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CURRENT AND FUTURE HABITAT SUITABILITY OF *Larix decidua* IN EUROPE AND ROMANIA

Alin M. ALEXANDRU[1] Emanuel STOICA[1,2]
Paula GÂRBACEA[1] Georgeta MIHAI[1]

Abstract: *European larch (Larix decidua) is one of the most important conifer species in Europe, with its natural and extended area covering around 1 million hectares. Gradual environmental changes may allow species to track suitable habitats, whereas rapid changes can cause maladaptation, reduced fitness, and population decline. Using climatic variables, we modelled the potential current and future habitat suitability for European larch in Europe and Romania, for three periods and two Shared Socioeconomic Pathways (SSPs) - SSP245 and SSP585. The GBIF database was used to download the occurrences of the species. Mean Diurnal Range (BIO2), Isothermality (BIO3), and Precipitation of the Warmest Quarter (BIO18) were the climatic variables with the highest relative importance regarding the habitat suitability for European larch. In Europe, the areas projected to be affected by a loss of habitat suitability (contraction) are between 24 and 44 times higher than those where conditions are predicted to improve (expansion). In Romania, for the 2081-2100 period and under the worst-case scenario (ssp585), the very highly suitable (excellent) area is projected to represent around 3% of the country. Modelling how climate change reshapes species distributions is essential for forest managers and policymakers who need robust mitigation and adaptation strategies. The models should be further developed to integrate more important variables for assessing the habitat suitability of European larch.*

Key words: *European larch, habitat suitability models, species distribution, shared socioeconomic pathways, expansion, contraction.*

1. Introduction

The ecological niche of a species was first defined as the set of ecological conditions within which it can survive and reproduce without immigration [20, 26]. Hutchinson [28] distinguished between the *fundamental niche* – the abiotic conditions

[1] Department of Forest Genetic and Tree Breading, "Marin Drăcea" National Institute for Research and Development in Forestry, B-dul Eroilor no. 128, Voluntari 077190, Romania;
[2] Department of Silviculture, Faculty of Silviculture and forest engineering, Transilvania University of Brasov, Șirul Beethoven no. 1, Brasov 500123, Romania;
Correspondence: Alin Mădălin Alexandru; email: alin.alexandru@icas.ro.

permitting indefinite persistence – and the *realised niche*, the portion of the fundamental niche constrained by biotic interactions such as competition or predation [36]. A species' geographic range thus reflects the combined effects of: *i)* suitable abiotic conditions for establishment and reproduction; *ii)* biotic interactions that allow persistence, and (iii) areas accessible through dispersal [53].

Ecological niche models are used to identify species' suitable habitats [21], reconstruct past and present distributions [61], and project future distributions under climate change scenarios [8, 43].

Because niche traits often evolve more slowly than environmental changes, gradual shifts may allow species to track suitable habitats, whereas rapid changes can cause maladaptation, reduced fitness, and population decline [1, 44].

Various terms are used to describe models of species niches and distributions, including "bioclimatic envelope models" [4], "habitat suitability models" (*HSMs*) [27], "species distribution models" (*SDMs*) [15], and "ecological niche models" (*ENMs*) [47].

According to Melo-Merino et al. [36], ecological niche models estimate a species' fundamental niche and are typically applied when assessing potential distributions (such as for invasive species or spatial-temporal projections), while species distribution models focus on the realised distribution in geographic space. Brown and Griscom [7] use ecological niche models as an umbrella term encompassing both *SDMs* and *HSMs*: *SDMs* aim to predict a species' current distribution, whereas *HSMs* aim to predict its potential distribution based on suitable habitat within the realised niche. Similarly, Peterson and Soberón [46] note that *SDMs* apply to actual distributions, while *ENMs* are suited for estimating invasive potential or assessing the impacts of environmental change, requiring an explicit estimation of the fundamental niche.

European larch (*Larix decidua* Mill.) is one of the most important conifer species in Europe [11]. It is valued for its rapid juvenile growth and the exceptional quality of its timber [51], capable of producing over 10 m^3 of wood per hectare annually under optimal conditions [34, 62]. It was proposed as a substitute for Norway spruce and Scots pine, considering the recent dieback and decline of the two species [62]. Its natural range covers approximately 500,000 ha, while plantations – often mixed with Japanese and hybrid larches – extend well beyond the native range, also covering more than 500,000 ha [34]. In Romania, the species occupies only 0.3% of the forested land, its natural distribution area being concentrated in Ceahlau, Ciucas, Bucegi, Lotru, and Apuseni Mountains [37].

The objectives of this study were: *i)* to identify the climatic variables that influence the distribution of European larch; *ii)* to predict potentially suitable areas for this species in Europe and Romania under current conditions; *iii)* to predict potentially suitable areas for this species under three future periods and two distinct shared socioeconomic pathways (*SSPs*); and *iv)* to evaluate the range shifts.

Information regarding the current distribution of forest tree species, how ecological factors such as climate and soil shape these distributions, and the possible decline or augmentation of habitat suitability, is necessary for decision-makers to identify affected and stable areas [45].

2. Materials and Methods

The occurrences of *Larix decidua* (Mill.) across the globe were downloaded from the GBIF database [19]. After cleaning the data using the CoordinateCleaner R package [64], 127,747 records remained (126,902 from Europe) out of 187,208.

The area of interest for our study was the continental part of Europe, from which Romania was subsequently cropped. The climatic variables for the 1970-2000 period were extracted with the *worldclim_global* function from the geodata package [25], at a resolution of 10 minutes. The 19 climatic variables were checked for collinearity, and those with collinearity problems were excluded from the model.

For the selected area, the sdm R package [39] was used to predict the current and future potential distribution of *Larix decidua*. For that, 1000 background (pseudo-absence) records were generated with the *gRandom* method.

