–Pinetum</i> , <i>Galio rotundifolii–Pinetum</i>
Lower mountainous beech forests on neutral or calcareous soils (FVT03)	<i>Hacquetio–Fagetum</i> var. geogr. <i>Geranium nodosum</i> , <i>Hacquetio–Fagetum</i> var. geogr. <i>Anemone trifolia</i> , <i>Hacquetio–Fagetum</i> var. geogr. <i>Ruscus hypoglossum</i> , <i>Hedero–Fagetum</i>
Mountainous beech forests on neutral or calcareous soils (FVT04)	<i>Arunco–Fagetum</i> , <i>Lamio orvalae–Fagetum</i> var. geogr. <i>Dentaria pentaphyllos</i> , <i>Lamio orvalae–Fagetum</i> var. geogr. <i>Dentaria polyphyllus</i> , <i>Aceri–Fraxinetum</i> s. lat.
High mountainous beech forests on neutral or calcareous soils in the Alpine region (FVT05)	<i>Homogyno sylvestris–Fagetum</i> , <i>Ranunculo platanifolii–Fagetum</i> var. geogr. <i>Hepatica nobilis</i> , <i>Anemone trifoliae–Fagetum</i> var. geogr. <i>Luzula nivea</i> , <i>Anemone trifoliae–Fagetum</i> var. geogr. <i>Helleborus niger</i> , <i>Lamio orvalae–Fagetum</i> var. geogr. <i>Sesleria autumnalis</i>
High Mountainous beech forests on neutral or calcareous soils in the Dinaric region (FVT06)	<i>Omphalodo–Fagetum</i> var. geogr. <i>Calamintha grandiflora</i> , <i>Stellario montanae–Fagetum</i> , <i>Ranunculo platanifolii–Fagetum</i> var. geogr. <i>Calamintha grandiflora</i> , <i>Polysticho lonchitis–Fagetum</i> , <i>Isopyro–Fagetum</i> , <i>Cardamini savensi–Fagetum</i>
Thermophilous beech forests (FVT07)	<i>Ostryo–Fagetum</i> , <i>Sesleria autumnalis–Fagetum</i> , <i>Ornithogalo pyrenaici–Fagetum</i>
Colline oak–hornbeam forests (FVT08)	<i>Ornithogalo pyrenaici–Carpinetum</i> , <i>Abio albae–Carpinetum betuli</i> , <i>Helleboro nigri–Carpinetum betuli</i> , <i>Epimedio–Carpinetum</i> , <i>Pruno padi–Carpinetum betuli</i>
Lowland willow, alder, and pedunculate oak forests (FVT09)	<i>Alnetum glutinosae</i> s. lat., <i>Alnetum incanae</i> , <i>Quercu roboris–Carpinetum</i> , <i>Pseudostellario–Quercetum</i> , <i>P.–Carpinetum</i> , <i>Salicetea purpureae</i>
Thermophilous hop–hornbeam, sessile oak, downy oak, Scots pine, and black pine forests (FVT10)	<i>Aristolochio luteae–Quercetum pubescentis</i> , <i>Ostryo carpinifoliae–Fraxinetum orni</i> , <i>Cytisantho–Ostryetum</i> , <i>Genisto januensis–Pinetum</i> , <i>Lathyro–Quercetum petraeae</i> , <i>Fraxino orni–Pinetum nigrae</i> , <i>Quercu–Ostryetum carpinifoliae</i> , <i>Sesleria autumnalis–Ostryetum</i>
Silver fir forests (FVT11)	<i>Bazzanio–Abietetum</i> , <i>Galio rotundifolii–Abietetum</i> , <i>Neckero–Abietetum</i>
Norway spruce forests (FVT12)	<i>Adenostylo glabrae–Piceetum</i> , <i>Luzulo sylvaticae–Piceetum</i> , <i>Asplenio–Piceetum</i> , <i>Rhytidiadelpho lorei–Piceetum</i> , <i>Mastigobryo–Piceetum</i> , <i>Laburno alpini–Piceetum</i> , <i>Sphagno–Piceetum</i> , <i>Hacquetio–Piceetum</i>
Dwarf mountain pine scrubs (FVT13)	<i>Hyperico grisebachii–Pinetum mugo</i> , <i>Rhodothamno–Pinetum mugo</i> , <i>Rhodothamno–Laricetum</i>

Table 2: Description of bioclimatic variables (adapted from O'Donnell and Ignizio 2012).

Variable	BI01	BI02	BI03	BI04	BI05
Description	Annual mean temperature	Mean diurnal range	Isothermality	Temperature seasonality	Max temperature of warmest month
Variable	BI06	BI07	BI08	BI09	BI010
Description	Min temperature of coldest month	Temperature annual range	Mean temperature of wettest quarter	Mean temperature of driest quarter	Mean temperature of warmest quarter
Variable	BI011	BI012	BI013	BI014	BI015
Description	Mean temperature of coldest quarter	Annual precipitation	Precipitation of wettest month	Precipitation of driest month	Precipitation seasonality
Variable	BI015	BI016	BI017	BI018	
Description	Precipitation of wettest quarter	Precipitation of driest quarter	Precipitation of warmest quarter	Precipitation of coldest quarter	

Twenty-one layers of environmental predictors were used in this study. Based on several examples (Portilla Cabrera and Selvaraj 2020; Du et al. 2021; Saha, Rahman and Alam 2021; Zeng et al. 2021), we used 18 bioclimatic variables (Table 2) and an additional 3 layers: the approximation of soil pH, the Euclidean distance of water bodies and the topographic wetness index (TWI). The last environmental predictor was calculated using SAGA software (TWI (one step)) (Conrad et al. 2015). The bioclimatic data were obtained from the WorldClim portal (Fick and Hijmans 2017). The layer to approximate the soil pH was calculated with GIS using the Slovenian soil map from 2007 provided by the Slovenian Ministry of Agriculture, Forestry and Fisheries, and theoretical assumptions about the response of soil types (Repe 2010). GIS was used to approximate the last two layers using DEM and a layer of linear Slovenian water bodies provided by the Slovenian environment agency (2006) and the Agency for real estate cadastre (2013).

All covariates were used with a spatial resolution of 500 m and extended to the entire study area, which is the Republic of Slovenia. The bioclimatic reference variables for present-day conditions represented the period 1970–2000. The bioclimatic data obtained had a spatial resolution of 2.5 arc minutes and were down-scaled using a combination of methods described by other authors (Ninyerola, Pons and Roure 2000; Ninyerola, Pons and Roure 2007; Poggio, Simonetti and Gimona 2018). The downscaling process in this study is described by Gregorčič, Rozman and Repe (2022).

The future bioclimatic data represent the projected climatic conditions in the period 2080–2100. Two climate scenarios (SSP1-2.6, SSP5-8.5) and three Earth System Models (CNRM-ESM2-1, BCC-CSM2- MR, and MIROC6) were used. The final future bioclimatic variables were produced by averaging the results of all three ESMs.

The bias files for each FVT were created using the buffered minimum convex polygon (MCP) method from SDM Toolbox and integrated into ArcGIS Pro (Brown 2014).

2.2 Modelling

The modelling was done using MaxEnt software, which has several advantages. The method requires species occurrence data, it can handle both continuous and categorical covariates, the output is continuous and allows fine distinction between suitability of different areas (Phillips, Anderson and Schapire 2006). However, there are also some disadvantages: the method is prone to overfitting (Radosavljevic and Anderson 2014). The most important measure of model quality is AUC (area under the curve) values. AUC is a measure of two-dimensional space under the receiver operating characteristic (ROC) curve. Nevertheless, some authors advise against using AUC values for various statistical reasons (Lobo, Jiménez-Valverde and Real 2008; Hanczar et al. 2010). Inference from presence-only data also requires strong assumptions that are often violated (Yackulic et al. 2013).

