Robust modelling of the impacts of climate change on the habitat suitability of forest tree species

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Publication Office of the European Union, Luxembourg

March 2017

European
Commission

JRC TECHNICAL REPORTS

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A European-wide study on silver fir maximum habitat suitability

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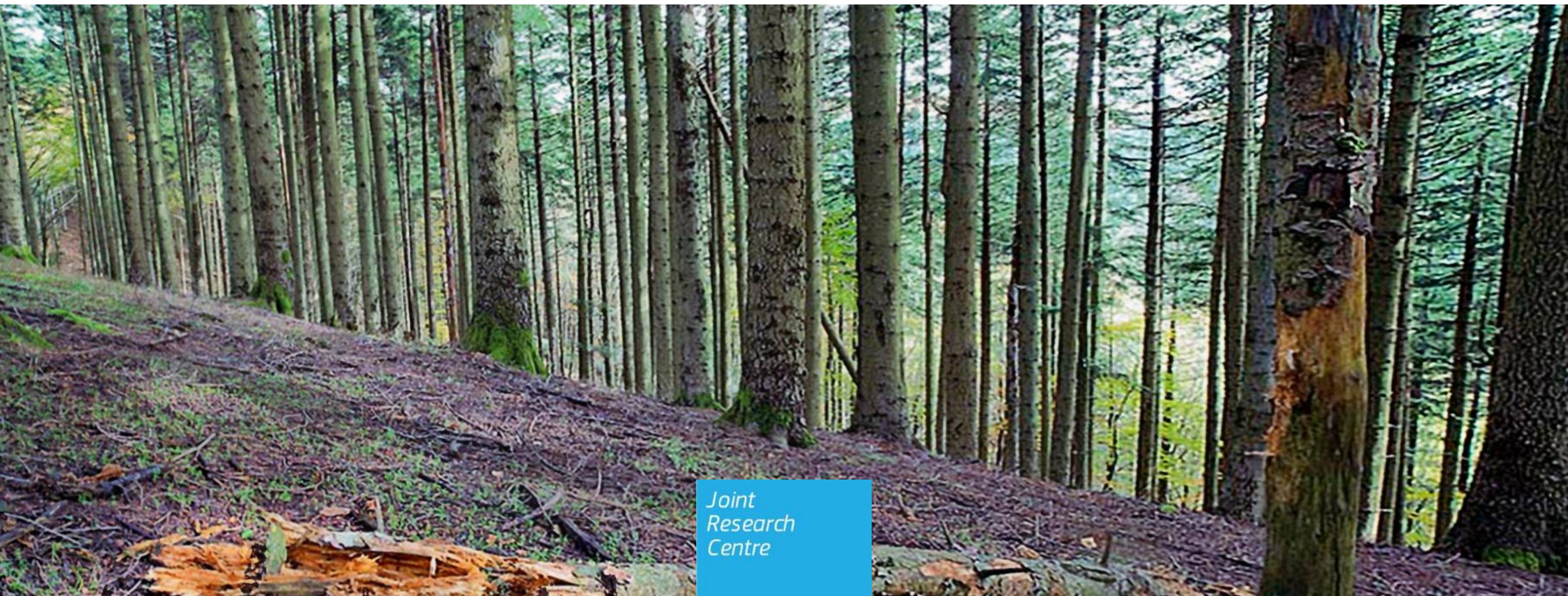
2017



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JRC105751

PDF ISBN 978-92-79-66704-6 doi:10.2760/296501

Luxembourg: Publications Office of the European Union, 2017

How to cite this report: de Rigo, D., Caudullo, G., San-Miguel-Ayanz, J., Barredo, J.I., *Robust modelling of the impacts of climate change on the habitat suitability of forest tree species*, doi:10.2760/296501

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Image in the front cover: mixed forest with *Abies alba* in the *Parco Nazionale delle Foreste Casentinesi, Monte Falterona, Campigna*, Italy – adapted from an image authored by Alessio Di Leo (CC-BY), http://archive.is/h2srd.

Foreword

In the European continent, forests play a strategic multifunctional role, serving economic, social and environmental purposes by offering a broad set of protective, provisioning, regulating and cultural functions [1, 2]. However, as they are among the most complex and influential systems [3, 4, 5, 6, 7, 8, 9], their interaction with the ongoing climate change – and the multifaceted chain of potential cascading consequences for European biodiversity, environment, society and economy – is far from being well understood and addressed; and requires robust science-based methods to support an integrated assessment of risks and options for mitigation and adaptation [10, 11]. This methodological task is rich in hidden challenges, some transdisciplinary, whose underestimation or oversimplification might hamper a sound science-based policy support.

- In Europe, forests play a strategic multifunctional role, serving economic, social and environmental purposes. However, their complex interaction with climate change is not yet well understood.
- The JRC PESETA project series proposes a consistent multi-sectoral assessment of the impacts of climate change in Europe.
- Within the PESETA II project, a robust methodology is introduced for modelling the habitat suitability of forest tree species (2071-2100 time horizon).
- *Abies alba* (the silver fir) is selected as case study: a main European tree species often distributed in bioclimatically complex areas, spanning over various forest types and with multiple populations adapted to different conditions.
- The modular modelling architecture is based on relative distance similarity (RDS) estimates which link field observations with bioclimatic patterns. Robust management of uncertainty is also discussed.

A core fact not to be neglected is that forest resources in Europe display a complex network of feedbacks with other natural resources and with the anthropic sphere [3, 12, 13]. They cover about one third of the European continent (Figure 1), providing a variety of ecosystem services and supporting the bio-based economy of the European countries [3, 12, 14]. Unfortunately, this vital ecological, cultural and economic value is threatened by the combined impact of multiple factors. These stressors include several disturbances, both abiotic and biotic; management practices not always shaped by pondering the importance for complex ecosystems of their richness and diversity – in particular for preserving their resilience [15]; and the subtle cumulative role of the changing climate which may severely exacerbate the stressors affecting European forests and the network of human systems affected by their state [3, 12].

Forest disturbances (such as wildfires, wind and storms, invasive species, forest pests and diseases) may be tightly linked with the changing bioclimatic conditions, and the impact of the anthropogenic components underpinning the array of disturbances is intrinsically coupled with the climate evolution. For example, a certain habitat may become less suitable for a given forest tree species to thrive, irrespective of forest management efforts and even ignoring ecological competition among different taxa. This typology of habitat suitability loss may be estimated by considering the slowly changing local bioclimatic patterns – this is the object of the present study – even if the particular modality with which the suitability loss may become evident could occasionally imply a sudden transition, e.g. due to a resilience failure, a previously unlikely prolonged drought, an exceedingly wet period or an abrupt pest outbreak [15, 16, 17, 18, 19, 20, 21].

Although the specific future occurrence of one among the potentially sudden homeostasis/resilience failures [22, 23] is virtually impossible to predict, nevertheless the general bioclimatic trends may be modelled with the help of robust statistical or fuzzy-possibility analysis. Discussing the characteristics of a robust methodology for linking bioclimatic components with the observed patterns of occurrence for a certain tree species is the aim of this study. A novel modelling approach is proposed for estimating the maximum extent of suitable habitats (*maximum habitat suitability*) for focal taxa, where the focus is here exemplified for tree species. Both technical and interpretation core aspects are presented in an integrated overview. The semantics of the array of quantities under focus and the uneven sources of uncertainty at the continental scale are discussed (following the *Semantic Array Programming* paradigm [24, 25, 26]).

The PESETA projects

The context underpinning this study is based on a series of cross-disciplinary projects mainly developed within the Joint Research Centre (JRC) of the European Commission. This project series is denoted as PESETA (Projection of Economic impacts of climate change in Sectors of the European Union based on bottom-up Analysis, https://ec.europa.eu/jrc/en/peseta). In particular, the focus of the second instance (PESETA II) is on making a consistent multi-sectoral assessment of the impacts of climate change in Europe for the 2071-2100 time horizon.

The methodology of the project is characterised by two distinctive features. First, the results rely on the bottom-up biophysical impact estimated by sectoral models. Bottom-up models can approach the relationship between climate change and biophysical impacts in a structural way, including the main required interactions and mechanisms. Second, the assessment follows a consistent approach, where all biophysical impact models use the same climate data, and take into account other horizontal issues. The PESETA II project includes the results of this study [27], which also serve as the basis for the modelling of maximum habitat suitability estimates as published in the European Atlas of Forest Tree Species [28].

Following the conclusion of the PESETA II project, a new instance (PESETA III) of the cross-disciplinary exercise has been active since January 2016. The new JRC PESETA III project is specifically focused on supporting the implementation of Action 4 of the EU Adaptation Strategy by deepening and further refining existing JRC bottom-up analyses of climate change impacts. Furthermore, it will contribute to report on the Strategy's implementation that the Commission will have to present to the European Council and Parliament in 2017. The JRC PESETA III project, compared to JRC PESETA II, will develop projections for a shorter time horizon (2030-2040, in addition to the end of the century analysis) use the new family of climate futures (Representative Concentration Pathways, RCPs, and Shared Socioeconomic Pathways, SSPs), and have an explicit emphasis on assessing impacts of extreme events and their costs. In PESETA II, the focus of the analysis on habitat refers to the specific vegetation characterising European forests, with a demonstration case study centred on *Abies alba*, here discussed. In PESETA III, the analysis on habitat focuses on the vegetation characterising the Mediterranean habitat, with first results based on the same climate projections applied in this study [29].

Among the climate change impacts considered within the JRC PESETA project series, it is worth mentioning – as especially relevant to key European forest habitats – the analysis on droughts [30] and wildfires (as a key abiotic disturbance for forest resources).In particular, a link exists between weather, climate and fire danger with the future evolution of arid climate patterns over Europe. The combined effect of these emerging patterns may be considered as a major threat for the bioclimatic conditions supporting the habitat of several forest tree species [3]. The evolution of the arid climate conditions are analysed in the PESETA III module on the Mediterranean habitat, while a drought analysis from a perspective on fire danger is considered in the module on wildfires.

Robust modelling of tree species habitat suitability

How resilient are the European forests? How robust is our understanding of the potential impacts of the changing climate on the future forests in the European continent? Recalling the aforementioned inherent complexity of forest systems, and the significant share of forested areas in Europe (Figure 1), an articulated response may be expected.

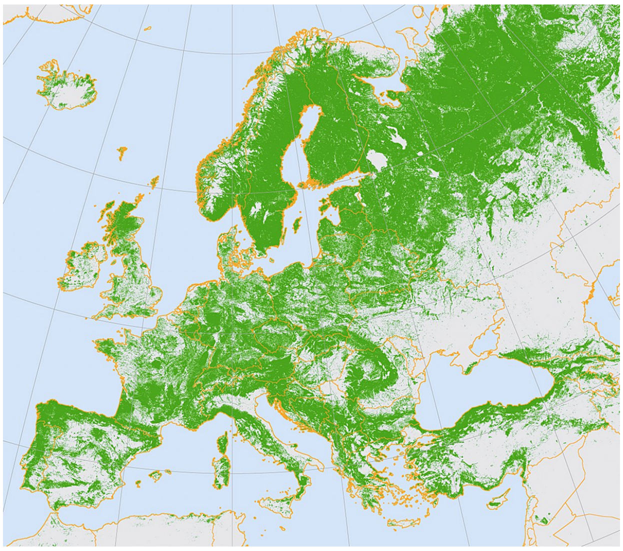

Figure 1: Distribution of forest areas in Europe. Forest resources cover about one third of the European continent, providing a variety of ecosystem services and supporting the bio-based economy of the European countries [3, 12, 14]. If mixed landscapes are also considered (quite a frequent category of land-cover in the complex anthropic context of Europe), then the extent of areas with a non-negligible share of forests dominates several regions of the continent. In green, areas with at least 5 % of forest cover. Derived after de Rigo *et al.* [3, 28] from a pan-European harmonisation based on existing land-cover maps [31, 32, 33, 34, 35, 36].

Forests in Europe span over a variety of types [37, 38] and even a basic broad characterisation requires multiple, quite different ecological domains to be considered, from the subtropical domain in the Mediterranean areas to the temperate and boreal domains in the northern areas of the continent [39].

The literature on tree species distribution is huge. Unfortunately, terminology, meaning and methodological limitations of reported findings might be ambiguous – an ambiguity which could potentially reverberate at the science-policy interface [40, 41, 42, 43, 46, 47]. A confusion exists between distinct concepts such as the distribution range of a certain tree species, its frequency or probability of presence, its habitat suitability (and which kind of statistical operator is exploited to compute this suitability), the realised niche of the species versus its potential niche [48, 40, 41, 42, 43]. Furthermore, available pan-European forest field data are collected with challenging harmonisation efforts from multiple regional (e.g. country-level) sources. Regional datasets are typically collected and organised independently, with uneven spatial density of sampling and uncertainty; and sometimes following non-homogeneous definitions of the collected information [28, 49, 50]. Therefore, semantic, modelling and data uncertainties characterise tree species distribution and suitability modelling at the European scale, *requiring robust modelling strategies to mitigate their combined uncertainty*.