For the ensemble prediction of European larch occurrences, five commonly used methods of presence−absence modelling for the ensembling of *SDMs* were applied [22, 41, 45]. These were regression techniques (generalised linear models – GLM [35] and flexible discriminant analysis – FDA [23]), and machine-learning methods (boosted regression trees – BRT [17], random forest – RF [6] and maximum entropy – MaxEnt [49] (maxNet in R [48])). Thirty percent of the data was randomly selected and used to test the models, three times for both subsampling and the bootstrapping procedures, resulting in a total of 30 models for the ensemble.

The performances of the models were assessed using the True Skill Statistic (TSS) and the Area Under the Receiver Operating Characteristic Curve (AUC). Both range from 0 to 1, but have different scales. For TSS, the model performance can be: poor (0.00 – 0.20); fair (0.21 – 0.40); moderate (0.41 – 0.60); substantial (0.61 – 0.80); or excellent (0.81 – 1.00) [29]. Using AUC, the model performance can be: counter-predictions (similar to negative correlation coefficients) (< 0.50); fail (0.51 –0.60); poor (0.61 – 0.70); fair (0.71 – 0.80); good (0.81 - 0.90); or excellent (0.91 –1.00) [3].

To compute the range shifts of the potential habitat suitability, the values of predicted probability of occurrence were transformed to presence/absence data (1 or 0), based on the threshold that maximises specificity and sensitivity. After that, the differences between the predicted future suitability and the current suitability were calculated for the analysed areas. The differences were defined as: unsuitable and stable, when there are no changes between the present and the future; expansion, when an unsuitable present area becomes suitable; and contraction, when a suitable present area becomes unsuitable in the future.

Hirzel et al. [26, 27] recommend the use of a reclassified map, with only a few levels of suitability, instead of maps showing continuous gradients of suitability, for easier communication to policymakers and the public, and because a continuous scale is often misleading. Following this approach, habitat suitability was also classified into five levels, proposed by Hending et al. [24], which are a slightly modified version of the limits suggested by Yang et al. [60]. The levels are the following: very unsuitable (less than 0.20), less suitable (0.21-0.40), moderately suitable (0.41-0.60), highly suitable (0.61-0.80), and very highly suitable (above 0.80). The same limits were used by Brown and Griscom [7], who defined the habitat classification as: unsuitable, poor, fair, good, and excellent.

Future climate projections were obtained for two Shared Socioeconomic Pathways (SSPs) - 245 (middle of the road) and 585 (Fossil-fuelled development), at a resolution of 10 minutes. We utilised the cmip6_world command from the geodata R package for the periods 2041-2060, 2061-2080, and 2081-2100. We used the average of the climate variables from the following 10 recent models: ACCESS-CM2 [12], BCC-CSM2-MR [63], CMCC-ESM2 [31], EC-Earth3-Veg [14], FIO-ESM-2-0 [54], GISS-E2-1-G [40], HadGEM3-GC31-LL [59], INM-CM5-0 [58], IPSL-CM6A-LR [5], and MIROC6 [55].

The Shared Socioeconomic Pathways (SSPs) are a set of alternative futures of societal development, which is a part of developing new scenarios integrating future changes in climate and society to investigate climate impacts, as well as options for mitigation and adaptation [42]. The first number represents the scenario, while the last two indicate the additional radiative forcing achieved by the year 2100 in units of tenths of watts [56]. SSP245 is an update to scenario RCP4.5; it assumes that climate protection measures are being taken. SSP585 can be seen as an update of the CMIP5 scenario RCP8.5, now combined with socioeconomic reasons [56].

3. Results

3.1. Climatic Variables

Of the 19 climatic variables, 11 had collinearity problems and were excluded from the analysis. For the remaining variables, the linear correlation coefficients range from -0.011 (BIO19 with BIO15) to 0.781 (BIO9 with BIO1). The values of the Variance Inflation Factor (VIF) of these are presented in Table 1.

The relative variable importance of the climatic variables based on Pearson correlation and the AUC metric is presented in Figure 1.

The response curves of the climatic variables are presented in Figure 2. All climatic variables present a bell shape, except the BIO15-Precipitation seasonality, which is a coefficient of variation, and BIO18-Precipitation of the Warmest Quarter, which is flat-topped.

The climatic variables, their descriptions, and the variance inflation factors Table 1

Variables	Description	VIF
BIO1	Annual Mean Temperature	7.272
BIO2	Mean Diurnal Range	2.255
	(Mean of monthly (max temp - min temp))	3.766
BIO3	Isothermality	3.938
	[(BIO2/Temperature Annual Range) ×100)]	7.761
BIO8	Mean Temperature of Wettest Quarter	1.247
BIO9	Mean Temperature of Driest Quarter	3.288
BIO15	Precipitation Seasonality (Coefficient of Variation)	4.052
BIO18	Precipitation of Warmest Quarter	7.272
BIO19	Precipitation of Coldest Quarter	2.255