The modelling was based on 4 theoretical (A) and 3 methodological (B) assumptions (Guisan, Thuiller and Zimmermann 2017):

- A1 – The relationship between species and environmental needs is considered to be in equilibrium.
- A2 – It is assumed that all environmental predictors required to capture the desired niche of the modelled FVT are available at the resolution relevant to the modelled FVT.
- A3 – It is assumed that the likely future environment is accessible to the species to the same extent as it is today.
- A4 – The entire realised niche is captured in the model.
- B1 – The statistical modelling methods used are appropriate for the data being modelled.
- B2 – There are no errors in the independent variables.
- B3 – The data on the occurrence of FVT are unbiased.

Prior to final modelling, a pre-selection of variables was made, testing collinearity between bioclimatic covariates to avoid multicollinearity in the model. An approximation of soil pH from the digital soil map was used to model the potential ecological niche of each FVT. The distance between the water body level and the ITV level was only used for modelling the ecological niche of FVT09. The selection of bioclimatic covariates for a given FVT was based firstly on a collinearity test and secondly on the significance of the covariates for the respective FVT. A total of 10,000 random sample points were created in the study area. The bioclimatic covariates were included in the sample and the Pearson coefficient matrix was calculated. If two covariates had a correlation greater than 0.8 or less than –0.8, one was excluded from the final model. To exclude the independent variable that was less important for the modelling results, we ran 13 test-MaxEnt

Table 3: The final selection of independent variables per FVT.

	BI01	BI02	BI03	BI04	BI05	BI06	BI07	BI08	BI09	BI010	BI011	
FVT01	X	✓	X	X	X	✓	✓	✓	✓	✓	X	distance to hydro- logical network.
FVT02	✓	X	✓	✓	X	X	✓	✓	✓	X	X	
FVT03	X	X	✓	✓	✓	✓	✓	✓	✓	X	X	
FVT04	X	X	✓	X	X	✓	✓	✓	✓	✓	X	
FVT05	X	✓	X	✓	✓	✓	✓	✓	✓	X	X	
FVT06	X	X	✓	X	X	✓	✓	✓	✓	✓	X	
FVT07	X	X	✓	✓	✓	X	✓	✓	✓	X	X	
FVT08	X	X	✓	✓	✓	✓	✓	✓	✓	X	X	
FVT09	X	X	✓	X	X	✓	✓	✓	✓	✓	X	
FVT10	X	X	✓	✓	X	X	✓	✓	✓	X	✓	
FVT11	X	X	X	✓	X	X	X	✓	✓	X	✓	
FVT12	X	✓	X	X	X	✓	✓	✓	✓	✓	✓	
FVT13	X	✓	X	X	X	✓	✓	✓	✓	✓	X	
	BI012	BI013	BI014	BI015	BI016	BI017	BI018	BI019	soil pH approximation	TWI		
FVT01	✓	X	X	✓	X	X	X	X	✓	X	X	
FVT02	✓	X	X	✓	X	X	X	X	✓	X	X	
FVT03	X	X	X	✓	X	X	✓	✓	✓	X	X	
FVT04	X	X	X	✓	X	X	X	✓	✓	X	X	
FVT05	X	X	X	✓	X	X	✓	✓	✓	X	X	
FVT06	X	X	X	✓	X	✓	X	X	✓	X	X	
FVT07	X	X	X	✓	X	X	✓	✓	✓	X	X	
FVT08	X	X	X	✓	X	X	✓	✓	✓	X	X	
FVT09	X	X	X	✓	X	X	✓	✓	✓	✓	✓	
FVT10	X	X	X	✓	X	X	✓	✓	✓	X	X	
FVT11	X	X	X	✓	X	X	✓	✓	✓	X	X	
FVT12	✓	X	X	✓	X	X	X	X	✓	X	X	
FVT13	X	X	X	✓	X	X	✓	✓	✓	X	X	

models for each FVT with 20 or 22 covariates for the period 1970–2000 and bias files. 20% of the FVT sample points were used for data validation using a cross-validation test, and the regularisation multiplier had a default value of 1.0. Based on the results of the Jackknife test, the one with the least significance among two highly correlated independent variables was excluded from the final selection (Table 3). Sometimes the Jackknife results showed a negative value for a particular covariate, which meant that this covariate was detrimental to the final results (Phillips 2017). In these cases, we excluded the covariate from the final selection. This was necessary for FVT04 – BIO2, FVT07 – BIO6 and FVT11 – BIO2, BIO7 (Table 3).

The final potential ecological niche modelling of FVT was conducted with the same settings as in the test phase and new selection of independent variables. In addition, a regularisation multiplier value of 0.8 was used for FVT01 and FVT02 because the probability distribution for 1970–2000 was too wide when using a regularisation multiplier value of 1.0.

Separate spatial results were merged into one layer using the GIS software. Each raster cell in the study area maintained the highest probability value from all 13 ecological niche distribution layers. Each ecological niche distribution layer was subtracted from the merged layer. In the final step, raster cells with a value of 0.0 were classified as the result of the ecological niche distribution modelling of the specific FVT. To evaluate the results, the area and centroid differences between the present FVTs and the modelled ecological niches were calculated. This enables a holistic assessment of the results (Guisan, Thuiller and Zimmermann 2017).

3 Results

3.1 Performance Statistics

The performance of the models was statistically analysed by assessing the area under the curve (AUC) values. The AUC test value of each modelling procedure was higher than 0.7. The FVT03, FVT01 and FVT07 scored 0.71, 0.77 and 0.78, respectively. The FVT04, FVT11, FVT10, FVT08, FVT05 and FVT06 scored 0.84, 0.84, 0.86, 0.86, and 0.87 respectively. The FVT02, FVT12, FVT13 and FVT09 scored 0.90, 0.92, 0.92, and 0.94 respectively, indicating excellent results (Araújo et al. 2005). Table 4 summarizes the response curves for all covariates for each selected FVT.

3.2 Changes in the ecological niche areas based on the selected SSP scenarios

Currently, *Fagus sylvatica* forests dominate in Slovenia, covering 72.83% of the total national forest area (Bončina et al. 2021). Within the structure of *Fagus sylvatica* forests, FVT01 is the most widespread, while FVT07 make up the smallest proportion. The FVT09 have the smallest share of Slovenia's total national forest area with only 1.52%.

In the optimistic scenario, the results show that the areas of FVT06, FVT13, FVT12 and FVT11 would decrease by 92.81%, 87.19%, 84.42% and 41.30%, respectively. All areas of *Fagus sylvatica* FVTs decreased, except for the FVT07. Thus, the combined area of *Fagus sylvatica* would decrease to 38.81% of the total forest area. Based on current knowledge of successional processes FVT08 could partially replace FVT03, which is consistent with our results. FVT02, FVT07, FVT08 and FVT10 would expand their ecological niches by 67.37%, 126.06%, 201.12% and 327.59%, respectively. Based on these dynamics, FVT10 makes up the largest share of the national forest area.

In the pessimistic scenario, all FVTs would experience a decrease in area, except for FVT07 and FVT10. They expanded by 282.54% and 804.25% respectively. In this scenario, no areas would be suitable for FVT12. Almost 100% decrease would be experienced by FVT01, FVT04, FVT05, FVT03, FVT13 and FVT06, which also experience 97.23%, 98.26%, 98.34%, 99.13%, 99.38% and 99.97% respectively. Although FVT08 could experience expansion in the SSP1-2.6 scenario, the results show that their area would decrease by 78.25% in the SSP5-8.5 scenario. The same pattern is seen for FVT09, although they would experience the smallest area decrease of all FVTs (8.03%). When analysing absolute numbers, FVT10 and FVT07 would occupy the largest share of the total forest area (6,951.64 km² or 65.26% and 3,089.88 km² or 29.01%, respectively). All other FVT area sizes would be negligible.