This work mainly deals with the habitat suitability (HS) of a tree species, frequently linked to the bioclimatic conditions characterising the habitats under which the species is suitable to thrive. Here, a distinction should be made between:

- the average HS – derived by considering the frequency of observed occurrences for a given bioclimatic pattern as a proxy for the corresponding fitness of the species – and
- the maximum HS (MHS or *survivability*) – which equally considers also less frequent occurrences, so as to detect where the species can survive irrespective of whether it would be dominant or secondary within a certain bioclimatic habitat.

The first definition is the typical one implicitly considered by most HS applications, even because computing it is faster (if not the only possible option) with several available tools. The latter definition is the one on which this work focuses. Since the maximum HS is also based on available field observations (which are by definition limited to the realised niche, as altered by the anthropic influence), the estimated maximum HS of a species should not be confused with its potential niche – which may be a challengingly elusive concept from a data-driven perspective. Nevertheless, maximum HS might support the assessment of the areas whose bioclimatic conditions may allow a given species to survive (including conditions observed less frequently, thus more robust to the typically uneven sampling of the data available at regional or wider scale); and the potential spatial shift of these areas under changing climate scenarios.

HS is sometimes exploited as proxy information for crudely approximating the current distribution range (if not even the probability of presence) of the species. Extrapolating this approximation to future climate change scenarios might be tempting. However, there are several reasons why some geographic areas might be bioclimatically suitable for a species even if the species is not observed there. Among them, three may be mentioned, because of their policy relevance:

- **ecological competition**: although the species may be bioclimatically suitable if considered in isolation, under natural conditions other taxa might prevail because of their higher fitness in taking advantage of the local bioclimatic conditions. In this case, the species may simply be unable to survive the competition with the other taxa, or it may instead be severely limited in its potential dominance, thus locally resulting as a secondary or rare species. Under these circumstances, plantations or managed forest stands (where natural competition is artificially limited) may enable the species to exploit its full habitat suitability. Biotic disturbances (e.g. forest tree species pests or diseases; grazing, browsing or bark peeling) may act in a way similar to competition, by selectively reducing the fitness of the affected tree species population – or even potentially impeding the survival of the population. Concerning only *Abies alba*, several examples of biotic disturbances have been discussed in the literature [51, 52, 53, 54, 55, 56].
- **Dispersal limitation**, distance from the borders of the current distribution: an otherwise suitable area may not yet have been colonised by the species [44, 45]. The changing bioclimatic patterns under climate change may amplify the impact of dispersal limitation, so as for areas expected to become suitable bioclimatically to remain not colonised by the species under focus. The departure from this natural phenomenon is unfortunately exemplified by considering invasive species, when they are introduced and established in suitable areas

which are remote from the initial distribution range. Among the consequences of invasive taxa, an increased (sometimes overwhelming) ecological competition – see previous point – may potentially have an impact on the distribution of a species of interest.

- **Anthropogenic elimination**: for example, eradication of the species as a consequence of systematic anthropic interventions to favour other taxa which may be locally more convenient (e.g. from an economy perspective). In this case, an area suitable from a bioclimatic perspective *and* already belonging to the current distribution range is artificially removed from it. The opposite typology of anthropic interventions – namely the introduction of a species outside its natural range, and the protective management operated to favour the introduced species over other potentially competing taxa – is instead limited by the suitability for the species of the local bioclimatic conditions[1]. Therefore, anthropic elimination may be effective despite favourable local bioclimatic conditions, while anthropic introduction may be ineffective under unfavourable bioclimatic conditions.

These three phenomena have in common a straightforward mechanism with which the habitat suitability influences the species distribution. The maximum extent of the HS acts as a logical constraint for the actual species distribution, so that the latter is strictly included within the maximum HS. Therefore, while a future expansion of the maximum HS might not automatically imply an expanding distribution range, *a future MHS contraction would likely affect the distribution range by imposing a contraction to it*.

Discussing on robustness of habitat suitability modelling under climate change scenarios, another key source of uncertainty deserves to be mentioned. Projections on potential future climate scenarios predict broad areas of Europe to possibly shift towards geoclimatic patterns which are far from *any* currently observed pattern in Europe (See also Figure 12, in particular maps G to J). This wide shift introduces an intrinsic source of modelling uncertainty due to climate-driven *extrapolation* [61]. Elementary models which are based on relatively small subsets of the information on the climate signal – as made available by global circulation models and regional climate models – may be able to limit the impact of the forced extrapolation, although at the price of a more simplistic description of the biophysical conditions (higher modelling uncertainty [28]). Unfortunately, this might be a reassuring overoptimistic consequence of the low-dimensionality of the simplified climate signal considered [62, 63, 64, 65, 66].

The approach we propose is robust even in exploiting a rich set of bioclimatic predictors (not to oversimplify the climate signal) while transparently highlighting the extent of extrapolation, which is intrinsically computed by the underpinning mathematical methods. The proposed modelling architecture to estimate maximum HS is based on the relative distance similarity (RDS) approach, which estimates a dimensionless score of how similar/dissimilar the bioclimatic patterns of a tested area are compared with the available species observations.

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[1] Except where management practices alter the natural bioclimatic conditions, e.g. with irrigation or by means of greenhouse control of the temperature patterns. Under these circumstances, a specific maximum habitat suitability might nevertheless be estimated, by introducing the modified bioclimatic conditions in the analysis.

Box 1. From observed occurrences to adaptation scenarios: the role of the (often unavailable) information on phenotypic and genetic diversity

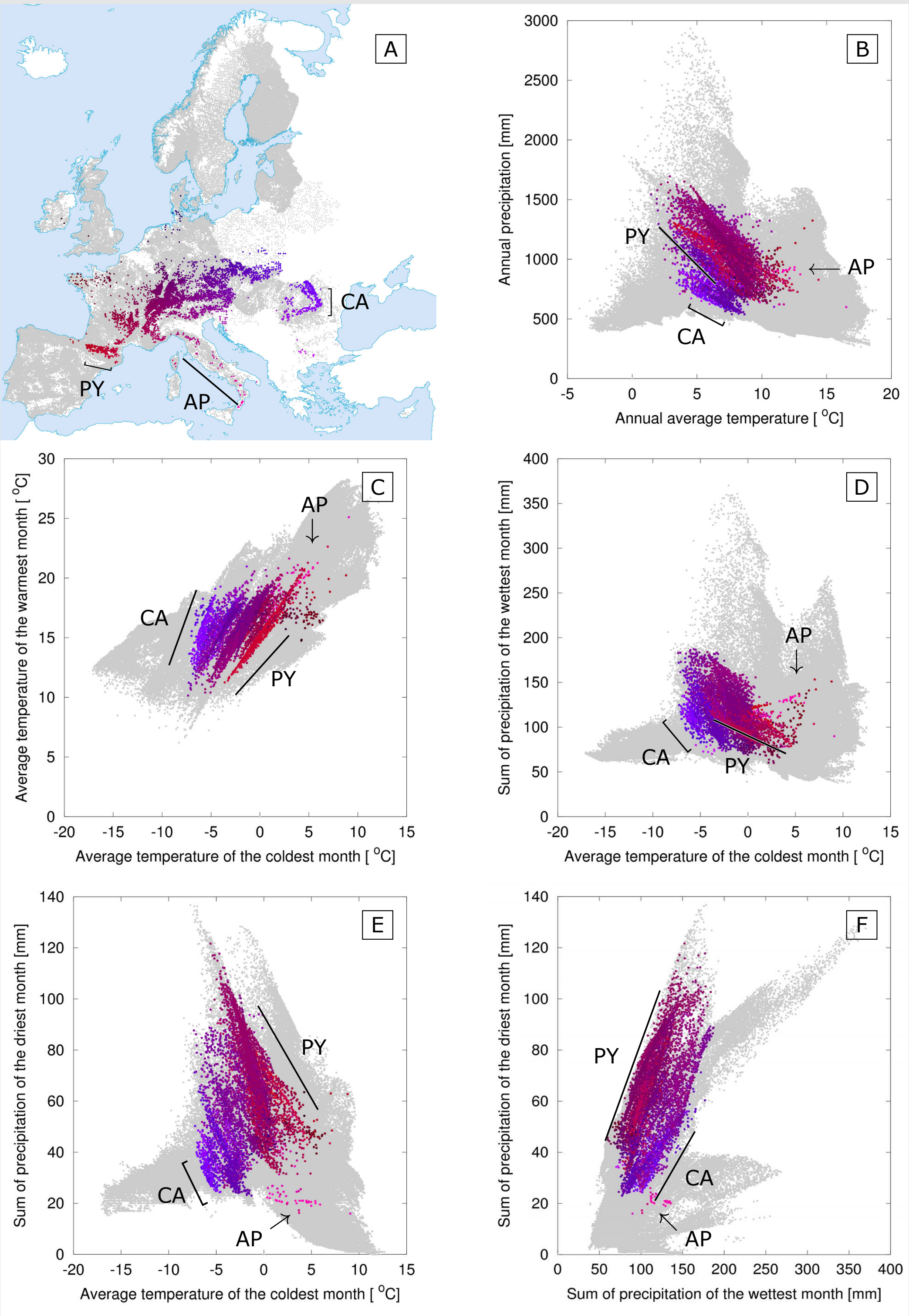
The outcome of a habitat suitability analysis relies on the available information on the taxon under focus and is subject to the propagation of its unavoidable uncertainty. The characterisation and definition itself of the taxon, whether a certain taxon is composed of multiple sub-species, and the role of its populations, are important topics. It is not infrequent to find cases where what has previously been considered a single species should instead be reclassified, with hybridisation between different taxa and intraspecific diversity sometimes also playing a role on the suitable bioclimatic ranges associated with local populations and the corresponding past, current and future spatial distribution of the taxon (e.g. this is also the case of some taxa in the genus *Abies* [57, 58, 59]). This source of uncertainty may be summarised even by referring to the debated potential confusion of population structure with species boundaries [60].

Within a robust approach to habitat suitability analysis for supporting adaptation policy, intraspecific diversity and its typically complex spatial pattern need to be pondered, and a modelling decision/scenario should be clarified on how to process the various subsets of observations referring to more homogeneous species' populations. Depending on the particular criteria with which the maximum extent of the HS is modelled, the resulting estimated MHS may approximate different concepts – and thus support the answering of different policy questions. The terminology associated with these scenarios is heterogeneous and sometimes the corresponding assumptions are not even made explicit in the literature. Here, a simplistic taxonomy is offered as an incomplete summary contribution – also to better understand the potential applications of the proposed modelling architecture.

- **Local adaptation scenario**. If the observed presences of the species are considered without additional processing, the corresponding MHS of each "homogeneous subset" of observations will be modelled assuming the current geographical pattern of intraspecific diversity to be preserved. This modelling scenario may correspond to a "local adaptation" analysis, where the changing pattern of bioclimatically suitable areas under climate change is shaped following the observed potential of each *local* "homogeneous subset" of observations. *Locality* is here defined in terms of bioclimatic similarity, thus supporting even "bioclimatic twins" [67] assisted migration analysis (this definition satisfies the cryptomorphic partitioning property described in the introduction – see footnote 6). In the following, this local adaptation scenario is considered in the exemplified MHS analysis of *Abies alba*. An example of an additional constraint which may be imposed to a local-adaptation MHS analysis could consist of narrowing the definition of *locality* by adding the geographic proximity of the observations to their bioclimatic similarity.
- **Regional adaptation scenario**. The analysis interest could instead cover the overall bioclimatic envelope which might be associated with the species under the assumption that the full potential of phenotypic/genetic diversity of the species – as expressed within the analysed spatial extent – is to be exploited. This implies that even intermediate bioclimatic conditions between the conditions suitable for two distinct subsets (geographically and bioclimatically separated) would be considered as suitable.
- **General adaptation scenario**. Finally, the analysis might be interested in the global adaptation potential of a given species, even when its realised niche within the considered spatial extent is significantly incomplete compared with the fundamental niche which encompasses geographic domains outside the spatial extent. This scenario requires observations to be available even outside the studied spatial extent, so as for the MHS estimates to be informed about suitable bioclimatic patterns not associated with observations of the taxon within the spatial extent.

Depending on the typology of adaptation strategy to investigate, the mathematical workflow of the habitat suitability analysis needs to be adapted accordingly. Especially for the regional/general scenarios, genetic constraints and nonlinearities may highlight essential trade-offs [68, 69, 70, 71, 72] limiting the suitability for the species of some intermediate patterns between bioclimatic conditions for which field observations confirm the suitability (Figure 2).

Figure 2: Observed presences of *Abies alba* (coloured in A-F) with reported absences in grey. Observations are highlighted from populations in the Pyrenees (PY), Italian Apennines (AP) and Carpathians (CA). The bioclimatic space (autoecology diagrams B-F [28]) is multidimensional and rich of nonlinear patterns. An oversimplification of it might suggest false simplistic relationships. In B, the pattern of presences may resemble a Gaussian ellipsoid. However, in C-F the pattern reveals part of its real complexity (e.g. AP appears as an almost isolated fragment).



Why *Abies alba* as a case study

Figure 3: **Top**: Natural regeneration in a mixed stand with *Abies alba* and *Picea abies*. Adapted from Brang *et al.* [73], CC-BY. **Bottom**: An example of silver fir decline, Aragón Pyrenees, Spain. Defoliated crowns are visible in a forest landscape with an increasing rate of dead trees. Adapted from Linares and Camarero [74], CC-BY. On the complexity of the bioclimatic and anthropic factors influencing tree species decline, see e.g. Florentina and Io [75].