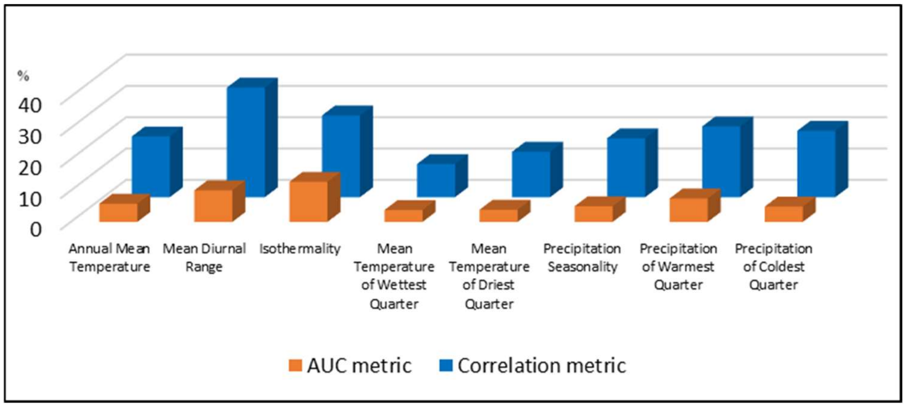

Fig. 1. *Relative variable importance of the remaining climatic variables*

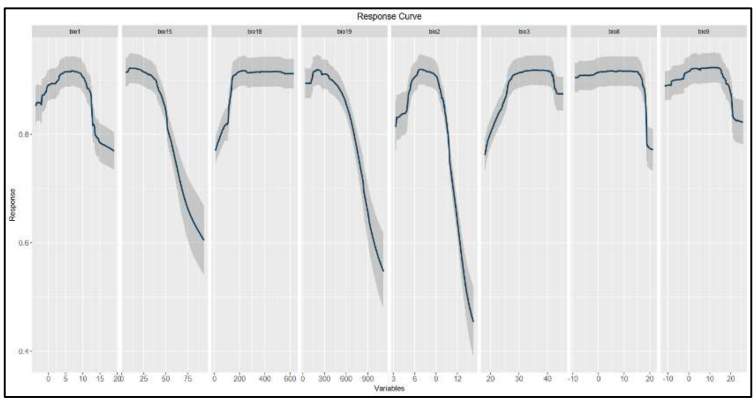

Fig. 2. *The response curve of the climatic variables from the model*

3.2. Model Evaluation

The mean area under the curve (AUC) of the four methods ranged from 0.77 to 0.94, indicating fair to excellent performance (Table 2). The highest True Skill Statistic (TSS) was 0.79 (substantial), obtained by the RF model; while for the other methods, the performances were moderate, with TSS values between 0.47 and 0.58.

Model mean performance Table 2

Methods	Name of the method	AUC	COR	TSS	Deviance
GLM	Generalised Linear Models	0.78	0.41	0.48	0.15
BRT	Boosted Regression Trees	0.82	0.46	0.58	0.14
RF	Random Forest	0.94	0.65	0.79	0.09
maxNet	Maximum Entropy	0.82	0.30	0.56	0.93
FDA	Flexible Discriminant Analysis	0.77	0.35	0.47	0.15

The ensemble result of the 30 models of the potential current habitat suitability for European larch is represented in Figure 3.

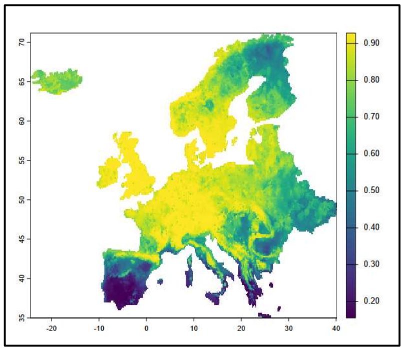

Fig. 3. *Potential current habitat suitability for European larch, based on the ensemble (average) of the 30 models*

3.3. Current Habitat Suitability of European Larch in Europe and Shifts

3.3.1. Based on the Threshold Method

The value of the threshold that maximised both specificity and sensitivity was 0.89468. The current potential habitat suitability of European larch in Europe, based on the threshold, is presented in Figure 4. The predicted changes of habitat suitability for the two SSPs and three periods are represented in Figure 5.

In Europe, under the two SSPs and for all three periods, the predicted unsuitable area is around 74% (Figure 6).

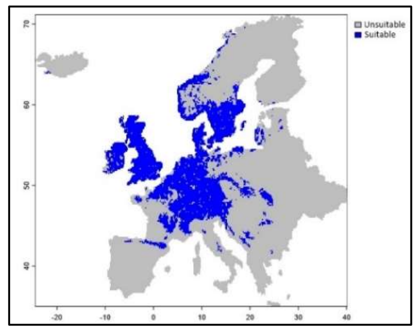

Fig. 4. *Current potential habitat suitability of European larch in Europe, based on the 0.89468 threshold*

For the period 2041-2060, while the predicted expansion area is similar for both SSPs, the contraction area for SSP585 is greater (18.7 vs 16.5%). The predicted stable area is 8.8 and 6.6% for SSP245 and SSP585, respectively.

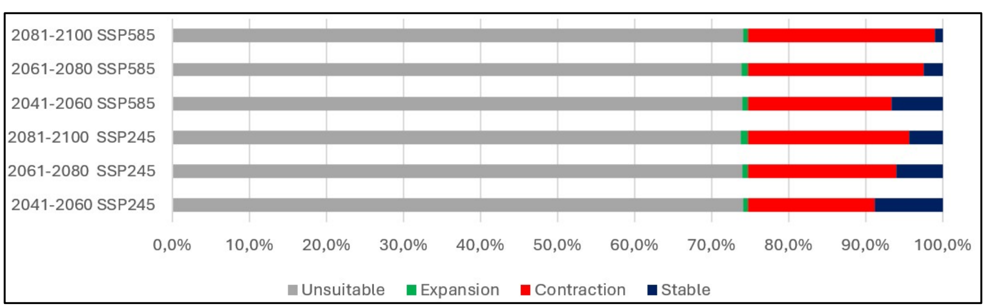

Fig. 6. *Percentage of shifts of the habitat suitability of European larch in Europe for the three periods and two SSP scenarios. Grey – unsuitable areas for both the current and future time periods; red – areas currently suitable, but unsuitable in the future; green – areas currently unsuitable, but suitable in the future; and blue – suitable areas for both the current and future time periods*