Table 4: Summary of the response curves of selected covariates for each FVT (The primary and secondary optima are referred to as (1) and (2), respectively. If there are two equally important optima, both are labelled (1). In the line for the approximation to the soil pH, (a) stands for automorphic soils with predominantly eutrophic properties and (b) for automorphic soils with predominantly dystric properties.)

	FVT01	FVT02	FVT03	FVT04	FVT05	FVT06	FVT07
BIO1 (°C)		9					
BIO2 (°C)	7				16,5 ⁽¹⁾ , 6 ⁽²⁾		
BIO3 (%)		34	34–37	42		41–44	8 ⁽¹⁾ , 48 ⁽²⁾
BIO4 (°C)		560–570		630			
BIO5 (°C)			25		18		21.5–23
BIO6 (°C)	–5.1		–4.5	–6	–8	≤ –9	
BIO7 (°C)	20–29	29	28–29.5	33	23	24.5	26
BIO8 (°C)	15.8	19 ⁽¹⁾ , 7 ⁽²⁾	17.5 ⁽¹⁾ , 6 ⁽²⁾	15.5 ⁽¹⁾ , 5 ⁽²⁾	13 ⁽¹⁾ , 3 ⁽²⁾	5 ⁽¹⁾ , 13.5 ⁽²⁾	15
BIO9 (°C)	–1.9 ⁽¹⁾ , 13 ⁽²⁾	–0.5	–1	–2 ⁽¹⁾ , 9.5–12.5 ⁽²⁾	–4 ⁽¹⁾ , 12 ⁽²⁾	9.5 ⁽¹⁾ , –3 ⁽²⁾	13 ⁽¹⁾ , –3 ⁽²⁾
BIO10 (°C)	18.5			14.5–16.5		11.5–13.5	
BIO12 (mm)	800 ⁽¹⁾ , 1050 ⁽²⁾	950 ⁽¹⁾ , 1300 ⁽²⁾					
BIO15 (%)	37	22.5 ⁽¹⁾ , 34 ⁽²⁾	20–27.5	22.5–32	23–24	16.5–18.5 ⁽¹⁾ , 31.5 ⁽²⁾	17 ⁽¹⁾ , 32 ⁽²⁾
BIO17 (mm)						480	
BIO18 (mm)			295–370		465		550–640 ⁽¹⁾ , 320 ⁽²⁾
BIO19 (mm)			195	460 ⁽¹⁾ , 155 ⁽²⁾	490 ⁽¹⁾ , 220 ⁽²⁾		390–460 ⁽¹⁾ , 155 ⁽²⁾
soil pH approx.	(b)	(b)	(a)	(a)	(a)	(a)	(a)

	FVT08	FVT09	FVT10	FVT11	FVT12	FVT13
BIO1 (°C)						
BIO2 (°C)					4–6	2–4 ⁽¹⁾ , > 15 ⁽²⁾
BIO3 (%)	36	32	40			
BIO4 (°C)	710		620–650	690		
BIO5 (°C)	27 ⁽¹⁾ , 25.5 ⁽²⁾					
BIO6 (°C)	–4	–4		–6	–8	–10
BIO7 (°C)	30–31	31	25		21–23	< 26 ⁽¹⁾ , > 28 ⁽²⁾
BIO8 (°C)	8 ⁽¹⁾ , 18.5 ⁽²⁾	19	9.5	15.5–16	4 ⁽¹⁾ , 12–12.5 ⁽²⁾	1–3 ⁽¹⁾ , 12 ⁽²⁾
BIO9 (°C)	0	0	15	–2.5	–4 ⁽¹⁾ , 8.5 ⁽¹⁾	–5
BIO10 (°C)		19.5			12	8.2
BIO11 (°C)			3	–2.5		
BIO12 (mm)					1700–1850	
BIO15 (%)	38 ⁽¹⁾ , 19.5 ⁽²⁾	29.5	18.5	33–35 ⁽¹⁾ , 18.5 ⁽²⁾	19.5 ⁽¹⁾ , 36 ⁽²⁾	23.5
BIO17 (mm)						
BIO18 (mm)	270–355	260 ⁽¹⁾ , 665 ⁽²⁾	245–280	420		580
BIO19 (mm)	95 ⁽¹⁾ , 180 ⁽²⁾	100 ⁽¹⁾ , 500 ⁽²⁾	250	130 ⁽¹⁾ , 320 ⁽²⁾		400
soil pH approx.	(b) ⁽¹⁾ , (a) ⁽²⁾	(b) ⁽¹⁾ , (a) ⁽²⁾	(a)	(b)	(a) ⁽¹⁾ , (b) ⁽¹⁾	(a)
TWI		11				
dist. from hydro. network (m)		0				

Table 5: Changes in the ecological niche areas based on the selected SSP scenarios.

	Today		SSP1-2.6			SSP5-8.5		
	km ²	%	km ²	%	% change	km ²	%	% change
FVT01	1,933.4	18.2	978.9	9.2	-9.0	53.6	0.5	-17.6
FVT02	217.4	2.0	363.9	3.4	1.4	152.9	1.4	-0.6
FVT03	1,888.3	17.7	436.0	4.1	-13.6	16.5	0.2	-17.6
FVT04	615.1	5.8	491.4	4.6	-1.2	10.7	0.1	-5.7
FVT05	947.2	8.9	314.2	3.0	-5.9	15.8	0.1	-8.7
FVT06	1,566.4	14.7	112.6	1.1	-13.6	0.5	0.0	-14.7
FVT07	807.7	7.6	1,801.7	16.9	9.3	3,089.9	29.0	21.4
FVT08	703.0	6.6	2,117.0	19.9	13.3	152.9	1.4	-5.2
FVT09	161.4	1.5	298.4	2.8	1.3	148.4	1.4	-0.1
FVT10	768.8	7.2	3,287.2	30.9	23.6	6,951.6	65.3	58.0
FVT11	680.2	6.4	399.3	3.8	-2.6	58.8	0.6	-5.8
FVT12	200.8	1.9	31.3	0.3	-1.6	/	/	-1.9
FVT13	162.8	1.5	20.9	0.2	-1.3	1.0	0.0	-1.5
Sum	10,652.6	100.0	10,652.6	100.0	0.0	10,652.6	100.0	0.0