Silver fir, *Abies alba* Mill. [57], is a particularly interesting tree species to serve as a case study for this kind of analysis. From an ecological perspective, it is regarded as an important functional balancer and it may serve as a keystone species to maintain high biodiversity in forest ecosystems [76, 77]. Within its range of bioclimatic habitat suitability, it shows a significant adaptation to temperature, soil and precipitation, with a genetic structure potentially influenced by geographical isolation and environmental gradients [78, 79].

As a main tree species in Europe, the distribution and history of silver fir is influenced by anthropogenic factors [76, 80]. However, compared with other broadly distributed conifers such as *Picea abies* or *Pinus sylvestris*, the current distribution of *Abies alba* in Europe shows a higher natural component, in particular over some areas where systematic forest inventory information on observed presence/absences is not available, and only simpler information on the bare occurrence at lower spatial resolution is known [81, 28].

Therefore, a habitat suitability analysis based on presence/absence training data may be also qualitatively corroborated (or rejected) – for the current climate – in areas quite remote from where training data are available (see Figures 11, 12 and 13). On the other hand, the intraspecific diversity of *Abies alba* may suggest some implications for oversimplistic modelling approaches. For example, the use within process-based models of sharp limiting factors (derived also from theoretic assumptions which simplify the rich set of empirical evidence) has been criticised and might potentially be suitable to significantly alter the reconstructed habitat suitability [82, 83, 59].

Furthermore, the future distribution of *Abies alba* in Europe is debated with partially contrasting studies suggesting reduction or expansion patterns in the species suitability in response to the expected warming [84, 76, 53, 85, 83]. In addition, the natural migration rate of the species has recently been revised to less than 250 m yr^{-1}, which would advise adaptation options to be considered in some critical areas of Europe where the species is too fragmented or where the speed of climate change would far exceed this migration rate [86, 80].

In this respect, this study aims to contribute with a novel approach on habitat suitability, focused on estimating the *maximum* extent of the bioclimatic-limited habitat (*maximum habitat suitability* or adult *survivability*) where an adult tree of *Abies alba* is potentially suited to live, irrespective of intra/inter specific competition and other factors not linked to the local bioclimatic conditions.

This offers a bioclimatic-driven *upper bound* to the habitat suitability of the tree species. The RDS survivability index is designed also to ease the integrated analysis with other ecological/anthropic limiting factors. As an upper bound, integrating other limiting factors to it would ideally reduce (but never increase[2]) the detected extent of areas actually suitable for a given tree species not only from a bioclimatic perspective.

The modelling architecture is easy to adapt to process arrays of components, e.g. both

- (a) aggregations of taxa; or
- (b) specific subsets of interest for a given species.

The case of interspecific cooperation – as an example of (a) – may be considered within the proposed approach wherever field observations are available in bioclimatic areas where some co-occurring taxa are known to display mutualism. In particular, the RDS survivability for a specific mutualistic *association* might be modelled instead of the survivability of each single taxon composing this association. The case of genetic diversity – as an example of (b) – within a given species may instead be addressed by independently modelling – where data are available – genetically homogeneous subsets of the species observations. The mathematical methodology allows exact composite survivability to be easily estimated starting from RDS survivability indices computed for components of a certain aggregated taxon. Therefore, the RDS maximum HS of multiple genetically homogeneous components of the species under investigation may easily be aggregated at the species-level (or even to higher taxonomic ranks).

This approach may support a less inaccurate/extrapolated decoupling of the bioclimatic components of tree species habitat suitability, based on the realised niche as depicted not by theoretical limiting factors estimated in laboratory under controlled conditions, but instead by the actual field observations – under the full range of observable conditions which result from the complex (and surely not yet fully understood) dynamic pattern of ecosystem disturbances and feedbacks.

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[2] See footnote 1.

Acknowledgements

This publication benefited from the peer-review of the PESETA II project (Projection of Economic impacts of climate change in Sectors of the European Union based on bottom-up Analysis)[3] with the comments and suggestions of its advisory board and the other external referees (see [27]). We also thank Alessandro Cescatti and Frank Dentener for their review comments.

We gratefully acknowledge Giuseppe Amatulli for the initial investigations on how to better apply environmental predictors to HS modelling (see also [87, 88]), Alessandro Dosio for suggestions on improving climatic downscaling/interpolation, Alessandra Bianchi for managing the dataset in NetCDF format, Thomas Huld for constructive discussions on the use of the *r.sun* GRASS-GIS module (see also [89]) and Tracy Houston Durrant for the compelling comments and suggestions on how to improve the readability.

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Please, cite as:

de Rigo, D., Caudullo, G., San-Miguel-Ayanz, J, Barredo, J.I., 2017. **Robust modelling of the impacts of climate change on the habitat suitability of forest tree species**. Publication Office of the European Union, 58 pp. ISBN:978-92-79-66704-6, https://doi.org/10.2760/296501

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[3] https://ec.europa.eu/jrc/en/peseta.

Abstract

In Europe, forests play a strategic multifunctional role, serving economic, social and environmental purposes. However, forests are among the most complex systems and their interaction with the ongoing climate change – and the multifaceted chain of potential cascading consequences for European biodiversity, environment, society and economy – is not yet well understood.

The JRC PESETA project series proposes a consistent multi-sectoral assessment of the impacts of climate change in Europe. Within the PESETA II project, a robust methodology is introduced for modelling the habitat suitability of forest tree species (2071-2100 time horizon). *Abies alba* (the silver fir) is selected as a case study: a main European tree species often distributed in bioclimatically complex areas, spanning over various forest types and with multiple populations adapted to different conditions[4].

The modular modelling architecture is based on *relative distance similarity* (RDS) estimates which link field observations with bioclimatic patterns, projecting their change under climate scenarios into the expected potential change of suitable habitat for tree species. Robust management of uncertainty is also examined. Both technical and interpretation core aspects are presented in an integrated overview. The semantics of the array of quantities under focus and the uneven sources of uncertainty at the continental scale are discussed (following the *semantic array programming* paradigm), with an effort to offer some minimal guidance on terminology, meaning and methodological limitations not only of the proposed approach, but also of the broad available literature – whose heterogeneity and partial ambiguity might potentially reverberate at the science-policy interface.

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[4] The PESETA project series is committed to further explore the analysis on European habitats. In the ongoing PESETA III project, the analysis on habitat – which in the present work refers to the specific vegetation characterising European forests – will focus on the vegetation characterising the Mediterranean habitat. The analysis on droughts and on key abiotic disturbances such as wildfires are also conceptually linked. In particular, a link exists between weather, climate and fire danger with the future evolution of arid climate patterns over Europe. The combined effect of these emerging patterns may be considered as a major threat for the bioclimatic conditions supporting the habitat of several forest tree species.

1 Introduction

Climate dynamics are imposing great pressure on Europe's forests [90, 91, 92, 93, 94, 95]. As a result, forests are increasingly exposed to climate-driven threats such as degradation, shifts in species distribution, extinction risk and changes in forest dynamics among others. Despite wide uncertainty [96] on the precise pattern of changes and yet unexplored feedbacks [97], several studies raised attention to the importance of the potential impacts. Computational modelling research estimated that "6 to 11 % of European plant species are projected to disappear from existing conservation areas by the mid-21st century due to climate change" [98, 99]. Boreal forests constitute a relevant part of European forests and a non-negligible carbon stock whose response to projected natural variability is considered highly uncertain [100]. For mixed forest ecosystems in the temperate zone, "even relatively small differences in phenological response types may significantly affect the competitive outcome when the trees grow in mixed stands" [95].

Although several studies investigate the response of forest tree species to climate dynamics, the key role of uncertainties for policy-guiding applications has been underlined [101]. Deriving robust and high-resolution spatially distributed estimates of the potential response of European tree species to scenarios of climate change is an environmental modelling task which poses several challenges. In particular, the well-known uncertainties and relatively coarse spatial resolution which are associated with global and regional climate change projections need to be coupled with highly nonlinear responses of tree species habitat suitability (HS) with varying climatic and geographic conditions. Not only are these conditions expected to change due to climate dynamics but also they currently (i.e. irrespective of climate change) show noticeable fine-

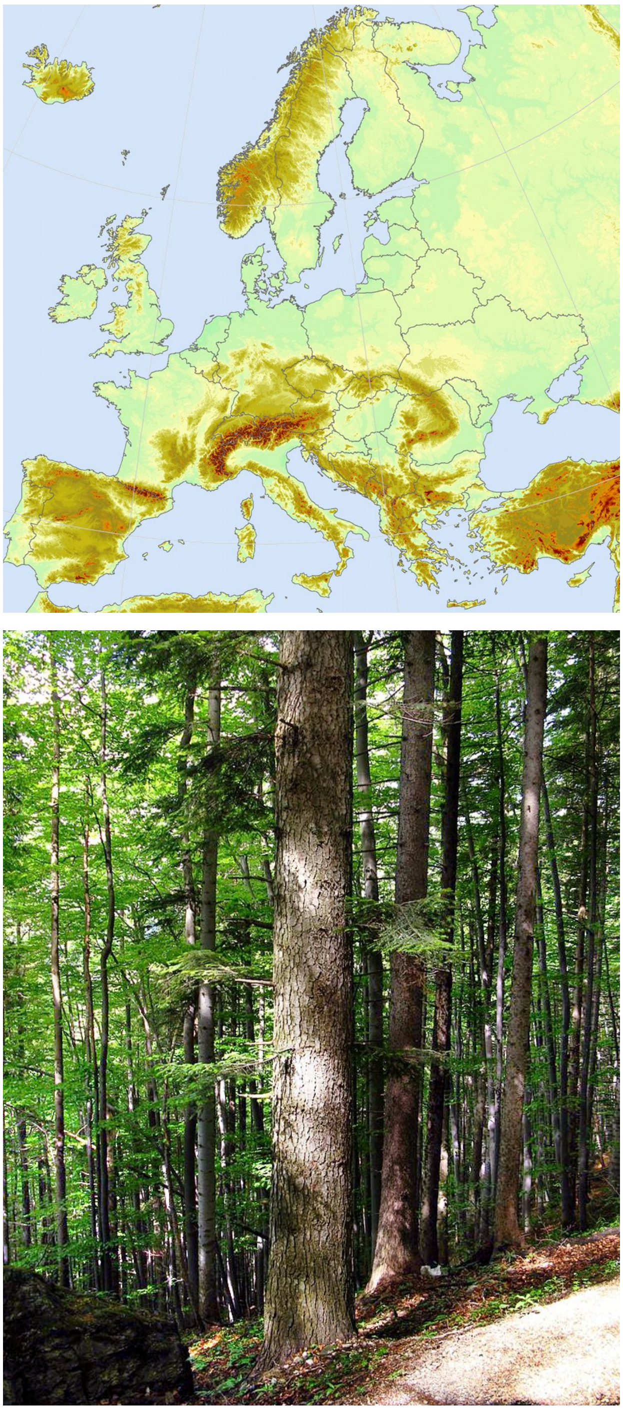

Figure 4: **Top**: The complex orography of Europe, adapted from de Rigo *et al.* [28]. Roughly one third of the continent is covered by mountain systems: depending on the variable elevation, slope and aspect, the bioclimatic conditions are subject to fine scale sudden changes of solar irradiation, temperature and precipitation patterns (e.g. rain shadow effects) [28]. **Bottom**: Malá Fatra, Slovakia, mixed forest with *Abies alba* – whose distribution range covers multiple mountain systems. Adapted from an image authored by Crusier (CC-BY), http://www.webcitation.org/6nxfEULaW.

Table 1: Presence and dominance of *Abies alba* following the European Forest Types (EFTs). The EFTs classification includes 14 categories, with sub-categories which are associated with the corresponding forest types, for a total of 78 classified forest types [37, 38]. *Abies alba* is able to span over multiple forest types with populations adapted to different bioclimatic conditions (or even sometimes hybridised with other firs [102, 103, 104, 105]). As a consequence, oversimplistic assumptions concerning the geometry of the projection of the realised niche in the covariate space (e.g. hyper-ellipsoid or Gaussian rudimentary approximations, sometimes imposed within elementary tools for habitat suitability modelling) are unlikely to be effective [40]. See also Box 1. Information derived after Pividori *et al.* [38].