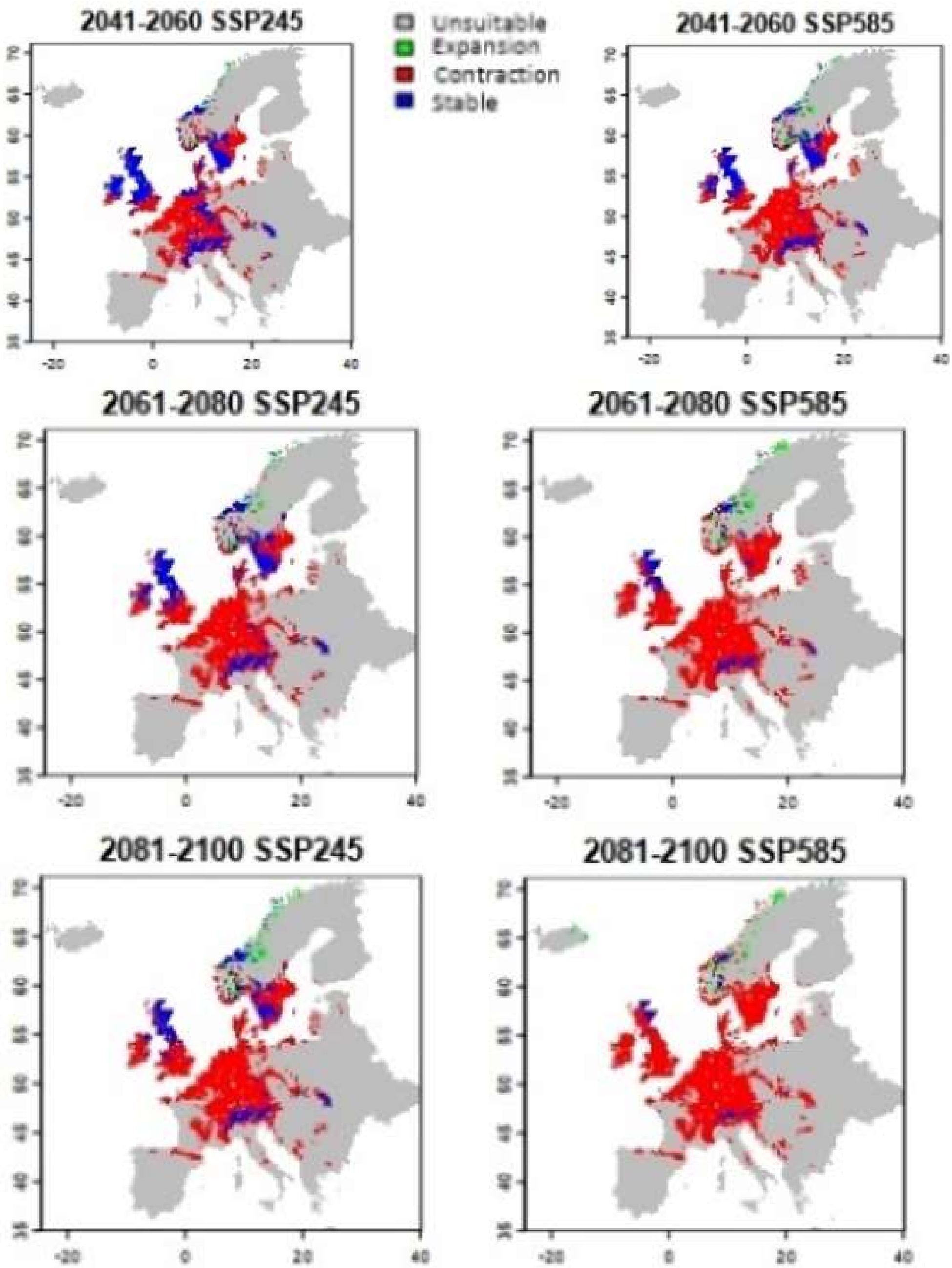

Fig. 5. *Predicted changes of habitat suitability for European larch in Europe, for three periods and two SSPs: grey – unsuitable areas for both the current and future time periods; red – areas currently suitable, but unsuitable in the future; green – areas currently unsuitable, but suitable in the future; and blue – suitable areas for both the current and future time periods*

For the period 2061-2080, the contraction area is 19.3% for SSP245 and 22.8% for SSP585. The predicted expansion area is similar for both SSPs (0.7% for SSP245 and 0.8% for SSP585). The stable area is predicted to be 6.0 and 2.5%, under SSP245 and SSP585, respectively.

For the period 2081-2100, the predicted contraction area is above 20% for both SSPs (20.9 and 24.3% for SSP245 and SSP585, respectively). The stable area is predicted to be 4.4 and 1.0% for SSP245 and SSP585, respectively.

3.3.2. Based on Levels of Suitability

The current potential habitat suitability of European larch in Europe, based on the levels of suitability, is presented in Figure 7. The levels of the predicted habitat suitability for the two SSPs and three periods are represented in Figure 8.

The present very highly suitable area (above 80%) for European larch in Europe is around 49% (Figure 9). For the period 2041-2060, this area is predicted to drop to 30.4% under SSP245 and to 28.1% under SSP585. For the period 2081-2100, the very highly suitable area is predicted to account for 24.6-16.7%, for SSP245 and SSP585, respectively.

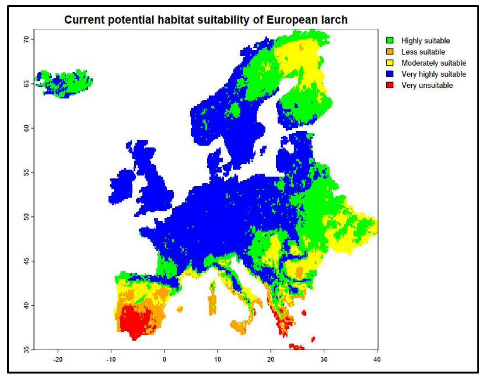

Fig. 7. *Levels of current potential habitat suitability of Larix decidua in Europe: Very unsuitable: less than 20% suitability; Less suitable: between 21 and 40% suitability; Moderately suitable: between 41 and 60% suitability; Highly suitable: between 61 and 80% suitability; Very highly suitable: above 80% suitability*