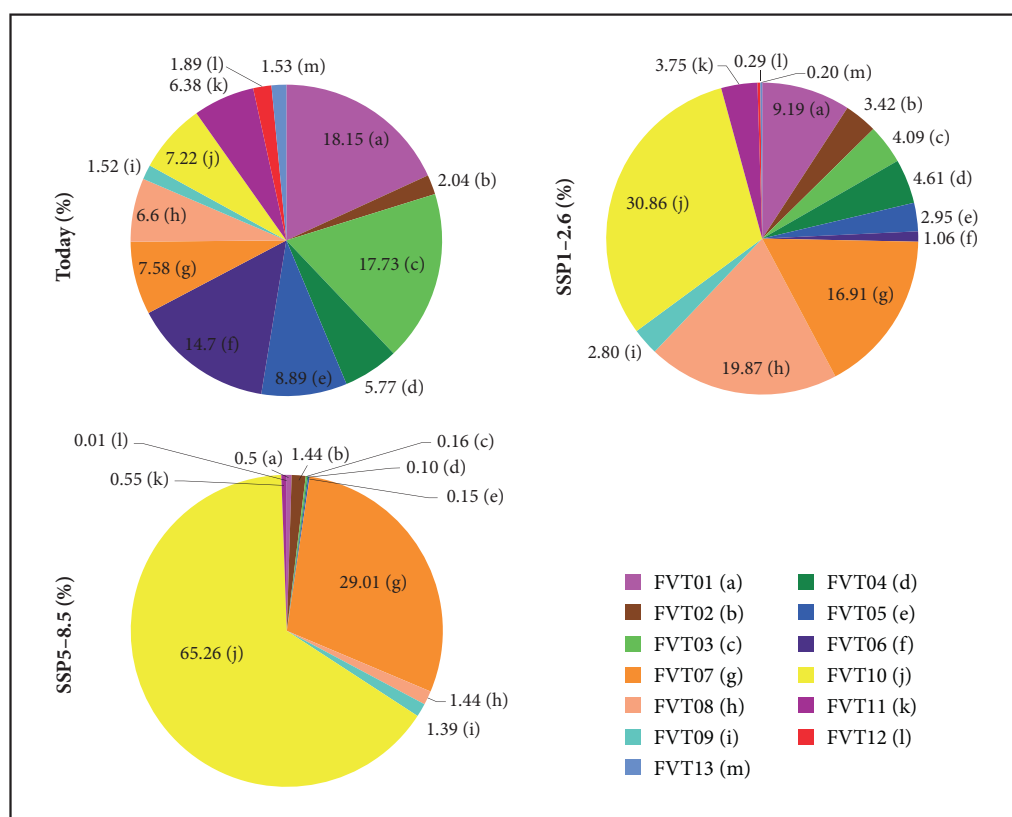


Figure 1: Shares of the ecological niche area changes based on the selected SSP scenarios.

3.3 Vectors between centroids of forest vegetation types for the selected SSP scenarios

In the optimistic scenario, Thermophilous beech forests (FVT07), Lowland willow, alder and pedunculate oak forests in the lowlands (FVT09) and High mountainous beech forests on neutral or calcareous soils in the Dinaric region (FVT06) experienced the greatest spatial changes in centroids (81.10 km, 58.64 km, 47.89 km) in eastern (77.89°), western (272.61°) and northern (2.95°) directions, respectively. Norway spruce forests (FVT12) experienced the least spatial changes in centroids (6.35 km) in east (90.34°) direction. All results are listed in Table 5.

In the pessimistic scenario, Lowland willow, alder and pedunculate oak forests (FVT09), Thermophilous beech forests (FVT07) and High mountain beech forests on neutral or calcareous soils in the Dinaric region (FVT06) would experience the largest spatial changes of centroids (89.35 km, 82.24 km, 72.56 km) in western (262.15°), eastern (77.52°) and northwestern (296.55°) directions, respectively. Dwarf mountain pine scrub (FVT13) would experience the least spatial change in centroids (21.60 km) in the west (286.59°) direction (Figure 2).

Table 6: Lengths and directions of vectors between centroids of forest vegetation types for the selected SSP scenarios.

	SSP1-2.6		SSP5-8.5	
	(km)	Azimuth (°)	(km)	Azimuth (°)
FVT01	12.33	north (348.35)	27.57	north-west (303.05)
FVT02	13.02	north-east (62.22)	31.12	north-east (60.47)
FVT03	32.11	west (265.69)	61.25	north-west (303.44)
FVT04	34.85	west (291.77)	50.5	north-west (304.14)
FVT05	20.94	west (277.49)	27.63	west (276.82)
FVT06	47.89	north (2.95)	72.56	north-west (296.55)
FVT07	81.1	east (77.98)	82.24	east (77.52)
FVT08	15.21	west (285.04)	55.47	north (356.21)
FVT09	58.64	west (272.612)	89.35	west (262.15)
FVT10	21.14	east (69.99)	38.78	north-east (60.41)
FVT11	46.55	west (261.13)	42.64	west (270.24)
FVT12	6.35	east (90.34)	/	/
FVT13	13.64	west (273.77)	21.6	west (286.59)

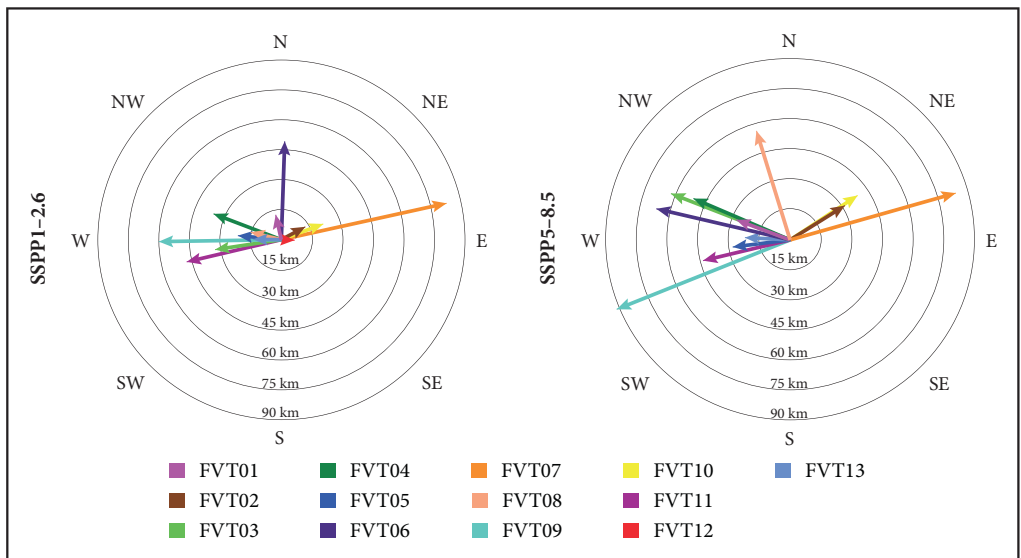


Figure 2: Graphical representation of vectors between centroids of forest vegetation types for the selected SSP scenarios.

3.4 Synthesis of the ecological niche changes for the selected SSP scenarios

Combining the results of changes in ecological niche areas and vectors between centroids, we obtained the final synthesis results for the potential impacts of climate change on Slovenian forests in the period 2080–2100 based on the selected SSP scenarios (Table 6, Figure 3). In the optimistic scenario, the ecological niche of Thermophilous beech forests (FVT07) would experience the greatest spatial change. High mountain beech forests on neutral or calcareous soils in the Dinaric region (FVT06) and Thermophilous hornbeam, sessile oak, downy oak, Scots pine and black pine forests (FVT10) would experience the second and third largest spatial changes, respectively. The least spatial changes would occur in the ecological niches of Norway spruce forests (FVT12), Acidophilous Scots pine forests (FVT02) and Dwarf mountain pine scrubs (FVT13).

Under the pessimistic scenario, the ecological niche of Thermophilous hop hornbeam, sessile oak, downy oak, Scots pine and black pine forests (FVT10) would experience the greatest spatial changes. Thermophilous beech forests (FVT07) and Beech forests in the lower uplands on neutral or calcareous soils (FVT03) would experience the second and third largest spatial changes, respectively. The least spatial changes would occur in the ecological niches of Norway spruce forests (FVT12), Lowland willow, alder and pedunculate oak forests (FVT09) and Acidophilous Scots pine forests (FVT02).

Table 7: Synthesis of the ecological niche changes for the selected SSP scenarios.