Category	Forest type	Dominance
2. Hemiboreal forest and nemoral coniferous and mixed broadleaved-coniferous forest	2.8 Nemoral silver fir	🟩
3. Alpine coniferous forest	3.2 Subalpine and mountainous spruce and mountainous mixed spruce-silver fir forest	🟦
6. Beech forest	6.3 Subatlantic submountainous beech forest	🟨
7. Mountainous beech forest	7.1 South western European mountainous beech forest	🟦
	7.3 Apennine-Corsican mountainous beech forest	🟦
	7.4 Illyrian mountainous beech forest	🟦
	7.5 Carpathian mountainous beech forest	🟨
	7.6 Moesian mountainous beech forest	🟨
8. Thermophilous deciduous forest	8.7 Chestnut forest	🟨
10. Coniferous forests of the Mediterranean, Anatolian and Macaronesian regions	10.2.1 Mediterranean Black pine forest	🟨
	10.6 Mediterranean and Anatolian fir forest	🟩

Legend		
	🟩	*Abies alba* is dominant in that forest type
	🟨	*Abies alba* is present but not dominant
	🟦	*Abies alba* is present in either category

scale spatial variability within Europe [39, 106]. For example, one third of European areas show a typically mountainous environmental characterisation (Figure 4) and corresponding complex stratification of forest tree species distribution at very fine spatial scale, far beyond available resolution of regional climate projections. Furthermore, forest tree species responses in term of HS may span over decades as their average lifetime is significantly greater than e.g. that of most plant species of agricultural interest. This also means that the complexity of projected climate dynamics requires a specific analysis so as to derive robust indices covering multi-decadal trends without losing the richness of high time frequency information.

This study discusses a sound modelling strategy which aims to contribute to integrating the best available European field observations referring to tree species presence with a set of climate and geography based bio-indicators in order to derive robust tree species HS estimates. The modelling framework outcomes are discussed with a case study (*Abies alba* Mill.) which introduces and exemplifies the systematic application of the model to the main European forest tree species (see the maximum habitat suitability maps in the European Atlas of Forest Tree Species [28]).

Due to the complex nonlinearities [90, 91, 95] with which tree species respond to changing pattern of bio-indicators and due to the variety of configurations which can be observed and projected for these bio-indicators, the proposed modelling framework is specifically designed to infer (by means of machine learning techniques) the HS response of each species directly from the observed data without a-priori assumptions about expected relationships between bio-indicators' configurations and observed presences of each species.

This approach intensively data-driven may be also helpful to mitigate the oversimplistic flattening of species-level observations which might otherwise be modelled completely discarding the intraspecific diversity, the peculiarities of different populations of the species and their adaptation to different forest types and corresponding bioclimatic patterns (see Table 1 and the section of the Foreword on the robust modelling of tree species habitat suitability). Unfortunately, the systematic availability of field data on the genetic and phenotypic diversity of tree taxa may still be considered a challenging open issue, thus delineating a *data-driven gap* still difficult to overcome. Nevertheless, it is sadly true that the "residual" richness in the field observations available at the species level may sometimes be underexploited simply due the widespread use of generic tools which might be inappropriate for some modelling tasks. This delineates a *model-driven gap* which might be less challenging to mitigate. For example, a possibly critical misconception in this respect may occur with rudimentary approximations introduced by elementary tools for habitat suitability modelling, which sometimes drastically oversimplify the observed pattern of bioclimatic conditions for a given species following potentially unrealistic assumptions (e.g. hyper-ellipsoid or Gaussian approximations for the geometric envelope of the covariate values associates to the *entire* pattern of observations). Tree species such as *Abies alba* consists of several populations spanning over a variety of forest types and corresponding bioclimatic conditions (with non-negligible phenotypic and genetic diversity and also hybridisation with other firs [102, 103, 104, 105]). The simple evidence would advise not to rely on unnecessary oversimplifications on the expected geometric envelope of the observed patterns of suitable bioclimatic conditions (see also Box 1).

A plain argument may help to illustrate this modelling recommendation. Even if we accepted these simplifications to be valid for a more "homogeneous" subset of field observations (e.g. a given subset of populations more similar between each other from a phenotype/genotype perspective, see also Box 1), then the resulting *aggregated* habitat suitability derived after modelling each homogeneous subset of observations this way would likely not satisfy the same modelling simplification[5]. Unfortunately, systematic and harmonised information to characterise the intraspecific diversity of forest tree species is not available for most of the field observations in Europe. As a consequence of this ignorance, in order for these aspects not to be completely neglected, a sound modelling architecture would require that the full pattern of observations is considered in a way consistent with *any possible clustering and re-aggregation of them* (which may be referred as cryptomorphic partitioning property on the available observations). Namely, the resulting es-

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[5] For example, assuming that each homogeneous subset might be modelled in the bioclimatic space as if it were occupying a simple (hyper-)ellipsoid, this would not imply that the overall resulting union of subset-specific ellipsoids is another (bigger) ellipsoid. Given the complex nonlinear relationship between genotypes and phenotypes [68, 69, 70, 71, 72], there is no general indication that *if* a certain bioclimatic pattern is associated with a subset of species observations, *and* another bioclimatic pattern is associated with another subset, *then* automatically all the intermediate patterns would be equally associable to potential genetic mixtures of the two subsets (see Box 1). Instead, what the proposed approach estimates is the degree of similarity between observed and tested bioclimatic conditions, taking into account also the field measurements where the investigated species was not found *and* also the bioclimatic signal of rarer reported occurrences. Very dissimilar patterns are detected, also highlighting the degree of modelling extrapolation (and thus the degree of uncertainty due to modelling and data) in the tested areas compared with the overall set of available observations.

Table 2: Emission scenarios and Regional Climate Models used for tree species habitat suitability modelling.

Scenario	Model (short form)	Temporal domain
A1B	KNMI-RACMO2-ECHAM5 (KRE)	1961-1990 1991-2099
	METO-HC-HadRM3Q0-HadCM3Q0 (MHH)	1961-1990 1991-2100
	DMI-HIRHAM5-ECHAM5 (DHE)	1961-2099
E1	MPI-REMO-E4 (ME4)	1961-2099

timates of habitat suitability should ideally not depend on any particular intermediate partition π in which the reported occurrences of the taxon $P = \{P_i\}$ may be clustered. As a consequence, given two generic partitions $\pi^A = \{P_1^A, P_2^A, \cdots, P_m^A\}$ and $\pi^B = \{P_1^B, P_2^B, \cdots, P_n^B\}$ (such that the union of each subset $P_j^\pi = \{P_{j_1} \cdots P_{j_{n_j}}\}$ of the partition π is again the whole set P), the corresponding habitat suitability as separately computed for each subset $\text{HS}_j^\pi = f(P_j^\pi)$ should be able to be combined to reconstruct the aggregated HS of the taxon *irrespective of the partition*, so that $\bigcup_{j^A} \text{HS}_{j^A}^A \equiv \bigcup_{j^B} \text{HS}_{j^B}^B$. To exemplify, for a given tree species a first partition might be a clustering of the field observations so as to classify them into a set of populations, e.g. based on a genetic criterion. The second partition might instead be based on a geographic classification. Other meaningful partitions might be based on bioclimatic classifications, ecological zoning [39, 106], phytosociology syntaxa or other assemblages [37, 38]. The described property would require that irrespective of the specific partition in which the disaggregated HS analysis is conducted, the merging of each cluster-specific HS is always the same aggregated HS[6]. Despite being so simple, this property is rarely satisfied by simplistic HS models – as the plain argument we illustrated highlights. As a trade-off for mitigating this kind of undue modelling oversimplifications, the proposed approach requires a more computationally intensive processing for observations and associated bioclimatic conditions. The modelling architecture here proposed considers each single observation in the training set without a-priori limiting assumptions on its relationship with the other observations. The HS is modelled observation by observation (i.e. modelling the most disaggregated partition π^* of the training data, where each each observation is considered as an atomic component of π^*), with a statistical resampling to support a robust aggregated estimation.

Results of this study show the potential response of European tree species to scenarios of climate change. This is achieved by modelling tree species HS on the basis of two emission scenarios and four climate models. Within the PESETA II project, the SRES scenario A1B [107] and the mitigation scenario E1[7] [108] have been assessed (Table 2). For the scenario A1B, the output of three Regional Climate Models (RCMs) has been considered.

The European Commission, Joint Research Centre (JRC) monitors the status and trends of European forests in relation to forest extent and fragmentation, forest fires, forest species distribution and dynamics, species habitat modelling and the influences of climate change. These fundamental aspects of forest resources in Europe reverberate in the multifunctional role of forests for economic, social and environmental purposes [1, 2]. The Forest Information System for Europe

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[6] Mathematically, this is equivalent to define as cryptomorphic – with reference to the final aggregated HS – all the collections of partial HS obtained following any possible conceptual partition of the reported occurrences (i.e. the partial HS estimates associated to any preferred partition of the presences which are observed in the field for a certain taxon).

[7] E1 is a mitigation scenario in which atmospheric concentrations of greenhouse gases are stabilised at 450ppm CO_2-equivalent.

(FISE[8]) hosted by the JRC is a focal point for the European Union policy relevant forest data and information [109, 1, 2]. FISE contains and points to relevant forest information, providing web-based tools for accessing this information. The tasks implemented in the framework of this project are built on the tools, models and datasets available in FISE and on established free scientific software and computational environments [110, 111] .

1.1 Relationship between potential suitability and distribution of tree species

Although there is no agreement on defining habitat within the ecological literature, a working definition for operational purposes has been proposed as “description of a physical place, at a particular scale of space and time, where an organism either actually or potentially lives” [48]. Hence, in the forestry context, habitat is a description of the physical nature of a place with respect to a tree species. The importance of climate to explain plant distribution has been long and widely recognised. Therefore climate in combination with other biophysical factors is used to predict the local suitability of a given tree species.

HS models relate tree species distribution data with local environmental characteristics at those locations. Hence HS models are used for predicting potential species distribution across the landscape. HS models are suitable not only to describe the environmental habitat variability corresponding to measured data, but also to infer the potential suitability for the analysed species where similar environmental patterns occur even outside the spatial (or temporal) domain of the available measures (“bioclimatic twins” [67]). Therefore, HS models can be used for predicting potential species suitability across landscape either for the current situation or for investigating potential suitability under future climate change scenarios.

The relationship between potential species suitability and potential species distribution lies in the environmental and ecological requisites to be satisfied in order for a given species to live. This means that potential suitability shapes the boundaries of potential distribution, while the opposite is not true: the spatial extent of potential distribution is a subset of the potential suitability extent. As summarised in the section of the Foreword on the robust modelling of tree species habitat suitability, different reasons may prevent a species from being observed within geographic areas which are bioclimatically suitable for it. Potential suitability alone is unable to predict potential distribution, because the latter is also influenced by anthropogenic activities (e.g. land cover changes), the cumulated effects and feedbacks of ecological competition, and sustainability of the natural migration pace of species (e.g. the spatial shift of environmental suitability due to climate change may exceed the natural spatial migration rate of the species). On the other hand, models based on hypotheses concerning anthropogenic scenarios and land-cover evolution cannot reliably predict potential tree species distribution without subordinating their predictions to the output of sound potential habitat suitability models. Therefore, HS models can be described as a highly critical bottleneck in a scientifically sound modelling chain which is required for assessing the economic impact of tree species distribution changes under climate change scenarios. Where evidence suggests a probable loss of HS, this could be interpreted as a probable local contraction of tree species distribution, with the inherent economic consequences. Where instead HS is predicted to grow, anthropogenic and species migration factors (either nat-

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[8] http://fise.jrc.ec.europa.eu/.

ural or due to anthropogenic adaptation efforts, e.g. assisted migration) would also be needed for assessing whether a corresponding local growth of tree species distribution is foreseeable. A simplistic taxonomy of adaptation scenarios which might be of interest in this respect, and a summary of corresponding implications for the HS analysis, are provided in Box 1.

Our modelling approach should be interpreted from the perspective of data limitations and assumptions considered. One main aspect is that the results of the modelling experiment are maps of potential HS. These maps are produced by using samples of observed species (presence/absence) harmonised from several National Forest Inventories (NFIs) in Europe [112, 113]. Therefore the observed distribution of tree species is the result of, first, a landscape modified as a consequence of anthropogenic effects (e.g. land-cover changes, afforestation, forest management practices), forest disturbances, and past climate events [59]. And second, sample biases [28, 113]. Thus, NFI data of observed distribution of tree species can be considered as the representation of a partial realised niche for specific species and not the complete realised niche; an issue common to most studies assessing habitat suitability of tree species [114, 48] .

1.2 Tree species HS modelling approach

So far a number of different modelling approaches have been developed. In this study we implemented a model based on grey-box Artificial Neural Network (ANN) architecture for modelling and predicting changes on HS resulting from changing climatic conditions. The mathematical formulation of the modelling architecture lies within the category of grey-box modelling because the model design explicitly included the use of data-based physical knowledge on the modelled system for intensely driving the ANN training.

The ANN data-transformation model relies on the Relative Distance Similarity (RDS) algorithm as implemented by the Mastrave[9] modelling library [24, 115, 116, 26]. Robustness and tolerance to outliers is achieved by systematically applying statistical resampling techniques (see also Figure 9), while reproducibility is improved by strictly adopting a set of coherent file naming conventions[10] directly supported by the modelling framework. The whole HS model is based on the Semantic Array Programming paradigm [24, 25, 26] and on the Mastrave library within GNU Octave[11] [117] and GNU Bash[12] [118, 119, 120] computing environments, with the use of the Geospatial Data Abstraction Library[13] [121] and of the Python computing environment[14] [122]. The resulting model is suitable to be either used as an unsupervised nonparametric estimator or as a supervised estimator of species HS. Within this project, modelling robustness has been favoured over more accurate model-fitting and the unsupervised approach has been exploited.