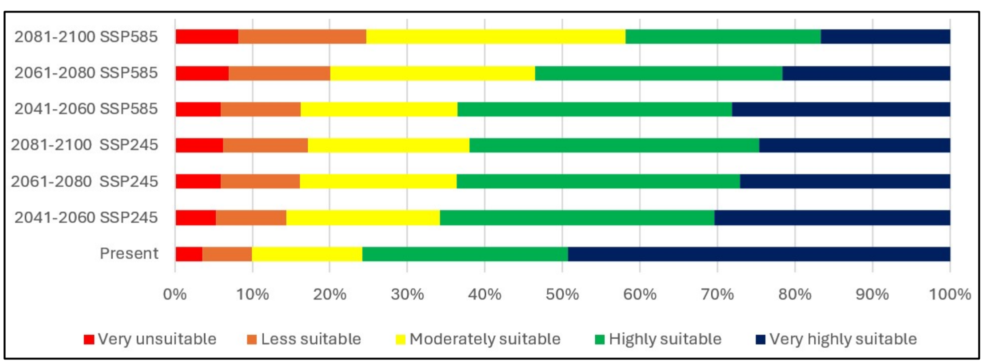

Fig. 9. *Evolution of the levels of suitability of European larch in Europe for the three periods and two SSP scenarios: Very unsuitable: less than 20% suitability; Less suitable: between 21 and 40% suitability; Moderately suitable: between 41 and 60% suitability; Highly suitable: between 61 and 80% suitability; Very highly suitable: above 80% suitability*

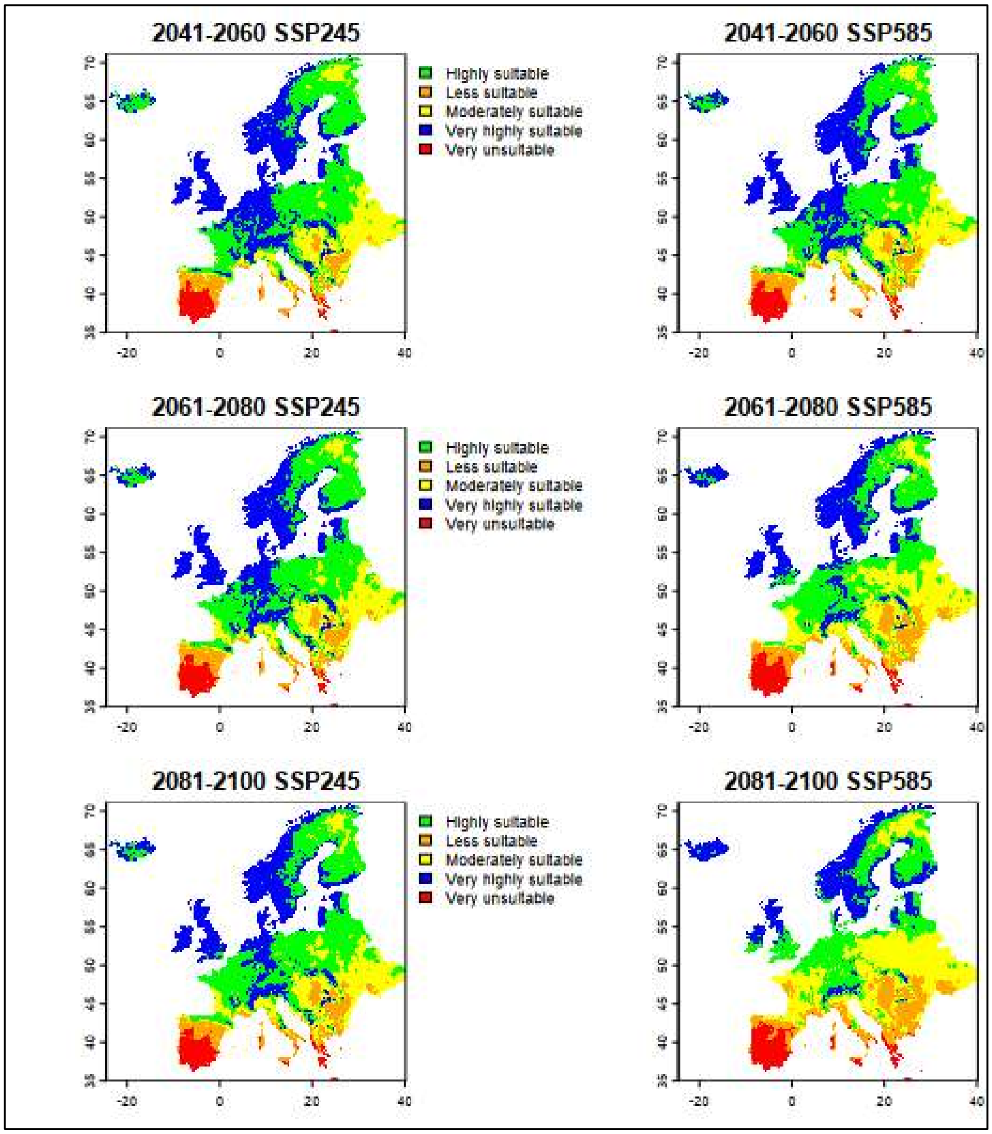

Fig. 8. *Levels of predicted habitat suitability of Larix decidua in Europe: Very unsuitable: less than 20% suitability; Less suitable: between 21 and 40% suitability; Moderately suitable: between 41 and 60% suitability; Highly suitable: between 61 and 80% suitability; Very highly suitable: above 80% suitability*

3.4. Current Habitat Suitability of European Larch in Romania and Shifts

3.4.1. Based on the Threshold

The current potential habitat suitability of European larch in Romania, based on the 0.89468 threshold, is presented in Figure 10. The predicted changes of the habitat suitability for the two SSPs and three periods are represented in Figure 11.

The unsuitable area of the species in Romania is predicted to be around 94%, for all three periods and both SSPs (Figure 12).

For the period 2041-2060, both SSP scenarios predict a low expansion area (0.4 and 0.1%, for SSP245 and SSP585, respectively). Regarding the predicted contraction area, it is 3.4% for SSP245 and 4.1% for SSP585. The stable area represents 2.2% of the total country under SSP245 and 1.5% under SSP585.