	SSP1-2.6				SP5-8.5			
	Area change factor	Vector change factor	Spatial change	Order	Area change factor	Vector change factor	Spatial change	Order
FVT01	0.38	0.15	0.057	8	0.30	0.31	0.09	5
FVT02	0.06	0.16	0.010	12	0.01	0.35	0.004	11
FVT03	0.58	0.40	0.232	4	0.30	0.69	0.21	3
FVT04	0.05	0.43	0.022	10	0.10	0.57	0.06	6
FVT05	0.25	0.26	0.065	6	0.15	0.31	0.05	9
FVT06	0.58	0.59	0.342	2	0.25	0.81	0.21	4
FVT07	0.39	1.00	0.390	1	0.37	0.92	0.34	2
FVT08	0.56	0.19	0.106	5	0.09	0.62	0.06	7
FVT09	0.05	0.72	0.036	9	0.002	1.00	0.002	12
FVT10	1.00	0.26	0.260	3	1.00	0.43	0.43	1
FVT11	0.11	0.57	0.063	7	0.10	0.48	0.05	8
FVT12	0.07	0.08	0.006	13	0.00	0.00	0.00	13
FVT13	0.06	0.17	0.010	11	0.03	0.24	0.01	10

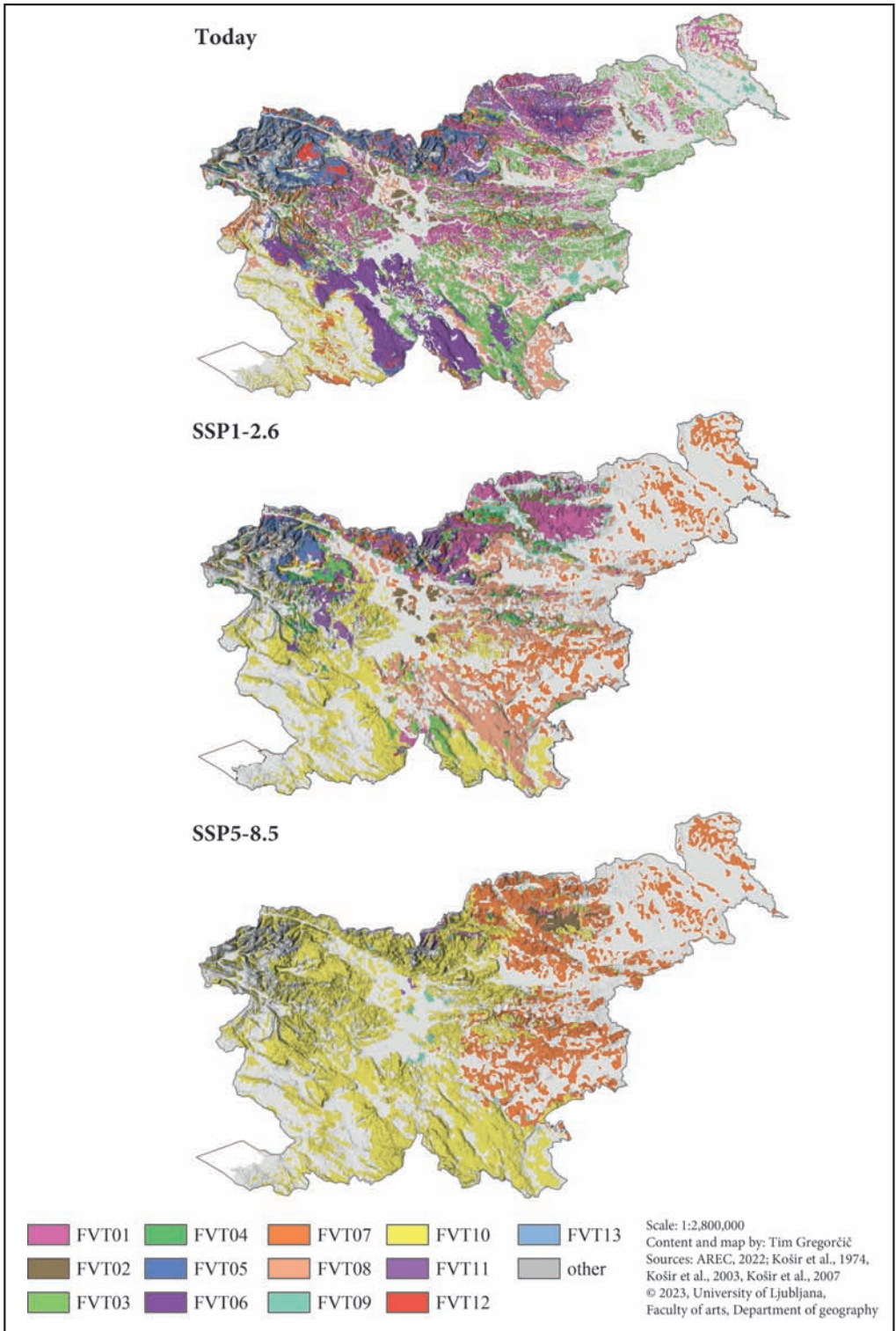
3.5 Changes in the altitudinal zones of the forest vegetation types

The analysis of the results indicates significant potential changes in the structure of the 7 altitudinal zones of the forest vegetation types occurring in Slovenia (Wraber 2008, cited in Ogrin and Plut 2012).

Today, most of the area of Acidophilous beech forests (FVT01) (50.59%) thrives in the lowlands. Most of the area suitable for Acidophilous beech forests (FVT01) (54.80% and 83.39%) would shift to the montane belt in SSP1-2.6 and SSP5-8.5, respectively. This FVT could also reach the lower alpine belt, where it does not occur today (Figures 4 and 5).

Most of today's Acidophilous Scots pine forests (FVT02) are found in the lowlands (89.67%). They can also grow at higher altitudes, with the highest representation in the montane belt. In scenario SSP1-2.6, the largest proportion of suitable area would be found in the lower montane belt (50.66%). In scenario SSP5-8.5, the largest proportion of suitable area would be found in the upper montane belt (97.00%). The pessimistic scenario also indicates potential areas in the lower alpine belt where it does not occur today.

Figure 3: Potential spatial ecological niche changes of Slovenian FVTs for selected SSP scenarios. ► p. 100



Lower mountain beech forests on neutral or calcareous soils (FVT03) is another type that is most widespread in the lowlands today (61.39%), but also reaches the montane belt with a relatively small area share (2.98%). In scenario SSP1-2.6, the largest proportion of suitable areas is in the montane belt (76.16%) and in the lower Alpine belt in scenario SSP5-8.5 (50.78%).

The largest proportion of today's Mountain beech forests on neutral or calcareous soils (FVT04) thrives in the lower montane belt (55.18%). In the optimistic and pessimistic climate scenarios, the most suitable areas would shift to the montane belt (58.11% and 61.84%, respectively). Mountain beech forests on neutral or calcareous soils (FVT04) could also disappear from the lowlands in the SSP5-8.5 scenario.

Most of today's high Mountain beech forests on neutral or calcareous soils in the Alpine region (FVT05) thrive in the montane belt (82.17%), although they are found in all altitudinal zones except the alpine and lower nival belt. The largest proportion of suitable areas would decrease in the optimistic scenario but would remain in the montane belt (73.66%) and could also spread into the alpine belt. In the pessimistic scenario, the largest proportion of suitable areas would shift to the lower alpine belt (62.91%).

Like the High mountain beech forests on neutral or calcareous soils in the Alpine region (FVT05), the High mountain beech forests on neutral or calcareous soils in the Dinaric region (FVT06) are mainly present in the montane belt (59.79%) and can be found at all altitudes, except for the alpine and lower nival belt. The largest proportion of suitable area would not only remain in the montane belt (87.80%) but would also increase as the area in the lowland and lower montane zones is reduced in the SSP1-2.6 scenario. In the SSP5-8.5 scenario, most of the suitable area for High mountain beech forests on neutral or calcareous soils in the Dinaric region (FVT06) would be in the upper montane belt (50.01%), while the other half would be in the lower alpine belt.