Since different bio-indicator configurations generally imply different dominance of the involved factors as driving the response of tree species, the RDS-based[15] modelling approach explicitly

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[9] http://mastrave.org/

[10] Several hundreds of gigabytes are involved with multiple intermediate data-transformations, e.g. for supporting the demanding data harmonisation process.

[11] http://www.gnu.org/software/octave/

[12] http://www.gnu.org/software/bash/

[13] http://www.gdal.org/

[14] http://www.python.org/

[15] Although the Mastrave modules implementing the RDS algorithm provide as default output a jack-knife based analysis of the relative importance of each bio-climatic indicator, this one-dimensional ranking should be considered a simplistic

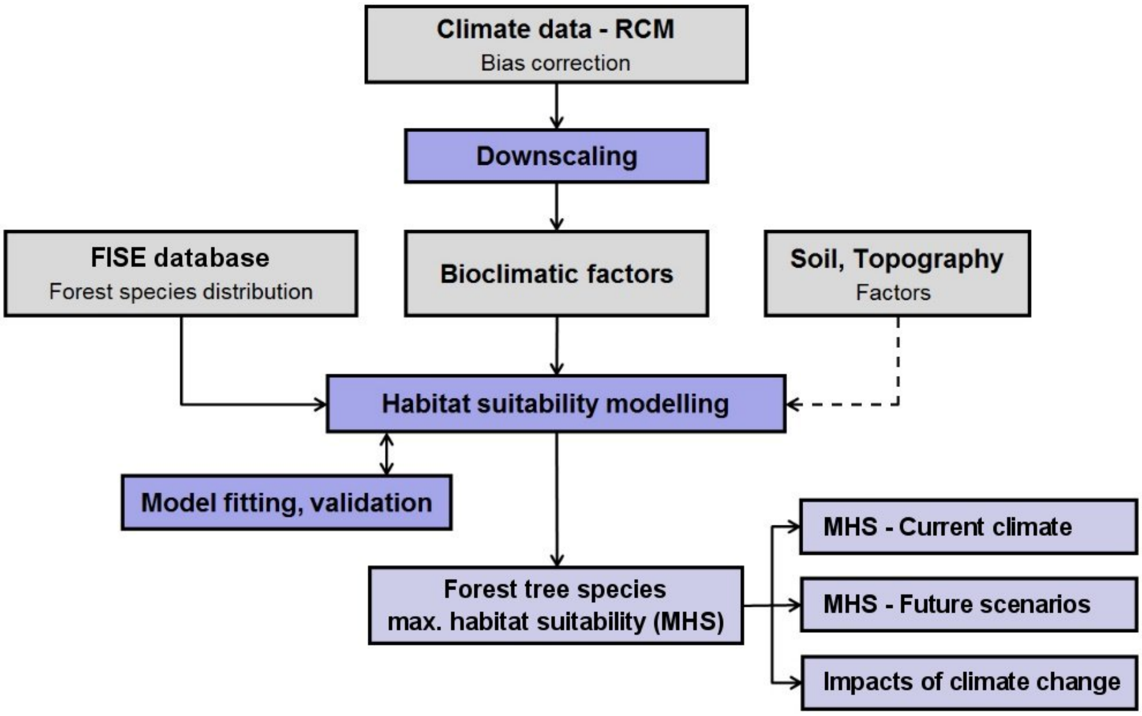

Figure 5: Tree species habitat suitability modelling approach.

does not attempt to limit the analysis to over-simplistic linear ranking of the relative importance of each driving factor.

2 Methods

HS models have been widely used to assess potential changes of species distribution under changing climatic conditions [123, 87, 114]. In addition, several modelling approaches and statistical techniques have been applied for modelling species HS [124, 125].

The methods of this study follow four main steps (Figure 5):

1. Data collection, pre-processing and setting, e.g. NFIs, BioSoil [126] and Forest Focus/Monitoring [127, 128] data from FISE, climate data, solar radiation, etc.
2. State-of-art and modelling strategy design
3. Modelling: model fitting, accuracy assessment and validation of generated spatially distributed HS maps under climate change scenarios
4. Impact assessment of climate change on species HS: difference analysis between current and future scenarios

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non-spatial (i.e. lumped) aggregation of the nonlinear response of each species to the complex variety of European climate and geographic conditions. Therefore, the proposed RDS-based analysis is instead spatially explicit while summarizing the aggregated contributes of all bio-indicators.

Steps 1) and 2) have been developed in parallel with a continuous feedback due to the high degree of dependence between the modelling design and both analysis and semantic interpretation of available datasets.

In this study HS is modelled integrating three main components:

- A georeferenced sample of observed tree species in Europe (NFIs, BioSoil and Forest Focus/Monitoring datasets available in FISE);
- a set of biophysical factors classified in three groups: bioclimatic, soil and topography; and
- a model describing the relationship of the presence/absence of species with the biophysical factors.

After model fitting and validation, climatic data from different scenarios are used as inputs into the model for assessing changes in HS between current climatic conditions and future scenarios. In this report we show HS maps of *Abies alba* as a pilot product of the modelling approach. The HS modelling of other species will follow the described methodological approach used for *Abies alba*.

The spatio-temporal setting of the assessment depends on the settings of the input datasets (climatic and other). This study follows a long-term approach with two time periods: 1960-1990 referred to as the current climate and 2069-2099 under two emission scenarios (and four models). The spatial resolution of the datasets is 1-km. Hence HS maps comparing current situation versus future scenarios are provided at this grid-size. On each grid cell the maps allow changes to be detected between present climate and future scenarios.

Not only differences but also initial and final absolute values of suitability are relevant. For example, the impact of a 50 % future decrease of HS may greatly differ from the case in which the current suitability is 50 % (thus suggesting complete local extinction of the species) to the case in which it is 100 % (predicting a noticeable worsening of future local health conditions). The relevance of the expected impact may also be influenced by local modelling uncertainties, so that the aforementioned 50 % future HS decrease would proportionally be more worrying where both current and future absolute HS estimates are affected by lower uncertainties. In order for possible economic analysis strategies to be based on the whole set of relevant information, absolute current and future suitability, along with local qualitative assessment of modelling uncertainties, are also provided as modelling outputs. Although simplified economic analysis could just consider HS differences, sound and robust economic assessment should not oversimplify intrinsic, structural HS modelling implications.

The geographical domain of the study covers the Members States of the EU, Switzerland, Norway and the Balkans. However, data availability is highly heterogeneous from country to country. The main FISE dataset (based on NFIs) has been complemented with the BioSoil and Forest Focus/Monitoring datasets (see also [28, 113] for a general description of the data and further improvements on their harmonisation). Figure 6 shows the density of plots which is computed by dividing the number of cells with at least one plot by the total number of cells per each country.

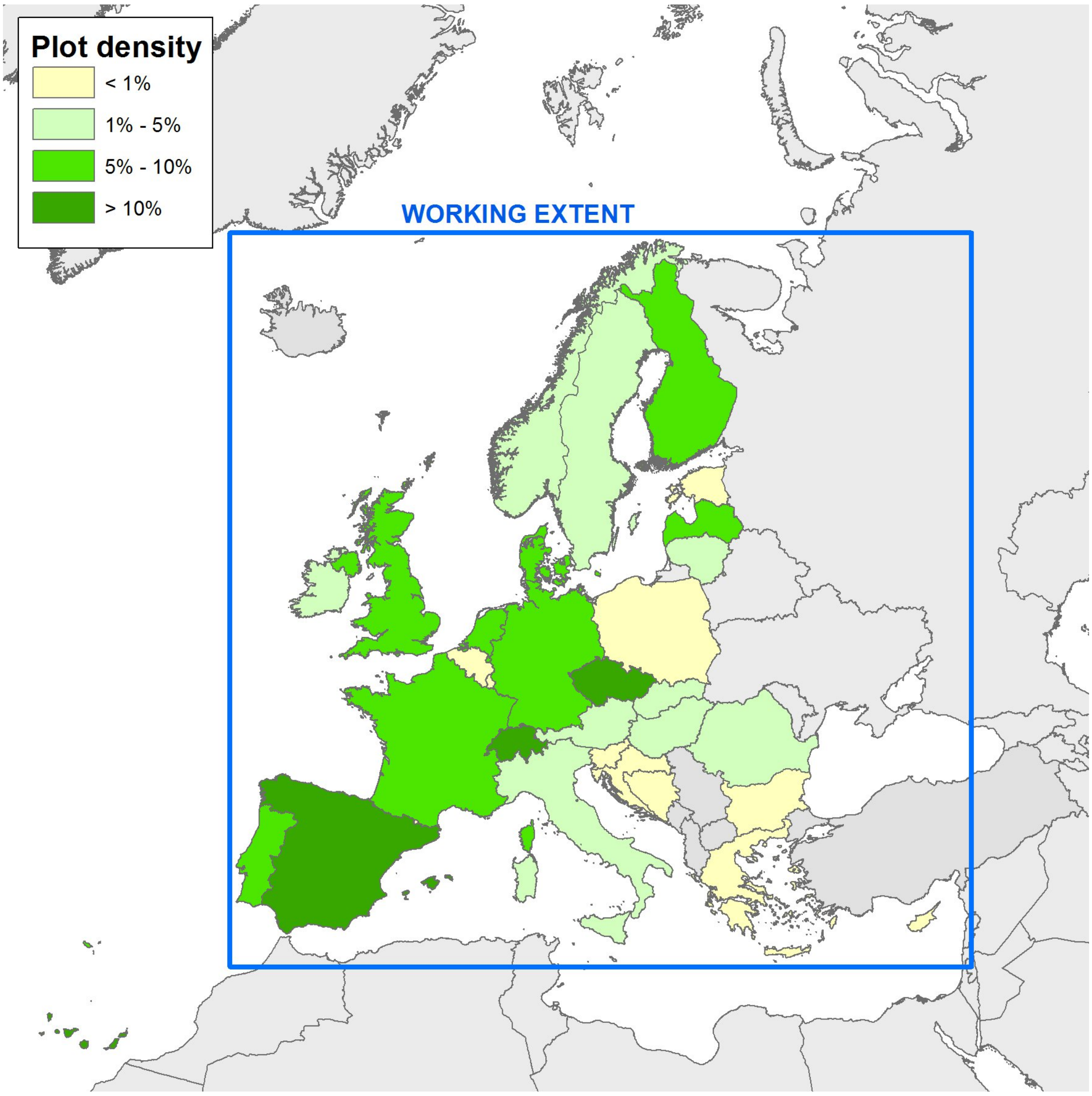

Figure 6: Country cover and plot density for available tree species presence/absence datasets. The main FISE dataset (based on NFIs) has been complemented with the BioSoil and Forest Focus/Monitoring datasets (see also [28, 113] for a general description of the data and further improvements on their harmonisation). The density of plots is shown by computing the number of cells with at least a plot compared with the whole amount of cells per each country. The blue square shows the working spatial extent of output maps.

2.1 Data

Two main categories of data are used in this study. First, a georeferenced sample of presence/absence of tree species in Europe, and second, a set of biophysical factors.

Information on tree species presence/absence and other tree characteristics is collected and maintained through NFIs [50]. The objective of NFIs is to collect information on tree species gathered from systematic sampling campaigns. However, the NFI methodology of sampling and data processing may vary from country to country [28, 113]. Harmonised NFI data is available at FISE for European countries, including information from European-wide datasets such as BioSoil [126] and Forest Focus/Monitoring [127, 128]. FISE hosts information from around 370,000 sample plots across Europe, including information for some 240 tree species [109, 113, 28].

The spatial resolution of tree species presence/absence is at 1 km^2 pixel size, using the ETRS89 Lambert Azimuthal Equal-Area as geospatial projection (EPSG: 3035, http://spatialreference.org/ref/epsg/etrs89-etrs-laea/).

The set of biophysical factors contains 39 grid-layers classified in three groups as shown in Table 3. Topographic factors were produced from a 100-m spatial resolution DEM [129, 130] derived from SRTM [131]. SD elevation, elevation range and slope were processed at the original DEM grid-size and then averaged at 1-km. The four aspect factors were processed at 100-m grid-size and then the ratio of cells of each major orientation added to a 1-km grid-size.

Annual potential global solar radiation was produced by using the r.sun[16] [89] model implemented in GRASS-GIS [132] and the DEM regridded to 1-km. We produced 12 grid maps of solar radiation (atmospheric turbidity and albedo coefficient absent) for the central day of each month. The annual potential global radiation was computed by integrating the data of the 12 grid maps using the trapezoidal rule.

Parental material data were obtained from the European Soil Database (ESDB) V2 [133]. The ESDB contains gridded datasets at a spatial resolution of 1-km for several soil parameters. One binary (0, 1) map was created for each class of the dominant soil parental material map. Within the model fitting phase, the resulting valuable harmonised information offered by these soil data was still too noisy, especially in some critical areas of the spatial extent (e.g. in the mountainous regions, where the variability of the soil characteristics may show very complex local patterns). This effect resulted from the cumulated effect of combining the uncertainty of the tree species field observations and of the soil data – an effect not as severe for the other biophysical factors. Furthermore, information on soil as a biophysical component for forest tree species HS analysis should ponder the intensity with which tree species influence the characteristics of soil (e.g. topsoil, rhizosphere; but also hydrogeomorphic processes) with a complex set of feedbacks – also involving understorey vegetation [134, 135, 136, 137, 138]. The overall impact of these local feedbacks may occasionally enhance or counteract the one due to the original parental material with noticeable effects [134, 139, 140, 141, 138] whose detailed extent is still uncertain with broadly missing information. Therefore, the analysis was finalised without considering the soil data.