For the period 2061-2080, the predicted area of expansion is 0.2% for SSP245, while for SSSP585, no expansion is expected. The contraction area is 4.1% under the SSP245 scenario and 5.0% under SSP585. The stable area for this period is 1.5% under SSP245 and 0.5% under SSP585.

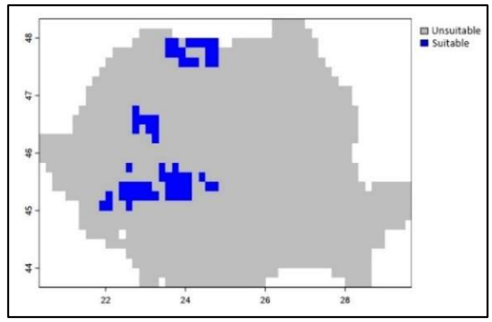

Fig.10. *Current potential habitat suitability of European larch in Romania based on the 0.89468 threshold*

For the period 2081-2100, under SSP245, the stable area is 1.3%, and an expansion of 0.3% is predicted, while the area under contraction is 4.3%. Under SSP585, a contraction of 5.6% is predicted, with no stable area and no expansion.

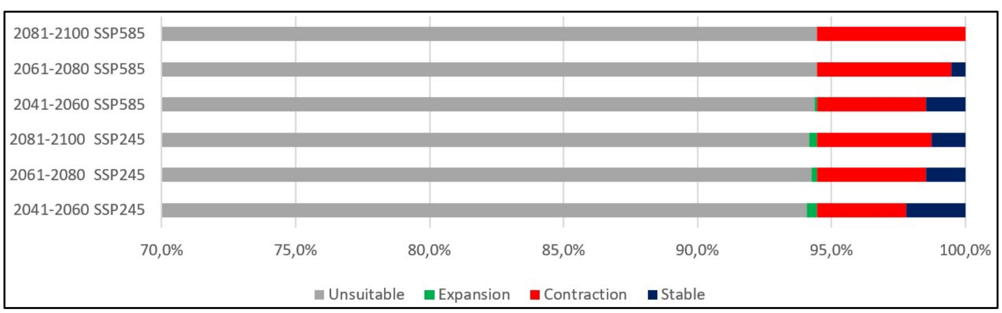

Fig. 12. *Shifts of the habitat suitability of European larch in Romania for the three periods and two SSP scenarios. Given that the predicted unsuitable area in Romania represents more than 90%, the x-axis purposely starts from 70%, for a better view of the other categories: grey – unsuitable areas for both the current and future time periods; red – areas currently suitable, but unsuitable in the future; green – areas currently unsuitable, but suitable in the future; and blue – suitable areas for both the current and future time periods*

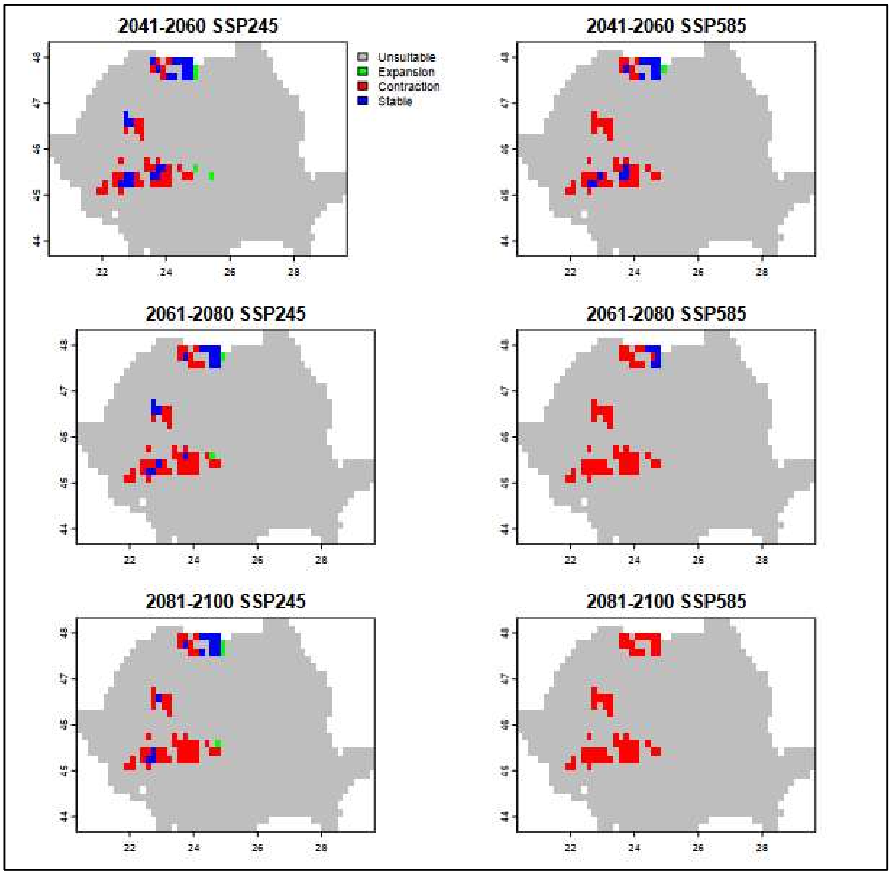

Fig. 11. *Predicted changes of habitat suitability for European larch in Romania, for three periods and two SSPs: grey – unsuitable areas for both the current and future time periods; red – areas currently suitable, but unsuitable in the future; green – areas currently unsuitable, but suitable in the future; and blue – suitable areas for both the current and future time periods*

3.4.2. Based on Levels of Suitability

The areas of the current predicted habitat suitability of *Larix decidua* in Romania, based on levels of suitability, are presented in Figure 13. The levels of the predicted habitat suitability for the two SSPs and three periods are represented in Figure 14.

Under current climate conditions, approximately 20% of the country has a predicted habitat suitability value for this species higher than 80% (Figure 15). For the period 2041-2060, this area is predicted to decrease to 11.1% under SSP245 and to 9.2% under SSP585. For the period 2081-2100, the very highly suitable area is predicted to account for 9.1-3.0%, for SSP245 and SSP585, respectively.