Thermophilous beech forests (FVT07) are most widespread in the lower montane belt and may occur into the upper montane belt. Suitable areas for this FVT would spread into the lower Alpine belt in the optimistic and pessimistic climate scenarios, while most areas would be found in the montane belt (86.09% and 73.46%, respectively).

The present Colline oak-hornbeam forests (FVT08) thrive in the first 3 altitudinal zones, with 94.06% occurring in the lowlands. In the SSP1-2.6 scenario, most suitable areas would remain in the lowlands (47.52%), although the proportion in the lower montane belt would be almost the same (46.61%). In the SSP5-8.5 scenario, suitable areas for Colline Oak-Hornbeam Forests (FVT08) would be found in the higher altitude zones, including the lower Alpine belt, with the majority in the montane belt (79.56%).

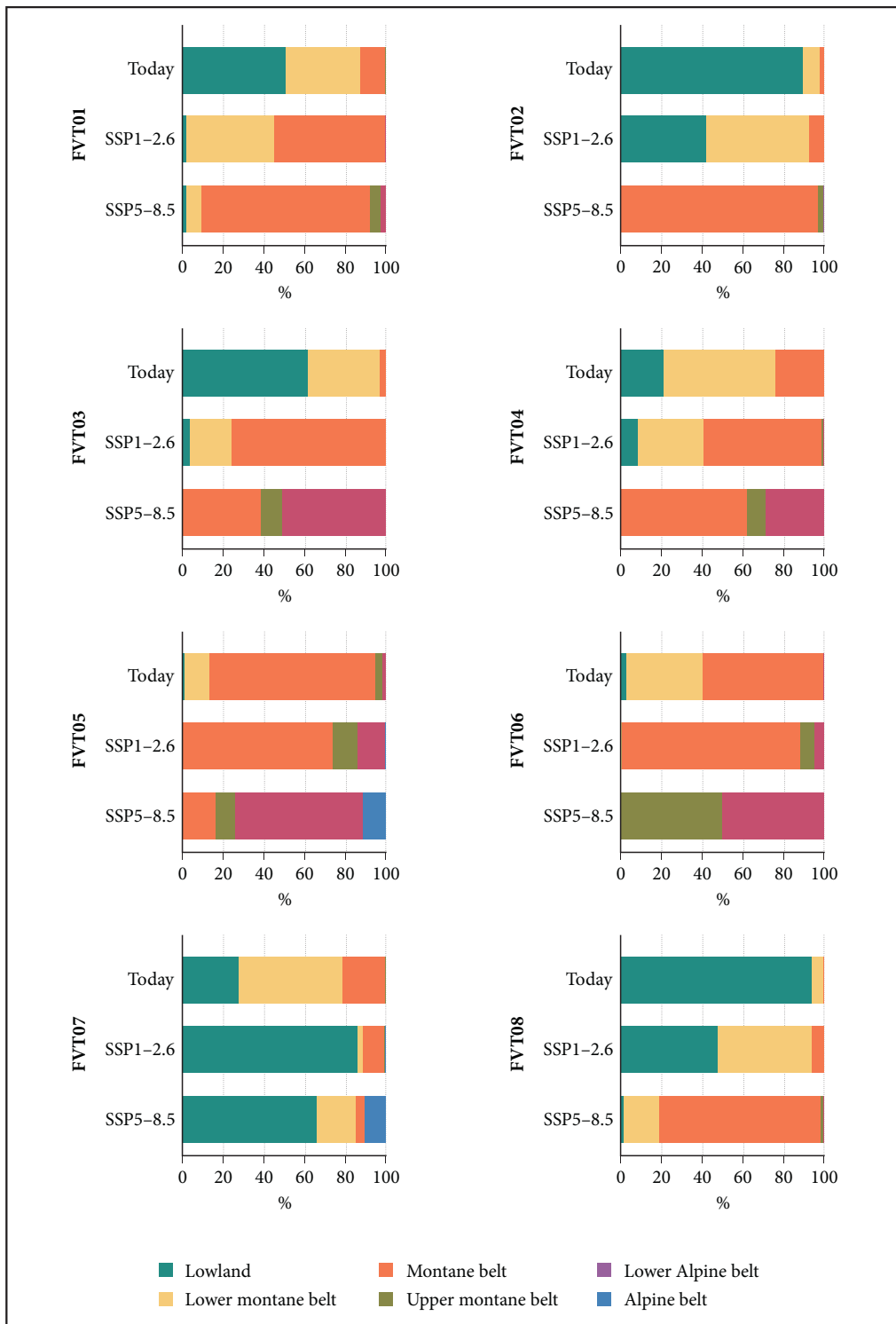
Like the Colline oak-hornbeam forests (FVT08), most of the present Lowland willow, alder and pedunculate oak forests (FVT09) grow in the first 3 altitudinal zones, with 99.35% in the lowlands. In the optimistic scenario, the areas suitable for these FVTs would remain in the same altitudinal zones, but most would grow in the lower montane belt (55.69%). In the pessimistic scenario, most suitable areas would remain in the lowlands (64.88%), but would increase in the higher latitudes, including the lower Alpine belt. As Lowland willow, alder and pedunculate oak forests (FVT09) depend on a high-water table, the spread of suitable areas at higher altitudes is questionable.

Thermophilous hop hornbeam, sessile oak, downy oak, Scots pine and black pine forests (FVT10) are most widespread in the lowlands (48.50%) and can be found at higher altitudes, including the lower Alpine belt. In scenarios SSP1-2.6 and SSP5-8.5, most suitable areas were located in the lower montane belt (42.98% and 41.32%, respectively). Under the pessimistic scenario, suitable areas would also be found in the alpine belt (Figure 4).

Most of today's Silver fir forests (FVT11) grow in the lower montane belt (51.40%) and are found as far as the lower Alpine belt. In the optimistic climate scenario, the areas suitable for FVT would remain in the same altitudinal zones, with the majority in the montane belt (63.00%). In the pessimistic scenario, the majority of the suitable areas would remain in the montane belt (56.24%) and increase in the alpine belt.

Spruce forests (FVT12) mainly thrive in the lower montane belt (87.65%). In the optimistic scenario, the largest proportion of suitable areas would be in the lower alpine belt, while the results for the pessimistic scenario indicate no suitable areas.

Dwarf mountain pine scrub (FVT13) is most widespread in the montane belt (41.35%) and can be found in all elevation zones except lowland. In the optimistic scenario, most suitable areas would be in the alpine belt (40.21%), while in the SSP5-8.5 scenario, the lower alpine belt would be most suitable (50.00%) and would only occur in the upper montane and lower alpine belts.