Modelling the impacts of climate change on HS of tree species requires high-resolution climate data. For instance, some studies in this field have used disaggregated climate data at 1 to 5-km grid size [87, 142, 143]. Therefore, 23 bioclimatic factors disaggregated at 1-km grid-size for current climate and future scenarios have been implemented using the change-factor (or Delta method) approach [144, 142, 145]. In the change-factor approach, the climate variables are disaggregated from the RCM resolution to the resolution of a target high-resolution observational data (baseline).

We used as a baseline the high-resolution WorldClim version 1.4 data at 30 arc-seconds (approx. 1 km) horizontal resolution [146] for implementing the change-factor method and modelling HS with current climate conditions. WorldClim contains monthly variables averaged for the period ~1950-2000 with most of the data for the 1960-1990 period. The WorldClim data layers were generated through interpolation of average monthly climate data from weather stations. We

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[16] http://re.jrc.ec.europa.eu/pvgis/solres/solmod3.htm and http://grass.osgeo.org/grass64/manuals/html64_user/r.sun.html

compiled baseline information from WorldClim of monthly mean, minimum and maximum temperature and precipitation. The 23 bioclimatic indicators were implemented using the baseline WorldClim datasets.

Climate data of future scenarios were originally produced by the ENSEMBLE project [108, 147]. Simulations were produced in the framework ENSEMBLES by using state-of-the-art Global Climate Models (GCMs) and Regional climate Models (RCMs) developed in Europe. The spatial domain of the RCM simulations listed in Table 2 cover the entire European continent at 25-Km horizontal resolution for A1B and 50-Km for E1.

We implemented the change-factor approach in the following steps. The 23 bioclimatic factors were produced at the spatial resolution of the RCMs for the modelled current (1960-1990) and future scenario period (2069-2099) for each model simulation listed in Table 2. We then subtracted the modelled current data from the future scenario to generate future climate anomalies for each bioclimatic factor. The climate anomalies were spatially re-gridded at 1-km by using thin plate spline interpolation [148, 149]. Finally, the last step of the approach is adding the interpolated anomalies to the current climate data to provide downscaled future scenario datasets. The change-factor approach assumes that the differences between model simulations and baseline current climate are maintained over time. Figure 7 shows an example of the input and output datasets of the change-factor approach for downscaling annual average temperature from the DMI-HIRHAM5-ECHAM5 scenario A1B.

2.2 Modelling tree species habitat suitability using observed presences/absences: definition of the problem

This section introduces the theoretical definition of the modelling problem that drove the design and implementation of the modelling architecture. Let us suppose having a set of observations measuring at regional scale whether or not a given quantity exceeds a threshold value. The regional scale, e.g. European scale, poses specific challenges because of the foreseeable lack of harmonization among the observations. Typically, even after an accurate harmonization preprocessing, the density of observations may vary widely between local areas within the region to be analysed. This also implies that the effects of sparsely and densely sampled areas should be properly modelled.

In this theoretical definition of the modelling problem, each measure is also supposed to be a record providing information on its localization within a certain spatial domain, irrespective of whether the localization refers to a given physical system (e.g. geographic coordinates, altitude, curvilinear distance along a certain curved line such as a river or a road, ...) or to non-geographical quantities which can be seen as localising the measure inside abstract spaces (e.g. the time at which the measurements are recorded; more abstract quantities which are derived by geographic ones, such as the local slope, aspect or potential solar radiation; climatic quantities such as the local temperature and precipitation; remote sensing quantities such as multiple satellite channels recording different wavelength bands, ...). In the following, geographical and climatic quantities to which the measures are logically correlated will be denoted as *predictors*.

Examples of these threshold-driven observations may include the detection of dominant tree

Table 3: Biophysical factors considered as predictors (see Figure 8) to model current and future tree species habitat suitability. Continuous/discrete variables are annotated along with the most straightforward array-based semantic constraints based on the *Semantic Array Programming* paradigm [24, 25, 26] (with the notation *::constraint::* and an associated active link to the formal definition). The factors are computed as ::matrix:: raster layers, all having the ::same_size:: .

Variable	Description	C: continuous D: discrete	Array-based constraint
Topography			
SD Elevation	Standard deviation (std. dev.) of elevation	C	::nonnegative::
Elevation range	Range of elevation	C	::nonnegative::
Slope (%)	Slope of terrain	C	::proportion::
Aspect N	Proportion oriented to North	C	::proportion::
Aspect S	Proportion oriented to South	C	::proportion::
Aspect E	Proportion oriented to East	C	::proportion::
Aspect W	Proportion oriented to West	C	::proportion::
	(the ::3-array:: composed by the four Aspect layers N-S-E-W is a ::1-partition::)		
Global radiation	Annual potential global solar radiation	C	::nonnegative::
Soils Parental material			
PM Consolidated	Consolidated-clastic-sedimentary rocks	D	::binary::
PM Sedimentary	Sedimentary rocks	D	::binary::
PM Igneous	Igneous rocks	D	::binary::
PM Metamorphic	Metamorphic rocks	D	::binary::
PM Unconsolidated	Unconsolidated deposits	D	::binary::
PM Unconsolidated glacial	Unconsolidated glacial deposits/glacial drift	D	::binary::
PM Eolian	Eolian deposits	D	::binary::
PM Organic	Organic materials	D	::binary::
	(the ::3-array:: with the 8 Soils Parental material layers is **not** a ::1-partition::)		
Bioclimatic			
Annual average T	Annual mean T	C	::real::
Max T of warmest month	Maximum of monthly mean of Maximum T	C	::real::
Min T of coldest month	Minimum of monthly mean of Minimum T	C	::real::
Annual T range	Max T of warmest month - Min T of coldest month	C	::nonnegative::
Mean T of warmest quarter	Mean T of the consecutive warmest 3 months	C	::real::
Mean T of coldest quarter	Mean T of the consecutive coldest 3 months	C	::real::
Winter mean T	Mean T of JFM	C	::real::
Spring mean T	Mean T of AMJ	C	::real::
Summer mean T	Mean T of JAS	C	::real::
Autumn mean T	Mean T of OND	C	::real::
Mean of monthly T range	Mean of monthly maximum T - minimum T	C	::nonnegative::
Isothermality	Mean of monthly T range / Annual T range	C	::real::
Annual P	Total annual P	C	::nonnegative::
Sum of P of wettest month	Total P of the wettest month	C	::nonnegative::
Sum of P of driest month	Total P of the driest month	C	::nonnegative::
Sum of P of wettest quarter	Sum of P of the consecutive wettest 3 months	C	::nonnegative::
Sum of P of driest quarter	Sum of P of the consecutive driest 3 months	C	::nonnegative::
Sum of P of Winter	Sum of P of JFM	C	::nonnegative::
Sum of P of Spring	Sum of P of AMJ	C	::nonnegative::
Sum of P of Summer	Sum of P of JAS	C	::nonnegative::
Sum of P of Autumn	Sum of P of OND	C	::nonnegative::
T seasonality	Std. dev. of monthly mean T / Annual mean T	C	::real::
P seasonality	Std. dev. of monthly sum of P / Annual P	C	::nonnegative::

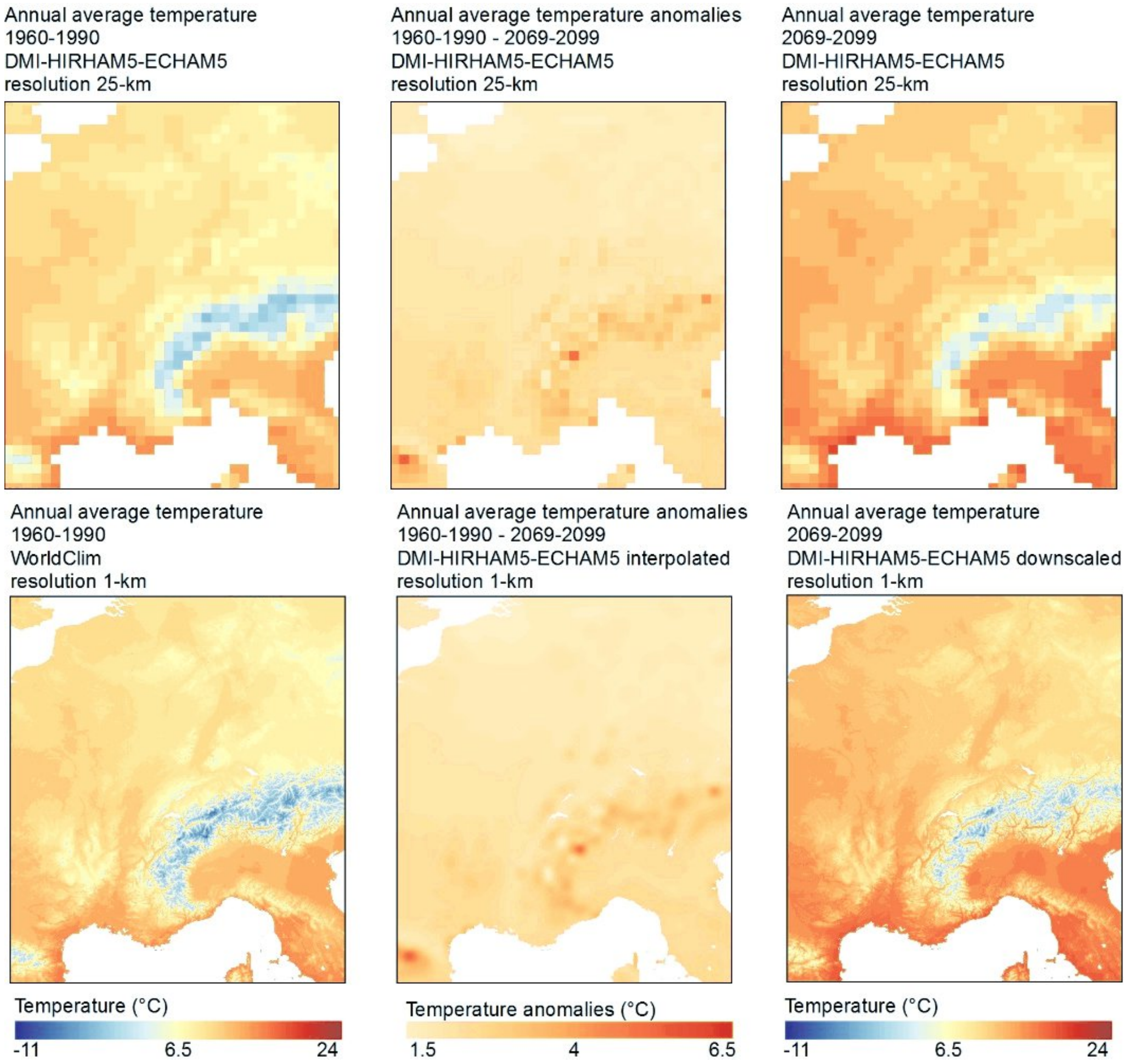

Figure 7: The change factor (or Delta method) approach to spatial disaggregation of climate scenarios [144, 142, 145]. Alpine and North alpine region annual average temperature from DMI-HIRHAM5-ECHAM5 model scenario A1B at 25-km (top row) and disaggregated datasets at 1-km (bottom right). WorldClim current climate at 1-km (bottom left) and temperature anomalies (central column) at the original model resolution and spatially interpolated at 1-km. Colour scheme derived from Harrower and Brewer [157] (see http://colorbrewer2.org/?type=diverging&scheme=RdYlBu).

species, or the height of a certain forested area with reference to the top canopy, or the share of young trees – detected by considering dendrometric measurements such as whether their trunk diameter at the breast height is small enough. As a special case, when the threshold – against which the observations have to be compared – is zero and refers to a particular species, the observation set collapses into a so-called presence/absence set (e.g. a set of records measuring whether a given tree species is present or not within several sampling areas). Hereafter, we refer to presence/absence [150, 151, 124, 88] in a generalised sense by extending the concept to include all kinds of information, which may be referred to as the abstract measure of a binary flag about the overpassing of some threshold. In this special case, the non-directly observable quantity to which the threshold overpassing refers can be properly described as a probability of presence, and the presence/absence measures can be conceptualized as a lossy conversion which degrades a continuous quantity to a discrete (binary) one.

The relevant structure behind such kinds of measures can be summarized as follows:

- The set of records does not only localize the occurrences of a given phenomenon but also the places in which it does not occur.
- The set of records is not required (and at regional scale is unlikely) to be uniformly sampled across the spatial domain as it is supposed to be when directly applying basic kernel-density like techniques, so that the sampling density (not the frequency of the sole presences) becomes an interesting statistic to be estimated.