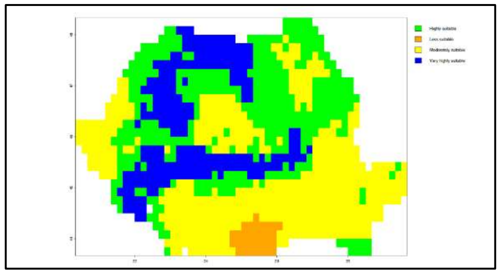

Fig. 13. *Levels of current potential habitat suitability of Larix decidua in Romania: Less suitable: suitability between 21 and 40%; Moderately suitable: suitability between 41 and 60%; Highly suitable: suitability between 61 and 80%; Very highly suitable: suitability above 80%*

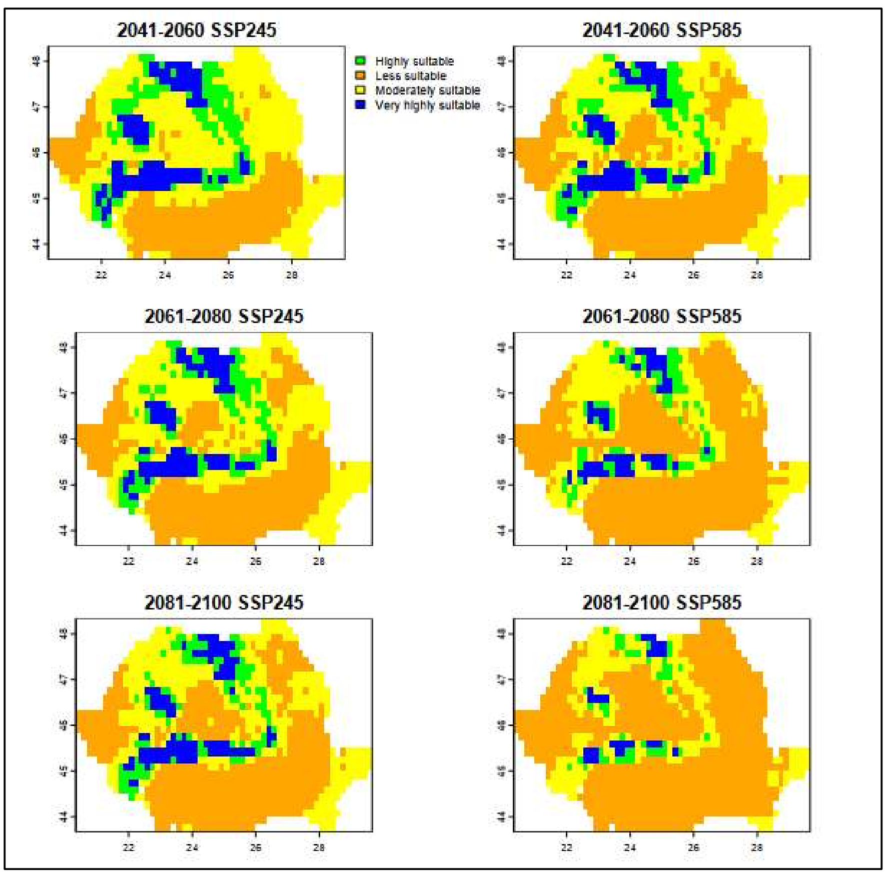

Fig. 14. *Levels of predicted habitat suitability of European larch in Romania: Less suitable: suitability between 21 and 40%; Moderately suitable: suitability between 41 and 60%; Highly suitable: suitability between 61 and 80%; Very highly suitable: suitability above 80%*

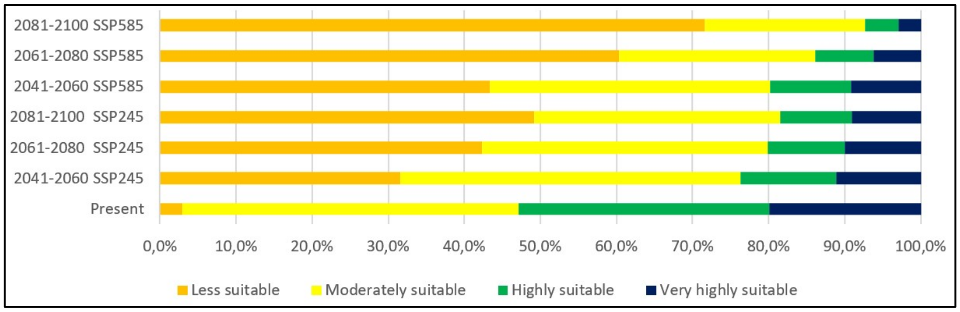

Fig. 15. *Evolution of the levels of suitability of European larch in Romania for the three periods and two SSP scenarios: Very unsuitable: less than 20% suitability; Less suitable: between 21 and 40% suitability; Moderately suitable: between 41 and 60% suitability; Highly suitable: between 61 and 80% suitability; Very highly suitable: above 80% suitability*

3.5. The Ecological Niche

Analysing the ecological niche described by BIO2 and BIO18 (Figure 16), it seems that optimal conditions for European larch are a BIO2-Mean Diurnal Range between 4.4 and 10.3°C; while for BIO18, at least 130 mm of precipitation in the warmest quarter seems to be ideal.

Areas with annual mean temperatures (BIO1) below 10°C present the best conditions for European larch, based on the ecological niche described by BIO1 and BIO18 (Figure 17), but also on the response curve (Figure 2).

Analysing the ecological niche described by BIO2-Mean Diurnal Range and BIO3-Isothermality (Figure 18), it seems that BIO2 below 8°C is suitable for European larch; as well as values below 42 for BIO3 - Isothermality.