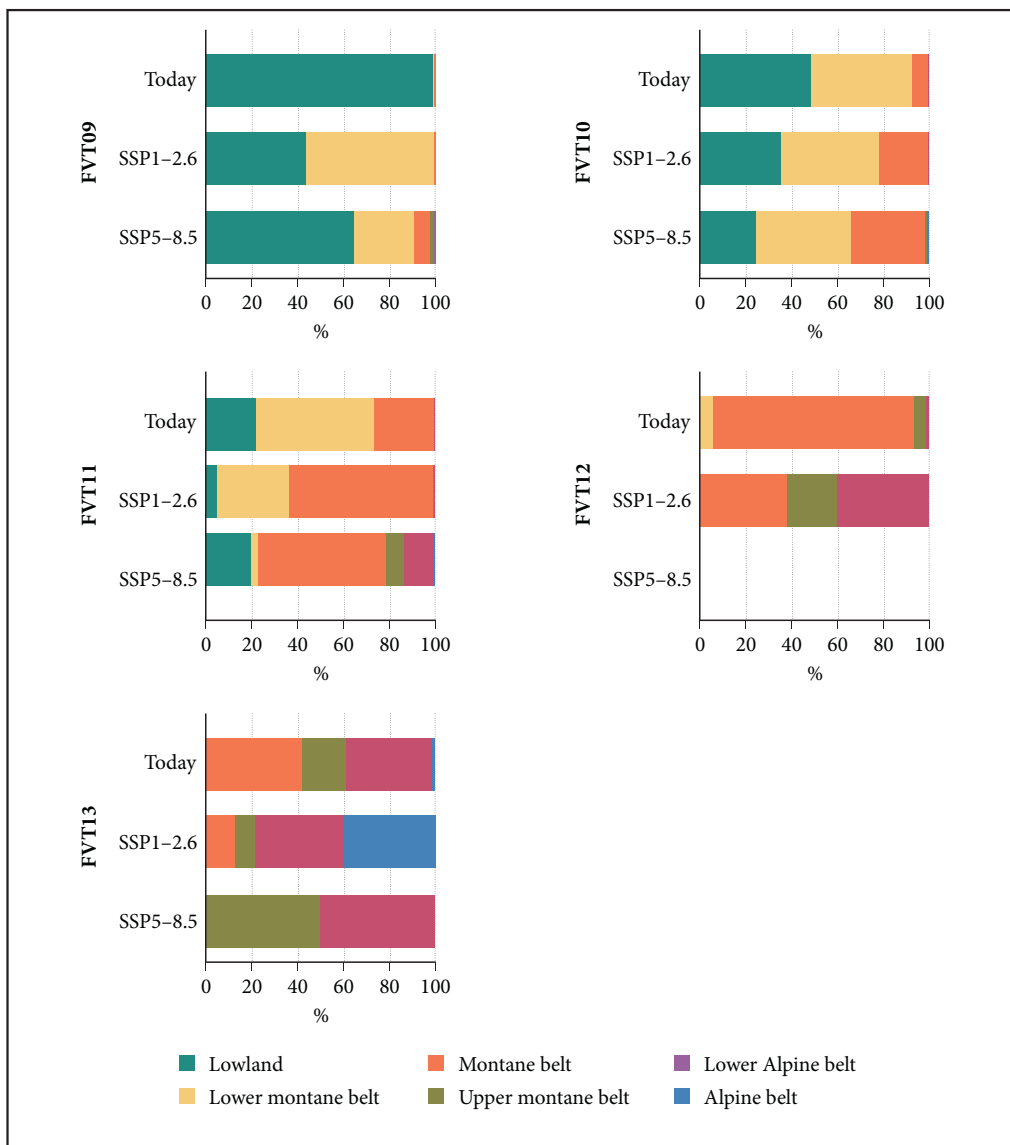


Figure 4: Potential altitudinal ecological niche changes of the first eight Slovenian FVTs for the selected SSP scenarios.

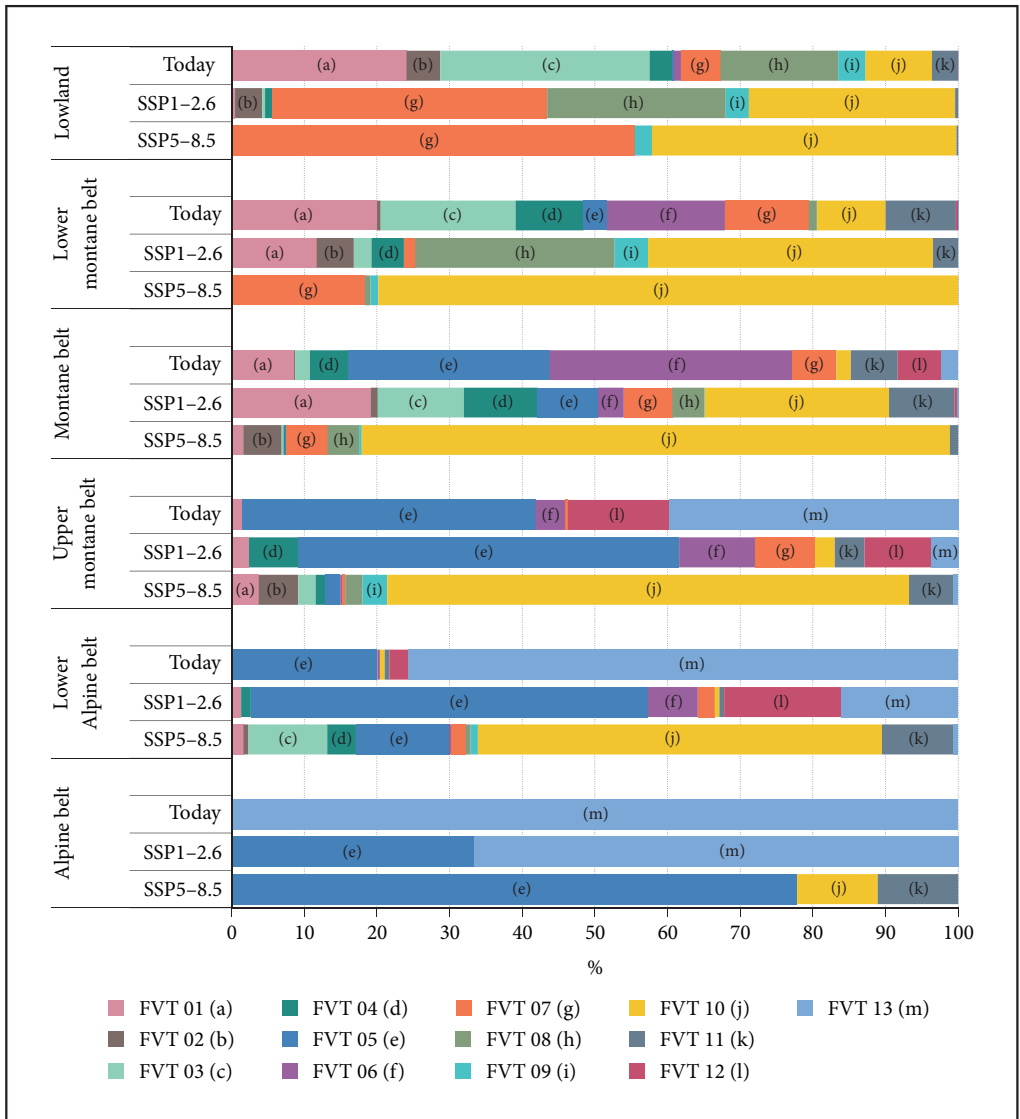


Figure 5: Potential structural changes of Slovenian altitudinal zones for the selected SSP scenarios.

4 Discussion

In SSP1-2.6, modelling results indicate that suitable areas for FVT02, FVT07, FVT08 and FVT10 would expand, while suitable areas of other FVTs would decrease. In Slovenia FVT02 are characterised as secondary FVTs. With the rise in temperature, intensification of droughts and their more frequent occurrence, the decline of suitable areas for FVT02 is more realistic. The expansion of FVT08 could be a consequence of the temperature increase at the time of winter temperature inversions. Currently, most FVT08 areas are located in the thermal belt, which is warmer than the bottoms of the valleys and basins during temperature inversions. In SSP5-8.5, only the thermophilous FVTs would expand. As the suitable areas of FVT06

and FVT13 are expected to be extremely small (0.51 km² and 1.02 km², respectively), it is possible that these areas remained due to possible methodological shortcomings (data quality, etc.) and would not exist in the SSP5-8.5 scenario, if realised. Based on these results, there could be a gradual decrease in suitable areas for FVT11. However, on a smaller spatial scale, they also thrive under warmer site conditions, such as in the low karst plain of Bela krajina. In shady gorges with appropriate humidity, they could therefore become even more competitive.