The uneven distribution density of the available observations at regional or wider scale suggests to apply kernel density estimation separately to model both the sampling density and the presence density. An estimator of the presence frequency is obviously the ratio between presence density (spatial distribution of the measured presences) and sampling density (spatial distribution of both measured presences and absences). The sampling density can be interpreted also as a rough indicator of the *local accuracy* associated with the statistical information which may be estimated starting from available observations across the spatial domain. When exploiting it as a qualitative proxy-indicator of the local error, it should be taken into account that for gaussian uncorrelated errors, the local variance is inversely proportional to the sampling density.

However, the choice of the optimal kernel bandwidth would still remain problematic due to the heterogeneity of the sampling density. The robust estimation of the spatial probability of presence under heterogeneous sampling density is addressed by adaptive approaches based on spatial multi-scale frequency analysis, a constrained version of which (constrained spatial multi-scale frequency analysis, C-SMFA) is summarised in de Rigo *et al.* [28, 113]. However, reconstructing the *spatial probability* of presence of a given tree species does not directly support the assessment of its *bioclimatic possibility* of presence. While an obvious weakness of a pure *spatial* kernel density approach would be the impossibility of modelling the effects of other predictors, combining heterogeneous predictors within a general modelling framework should require their corresponding quantities and units to be addressed in order to avoid the final model's parameters and structure depending on particular quantities and units.

2.3 Modelling: climatic and geographic similarity networks

The aforementioned considerations lead to the novel formulation we propose: a model suitable to manage heterogeneous predictors and designed to transform them into dimensionless quantities (features) whose combination estimates first, the *maximum habitat suitability* and second, the *probability of presence* of the selected set of tree species, potentially based on geospatial climatic, topographic and soil information. As already commented, the sole use of geospatial information on the position of the available observations collapses the approach into a classical spatial kernel density application to estimate the probability of presence of the species (with improvements referring to adaptive multi-scale frequency analysis supported by other semantic constraints, see [28, 113]).

In particular, estimating the *maximum habitat suitability* (MHS) is a novel aspect of this study and perhaps more interesting for supporting policy-makers in analysing adaptation strategies.

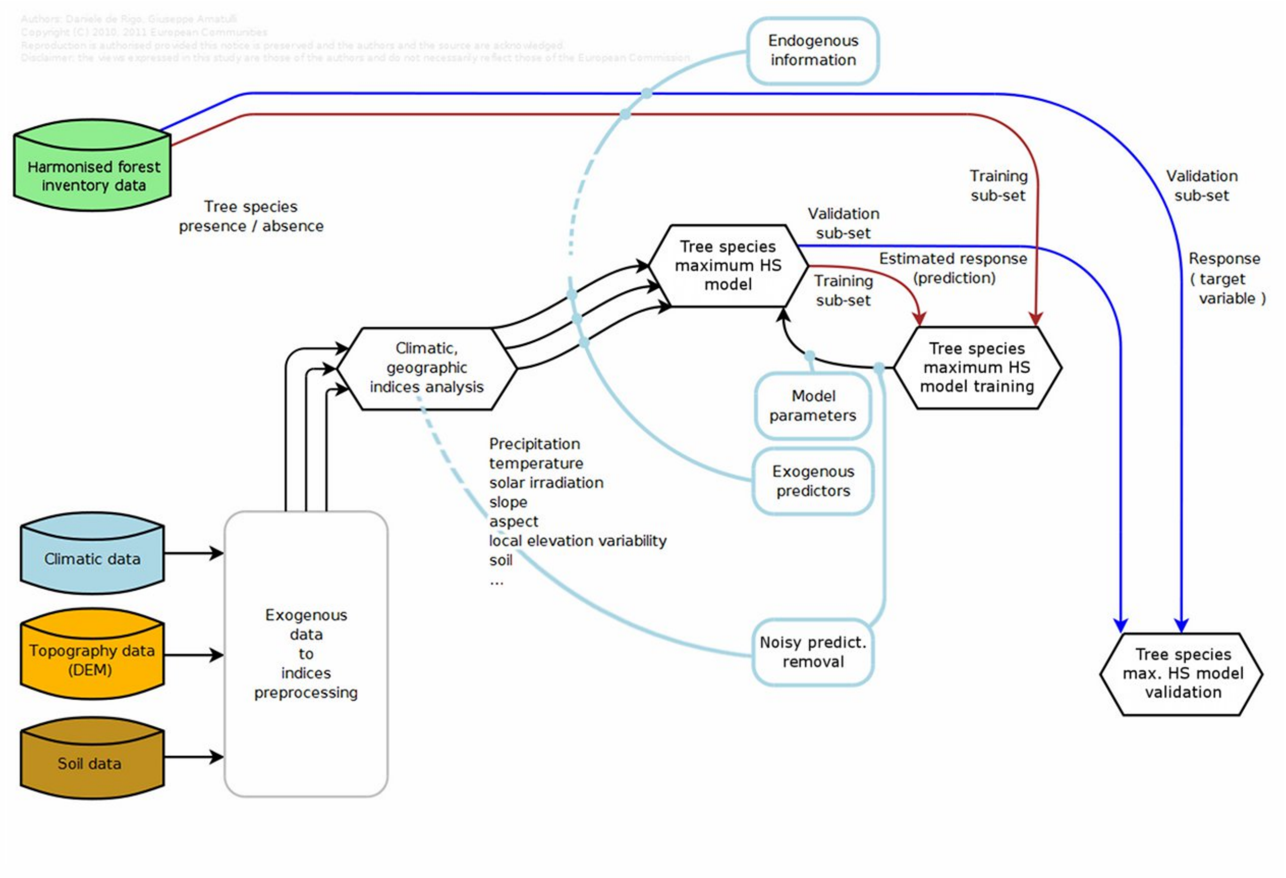

Figure 8: Modelling architecture. Information on the observed presence/absence (endogenous information) of a given tree species is split in two subsets respectively to be used in the training and validation phases of the corresponding model for the species. Proxy information based on climatic, topographic and soil data is processed and transformed into a collection of indices from which a series of n predictors are generated. Relative distance similarity is computed with respect to each predictor by considering the n predictor values of a given spatial cell as the n-dimensional coordinates of the corresponding climatic-geographic space. The similarities are used as intermediate layers (dimensionless features) of a neural network whose parameters can be finely tuned using a supervised approach or whose unsupervised (sub-optimal) estimation can directly be validated without tuning.

Furthermore, the C-SMFA modelling architecture is designed to easily exploit MHS information as an additional constraint to support a future improved estimation of the probability of presence for tree taxa of interest.

The data we used refer to the presence/absence of a given forest tree species with a spatial resolution of 1km grid size brought up into line with the INSPIRE 1 km^2 grid. In particular, the underlying information to assign the presence/absence value for a given grid-cell and a given tree species refers to observations within plot areas belonging to that cell. The overall area of those plots can be generally considered as negligible with respect to the 1 km^2 area of the cell.

The *maximum habitat suitability* is defined as a dimensionless quantity ranging between 0 and 1, conceptually constrained to have value 1 in all cells where a presence of the analysed species has been observed *in the current climate*. This means that in the current climatic conditions the maximum suitability of a given species is expected to be 100 % in correspondence with the subset of observed presences used in the training phase of the model (which in this application refer to adult trees). It is also expected to be close to 100 % in correspondence of the subset of observed presences reserved for the validation phase.

Under future climatic scenarios, the maximum habitat suitability can diverge from the current climate values: in particular (e.g. for climate scenarios peculiarly different from the current one), the maximum habitat suitability is not constrained to reach the maximum value of 1.

The modelling architecture (Figure 8) is based on an *ad-hoc* designed neural network structure to transform a customizable series of climatic, topographic and soil predictors into the estimated probability of presence and maximum habitat suitability [28, 113]. For the present work, the maximum habitat suitability modules have been exploited. One of the goals of the architecture is computational modelling robustness. Part of the robustness relies on transforming the predictors into dimensionless features which constitute the intermediate layer of the network. In particular, the Relative-Distance Similarity (RDS) approach has been used [26, 113, 106].

The architecture has been designed to support both unsupervised (robust despite sub-optimal) or supervised (better fitting with respect to training data, despite potentially less robust) applications. The RDS approach estimates how similar the current bioclimatic conditions for a given area are compared with the corresponding conditions where *Abies alba* has been observed. The aggregated RDS similarity of the given area considers each element in the available training set of observations, without relying on any assumption concerning the expected/plausible geometry of the underpinning realised niche (such as hyper-ellipsoidal simplifications of the niche), while statistical resampling is introduced to mitigate the effect of input data uncertainty, e.g. outliers[17]. This way, the complex potential interplay of genetic variability of the tree species (e.g. due to multiple populations) and different ecologically distinct forest communities with specific assemblages of trees (see Table 1) are modelled observation by observation without oversimplistic loss of details in the multi-dimensional bioclimatic pattern of occurrences. The RDS similarity may be considered as a fuzzy possibility set-membership, where the analysed area is not simply classified as bioclimatically suitable or unsuitable, but instead associated with a continuous score between these two extremes. Another way of interpreting RDS is as a constrained artificial neural network, where each training observation is linked to a single corresponding neuron. Unsupervised applications apply a global tuning of the bioclimatic predictors based on their overall pattern in the spatial extent. This robust tuning simplifies the integrated analysis of multiple species with simple exact mathematical rules for aggregating the suitability of single species into the one of aggregated taxa. In the present work, the unsupervised approach has been applied (see also [113, 27, 152]). Since supervising the training of the model is computationally intensive, the supervised training of the RDS network would instead rely on a selective parameter-improvement technique which has been already applied to computationally demanding training such as those involved in Neuro-Dynamic Programming [153, 154].

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[17] Potential sources of data uncertainty may include the wrong geolocation of the corresponding field observations; the misclassification in the reported data or even the additional uncertainty due to the administrative heterogeneity of Europe and the imperfect harmonisation of data autonomously collected by multiple administrative units (for an overview on data, modelling and software uncertainty related to European forest tree species modelling, see [28]). See also Figure 9 for details on the partitioning of presence/absence observations.

2.4 Modelling architecture: robustness and validation

As previously introduced, robust modelling of tree species HS at European scale requires heterogeneous datasets to be addressed. To mitigate the impact of outliers (e.g. peculiar outliers for a given tree species, geographic area, etc.), a statistical resampling technique with block-bootstrap approach was adopted. This approach is summarised in the following sequence of logical steps:

- Dataset splitting in random blocks (multiple training blocks and one validation block).
- Computing HS based on isolated blocks.
- Aggregation of blocks via block-bootstrapping (with multiple runs).
- Robust ensemble modelling:
  - from multiple runs to final estimation via weighted median
  - from multiple runs to qualitative spatial reliability assessment
- Final validation

The second logical step requires HS to be computed based on isolated blocks and is the actual core of the whole methodology. HS is computed by applying the Relative Distance Similarity (RDS) technique. Similarity maps with respect to the climatic conditions of each training observation (presence/absence) have been computed based on the relative distance (dimensionless) between climatic and topographic maps (predictors), and the corresponding predictors' value of training points.

The aggregated similarities of all predictors use a maximum-based aggregation criterion for estimating the maximum HS. It also allows a qualitative spatial reliability map to be estimated using observation density (Figure 9).

As a whole, the ensemble model is a reproducible, unsupervised data-transformation model applied to climate-geographic data to reconstruct habitat suitability.

The climate-topographic similarity of each spatial grid-cell varies from block-bootstrap run to run because of different training sets which are involved within each run computation. The HS estimations based on isolated blocks have been aggregated by means of a robust ensemble technique using Weighted Median Filters [155] as implemented by the Mastrave library by extending the algorithm to the case of multi-dimensional arrays [156] as required within the paradigm of semantic array programming. Weighted median is able to favour runs with higher similarity. Hence it mitigates the effects of outliers and stochastic fluctuations (runs with high dissimilarity) while preserving the more valuable information (Figure 10).

Maximum habitat suitability can only be validated by comparing estimated suitability versus observed presences. When validating this modelled quantity, reported absences are of no use because they refer to negligible plot areas within a given 1 km^2 spatial cell and not to the entire spatial cell. A tree species absent in a given plot does not imply the species to be absent in the corresponding entire spatial cell.