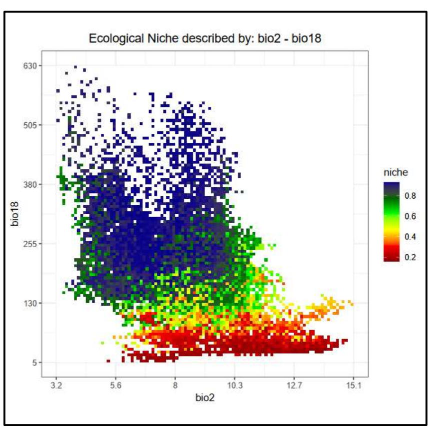

Fig. 16. *Ecological niche described by BIO2-Mean Diurnal Range and BIO18-Precipitation of Warmest Quarter*

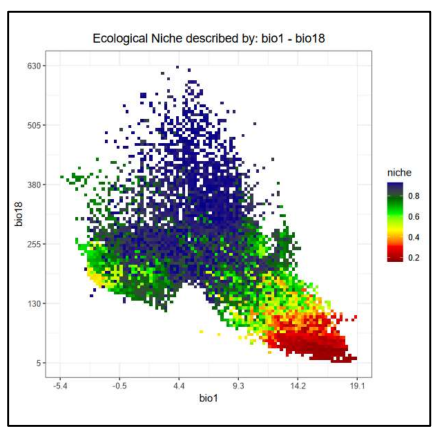

Fig. 17. *Ecological niche described by BIO1-Annual Mean Temperature and BIO18-Precipitation of Warmest Quarter*

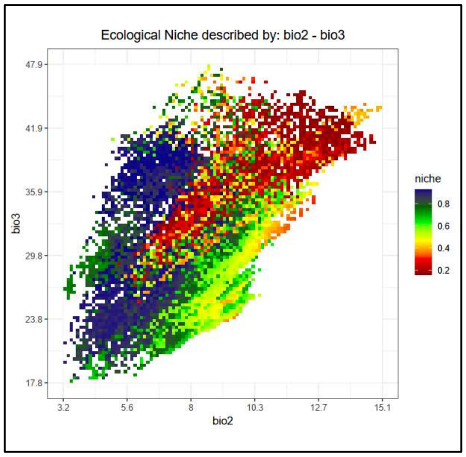

Fig. 18. *Ecological niche described by BIO2-Mean Diurnal Range and BIO3-Isothermality*

4. Discussion

In this study, the potential current and future habitat suitability of European larch in Europe and Romania, as well as the potential range shifts, were assessed based on climatic variables.

By predicting habitat suitability across landscapes, species distribution models help forest management and decision-makers prepare for range shifts, contractions and/or expansions [16]. They can play a key role in supporting assisted migration and ecological restoration efforts in local reforestation initiatives [2, 57].

Climatic variables – temperature above all – rank among the principal factors determining the species distribution [20, 21]. Their influence is especially pronounced for plants, which cannot evade or migrate to escape unfavourable conditions [26].

The primary climatic variables influencing the possible distribution range of European larch were BIO2-Mean Diurnal Range and BIO18-Precipitation of Warmest Quarter, based on the Correlation metric. European larch is known to develop well in areas without large temperature fluctuations [10].

For the analysed area, under SSP585, for the period 2081-2100, the suitable area (stable and expansion areas) is predicted to be 1.5%. In Romania, only under this scenario and period, no stable or expansion area of European larch is predicted.

Analysing the predicted changes of the habitat suitability for European larch in Europe (Figure 5), it can be observed that more than 50% of the current distribution is threatened, especially under the SSP585 scenarios. Our results are in agreement with Dyderski et al. [13], who evaluated changes in projected ranges for 12 species, for the 2061-2080 period, under three RCP scenarios.

By analysing the levels of current potential habitat suitability of European larch in Romania (Figure 13), the conditions in the five natural distribution areas (not shown on the maps) are very highly suitable, except the Ceahlau Mountains, where they are highly suitable. For the period 2081-2100 (Figure 14), under SSP245, the Ceahlau Mountains will be affected, and under SSP585, both the Ceahlau and Ciucas Mountains. Greater attention should be given to these areas in the effort to conserve forest genetic resources.

The Random Forests model was the only one classified as excellent based on AUC (0.94) and substantial based on TSS (0.79). In the study by Marchi et al. [32], the RF technique outperformed eight other algorithms in 10 out of 12 metrics used for data fitting assessment.

The predicted habitat suitability models consider only the climatic variables. Changes in the relationships among the variables could appear and represent the main risk to generalisation [26]. Other studies have incorporated more variables, such as soil types and land-cover data [9, 50], or biotic interactions [18].

Another limitation of this study is that the genetic variation and local adaptation of European larch were not considered, but the ability of tree species to survive and adapt under a changing environment depends on their intraspecific adaptive genetic variation [38, 52]. Using better-adapted tree species and selected provenances can strengthen forest system resilience and allow assisted migration strategies [33, 45].

Generally, models reflect only a partial view of reality [26]. Appropriate attention to the limitations of the models and continuous reassessment based on monitoring can reduce uncertainty [30].

5. Conclusions

Based on climatic variables, the current and future potential habitat suitability of European larch was modelled for the continental part of Europe and Romania.

The most important climate variables that influence the distribution of European larch were BIO3-Isothermality, BIO2-Mean Diurnal Range, and BIO18-Precipitation of the Warmest Quarter.

Across Europe, the contraction of potentially suitable areas for European larch is between 24 and 44 times higher than that of expansion, depending on the period and the SSP scenarios.

In Romania, under the worst-case scenario (SSP 585), for the period 2081-2100, very highly suitable areas (above 80% habitat suitability) are predicted to cover 3.0% of the country's area, which is larger than the current distribution range (0.3% of the forest area).

Greater attention should be given to conservation efforts for the European larch genetic resources from the Ceahlau and Ciucas Mountains, areas predicted to be affected by climate change.

The models should be further developed to incorporate other important variables for the habitat suitability of European larch.

Modelling the effects of climate change on species distribution could help develop better forest management strategies for mitigation and adaptation.

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