This was the first study to use MaxEnt modelling software and scenarios from SSP to assess the potential impacts of climate change on Slovenian forests. Our results show that even if the optimistic scenario occurs, site conditions may change drastically, potentially affecting the future distribution of Slovenian forest vegetation types.

The results generally confirm the direction of possible changes in the findings of Kutnar, Kobler and Bergant (2009). However, the methodology of their study was different, using different climate scenarios, independent variables, future time periods and modelling methods. Therefore, the comparability between these two studies is limited and will not be discussed in detail. Broadly, projected trends for *Fagus sylvatica* FVTs indicate a decline in suitable area, including for Thermophilous beech forests (FVT07), which is partly consistent with our results. However, in agreement with our results, the study also predicted an increase in area share for Colline oak–hornbeam forests (FVT08) and Thermophilous hop–hornbeam, sessile oak, downy oak, Scots pine and black pine forests (FVT10).

Kutnar and Kobler (2011; 2014) had similar comparability problems but they focused on predicting changes that would occur by the end of the 21st century. Therefore, a comparison of their results with our study is still useful. Nevertheless, we refrain from a quantitative comparison, as this would be inappropriate due to the impossibility of making quantitative comparisons between the climate scenarios of both studies. In summary, our results are largely consistent with theirs. Their 2011 paper also found an increase in suitable area for thermophilous FVTs and a decrease for other FVTs. However, the comparison raises questions about the mechanisms driving the spread of thermophilous FVTs and their ecological relationships. Moreover, our projections are rather conservative with respect to the possible disappearance of FVTs in the pessimistic scenario. These observations highlight the importance of further research into the mechanisms and dynamics of FVTs in a changing climate, and the need to be cautious when making projections about their future distribution.

There are some other studies that have analysed the potential impacts of climate change on forests in Europe using MaxEnt. Although they are only partially comparable with our results due to different target time periods, climate scenarios (RCPs), study areas, study area scales and ecological levels, some common general directions of change can be observed. Decolonisation of *Picea abies* (part of FVT12 in this study) at lower altitudes in Slovenia and spread of *Quercus petraea* were predicted by Mauri et al. (2022) for the moderate climate scenario (RCP4.5). The results of Dyderski et al. (2018) suggest that conifer species are more threatened by climate change intensification, which is consistent with our results. A case study in Greece by Fyllas et al. (2022) showed that Thermophilous *Quercus ilex* would be among the species with the lowest habitat loss under the pessimistic climate scenario (RCP8.5). High unsuitability for *Fagus sylvatica* with a 93% decline in habitat suitability was predicted.

When interpreting the changes in the altitudinal zones of the FVTs, one must be aware of their arbitrarily set altitudinal limits. This was necessary because of the analysis of the scale of the whole country. In reality, the elevation zones depend more on the ecological conditions of specific sites and less on the latitude zones themselves. Therefore, the same latitudinal zones may have different latitudinal boundaries across the country; however, this could not be taken into account (Kutnar et al. 2012). In summary, regarding the changes in latitude, the intensification of climate change shows a clear trend towards shifting FVTs to higher altitudes, which is related to the shift of current temperature conditions to higher altitudes.

Our results generally support similar research by Kutnar and Kobler (2011), who suggest that a rise in temperature and changing rainfall patterns due to climate change have the potential to cause a shift of FVTs from lower to higher elevations. However, we cannot directly and quantitatively compare our results with those of Kutnar and Kobler, as they used an intermediate scenario in their study to assess elevation, which was not the case in our study. This trend has already been recognised in several other studies that did not relate to our study area or species (Zhang et al. 2018; Zhao, Zhang and Xu 2020; Soilhi et al. 2022). The shift of FVT05, FVT10 and FVT11 in the Alpine belt is an indicator of one of the methodological shortcomings. According to the soil map of Slovenia, only lithosols are found in this altitudinal zone. From

the perspective of pedogenesis, this is a young and poorly developed soil type (Repe 2010). Therefore, the above-mentioned FVTs cannot thrive in this soil type, even though the bioclimatic conditions might make this possible in the coming decades. FVT12 include both primary and secondary FVTs. Thus, although they consist of boreal species, they are mainly found in the lower montane belt. Without human influence, these FVTs are likely to occur today only in frost depressions and at the upper timberline (Bončina et al. 2021), and there would most likely be no suitable areas for these FVTs in SSP1-2.6.

One of the main drawbacks of this study and other ecological niche modelling studies in general is that large-scale weather events and other natural hazards in forests are not taken into account, although they can have a strong impact on forest ecosystems (Vido and Nalevanková 2021). With the intensification and/or increasing frequency of extreme weather events as one of the consequences of global warming (Taccoen et al. 2019; Masson-Delmotte et al. 2021), their increasing influence on forest adaptation to climate change is also expected. Unfortunately, this factor cannot be quantified spatially.

However, many tree species have flexibility and adaptive abilities to adapt to the changing environment. These abilities are not yet fully understood by science (Lindner et al. 2010). Slovenian forests have already been exposed to a number of disturbance factors in recent years, such as bark beetle infestations, storms and ice storms, which may be related to climate change. As a result, the structure and composition of these forests have changed significantly. In the last 15 years, both Norway spruce (*Picea abies*) and silver fir (*Abies alba*) have declined, while the European beech (*Fagus sylvatica*) has increased, primarily due to the decline of the other two aforementioned species (Kutnar, Kermavnar and Pintar 2021).

The results and the methodology used in this study point to several future study topics and extensions. Further methods for modelling ecological niches should be tested and compared with the results of the MaxEnt software. Another approach to assess the potential impact of climate change on Slovenian forests is the analysis of palynological samples from warmer periods of Earth's history. Although we assumed that the upper forest boundary would not change due to the specifics of the methodology, we know that the boundary would most likely shift to higher elevations, which could be investigated using ecological niche modelling. With the rapid spread of several non-native invasive plant species in Slovenia (e.g. *Robinia pseudoacacia*, *Ailanthus altissima*, *Acer negundo*, etc.), the question arises as to how these species might affect forest structure in the future, especially since we already know that they can successfully spread to forest fire pits (Stančič and Repe 2018). Another study confirmed that *Robinia pseudoacacia*, as the dominant invasive species in Slovenian forests, has already significantly changed the composition of Slovenian forest ecosystems (Kutnar and Kobler 2013). Furthermore, the study suggests that the spread of *Robinia pseudoacacia* is likely to continue due to the intensification of climate change. However, it should be noted that modelling the ecological niche of invasive species can be problematic, as it violates the assumption that species are in equilibrium or pseudo-equilibrium with the environment, as Guisan, Thuiller and Zimmermann (2017) point out.

5 Conclusion

This study addresses the potential impact of climate change on Slovenian forests within the context of the SSP1-2.6 and SSP5-8.5 climate scenarios, employing the MaxEnt methodology. The modelling process has yielded statistically accurate results, which generally align with the expected trajectory of climate change effects on Slovenian forests, drawing from current understanding of the ecological requirements of Slovenian FVTs and previous investigations in this domain. Under both scenarios, an expansion of thermophilous FVTs is projected, accompanied by a significant decline in *Fagus sylvatica* FVTs. However, it is important to note that the results obtained are not scientifically provable in practice. While we have made efforts to incorporate all relevant independent variables into the modelling process, the complexity of natural systems renders it impossible to consider all factors that influence FVT development comprehensively. Therefore, caution must be exercised when interpreting the data. It is crucial for the reader to recognise that the outcomes do not constitute deterministic predictions. Instead, the results present potential areas that could exhibit suitability for selected FVTs during the specified time period, based on the current ecological characteristics of their habitats. We generally confirmed the expected trajectory of potential climate change impacts on Slovenian forests, based on current knowledge of the ecological needs of Slovenian FVTs.

6 References

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