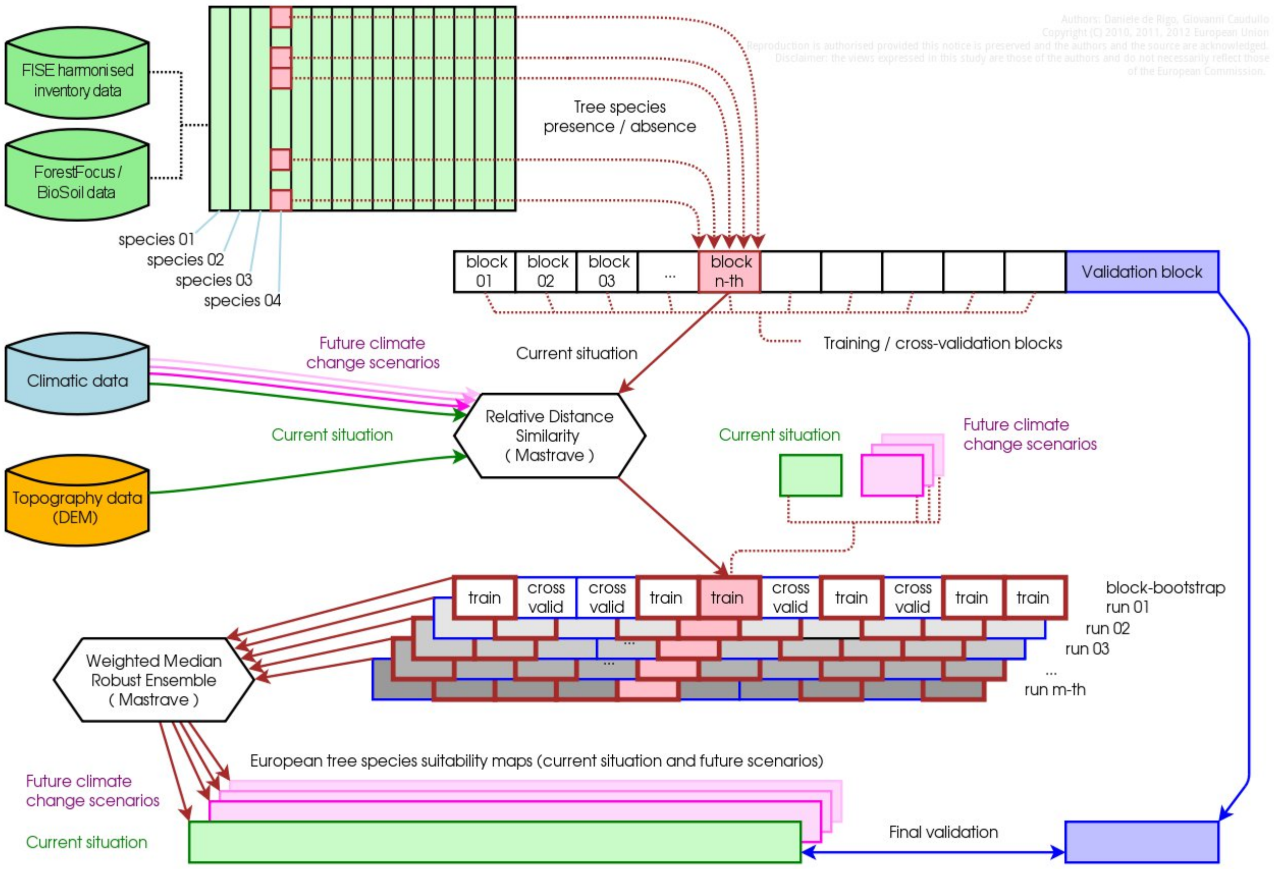

Figure 9: Detailed modelling architecture.

Because reported absences cannot directly be correlated with maximum habitat suitability, classical sensitivity and specificity analysis cannot be performed. Two indicators are instead computed:

- *accuracy*: observed presences vs. estimated MHS,
- (a proxy of) *specificity*: defined as the average for the whole continent of 1 - MHS.

If two estimates (computed with the same modelling technique so that they belong to the same family of estimators) have the very same accuracy, then the one having a higher specificity is preferable. This is because the more specific one has the same ability to explain presence observations as the other, while being able to provide a more cautious generalization. This concept may also be illustrated by thinking of a theoretical counter-example. The trivial model (constant 100 % suitability) explains all observed presences with the maximum accuracy. However its specificity is zero. A more detailed assessment of performances may of course be based on quantile analysis directly on the validation set (see Box 2 for an example where an extensive validation set and a limited training set are exploited).

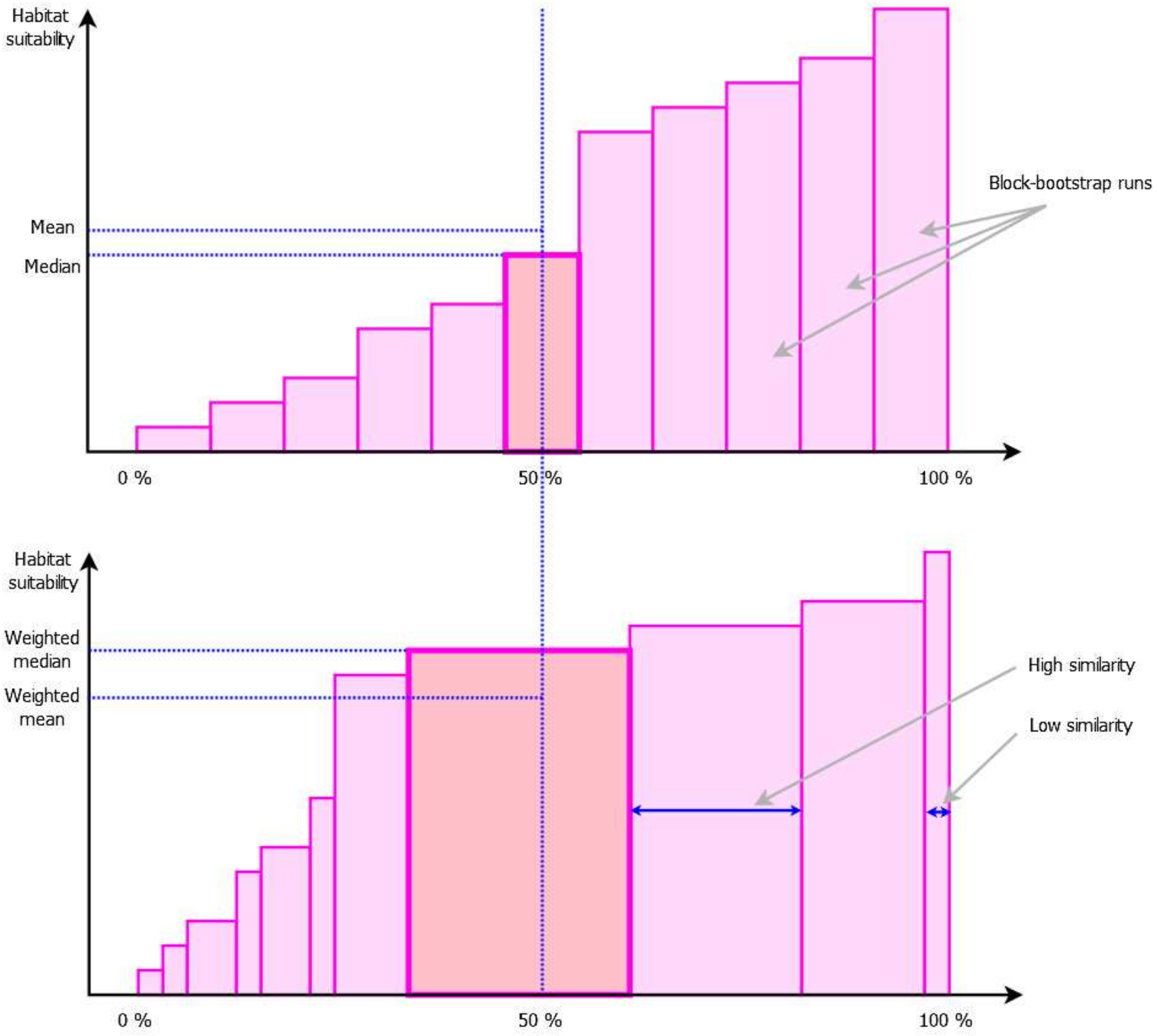

Figure 10: Example application of Weighted Median Filters.

3 Results

The most salient feature of this study is a shift towards northern and higher elevation areas of potential future habitat of *Abies alba* under scenario A1B. Figure 12 (A to E) shows the resulting HS maps implemented for *Abies alba*. The maps show HS of *Abies alba* under current climate, A1B and E1 future scenario conditions (Table 2 shows the RCM used for each scenario computed in Figure 12). In Figure 12 (A to E) HS is represented as a continuous probabilistic function with values ranging from 0 to 1.

Figure 12 shows *Density* (F to J) and *Variability* (K to O) maps. Density refers to the RDS of both presence and absence observations of a given training block. It provides a qualitative indication on how densely surrounded by observations a given spatial cell is. Here "density" of available observations refers to the abstract multi-dimensional space of predictors. Cells with low density underline the empirical fact that their environmental patterns show a scarce similarity with available observations. This qualitative information highlights these cells' HS estimation as potentially doubtful. The second series of maps show Variability, which refers to the degree of dispersion among the HS estimations provided by all runs. The density of each run is used to weight its corresponding HS prediction by means of weighted standard deviation.

Other maps that can be implemented departing from the maps of Figure 12 (A to E) are:

- Map of potential presence/absence (1/0) for the control period and future scenarios,
- Map of potential presence changes. In this case four values can be computed: no-presence under current climate and future scenarios, potential presence in current and future, new potential presence areas, and areas losing potential presence (potential extinction areas), and
- Maps of high HS as shown in Figure 13 (B to F).

Figure 13 (A) shows observed presence of *Abies alba* as recorded in the harmonised NFI samples. Figure 13 (B to F) shows areas of high HS (>= 0.75) of *Abies alba* under current climate (B) and future scenarios A1B (C to E) (medium emissions scenario) and E1 (F) (mitigation scenario). In the control period the HS of *Abies alba* covers several countries where little or no presence is recorded in the NFI dataset.

According to Flora Europaea and Euro+Med PlantBase, *Abies alba* is native in most Central European countries up to the Italian and Balkan Peninsulas. It is also recorded in Europe in other southern regions (Portugal, Cyprus, Sardinia) and northern regions (British Isles, Scandinavian Peninsula, Baltic States) as an introduced species and in some cases naturalized (Figure 11) [158, 159]. Although the NFI database covers a limited number of European countries, the current HS shows high values also in those zones where *Abies alba* is native but has low presence densities or is not recorded, such as the Balkan countries. High HS values are also evident in the Scandinavian Peninsula and British Isles where *Abies alba* is not native, confirming these areas are potentially suitable for this species, even if they are outside its known natural distribution.

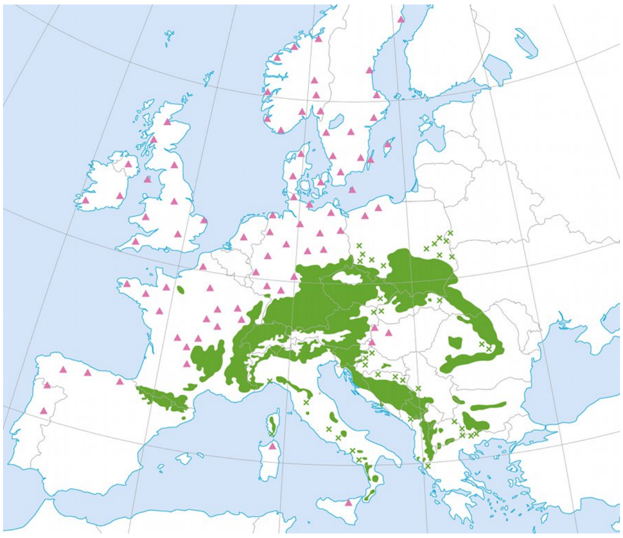

Figure 11: Distribution range of *Abies alba*. Green areas and crosses represent the natural range, purple triangles localize where the species has been introduced. The map is adapted from Caudullo *et al.* [81]. Colour scheme derived from Harrower and Brewer [157] (see http://colorbrewer2.org/?type=diverging&scheme=PiYG).

A shift in suitable areas towards Northern regions is evident in the A1B scenario maps of Figure 13 (C to E). New suitable areas are in the Scandinavian Peninsula, Poland, Northern British Islands and Ireland. Differences between different realisations of the scenario A1B are also evident in these maps, something that should be considered in assessing the uncertainty of using specific model realisations instead of ensemble scenario datasets. Differences between current HS and scenario E1 are less evident than in scenario A1B. Scenario E1 is considered a mitigation scenario with atmospheric concentrations of greenhouse gases stabilised at 450 ppm CO2-equivalent in comparison with A1B accounting for 850 ppm in 2100 [107]. However, in scenario E1 new suitable areas are in the Scandinavian Peninsula and Northern British Islands and Ireland, further increasing current HS in these regions.

Figure 14 shows absolute changes in HS of *Abies alba* between current climate and future scenarios A1B (A, B and C) and E1 (D). These maps show the difference (gain and loss) of HS for each grid-cell. Green and red areas are those respectively increasing and losing future HS. Green areas are more evident in Northern regions under A1B scenario (A to C). Green areas are less evident in scenario E1 (D). Some red areas are noticeable in specific regions of the Mediterranean, Iberian Peninsula and Central Europe that would need further investigation.

4 Discussion

Suitable areas of *Abies alba* are likely to suffer drastic changes as consequence of anthropogenic climate change. Changes would be more radical under A1B scenario environmental conditions than in E1 scenario. In addition to the evident shift to northern regions of suitable areas for *Abies alba* under the A1B scenario, there is also a remarkable shrinking of suitable areas in mountain regions such as the Pyrenees, Alps and Carpathian. This is consistent with an upslope shift towards higher elevation.

Results of this study should be interpreted in the context of limitations and assumptions adopted. HS defines the regions where the tree species actually or potentially lives. Therefore HS maps should be assessed from this perspective. An area exhibiting high values of HS will likely host individuals of the assessed species. However, several factors could prevent the species from being present in that area – e.g. competition between species, anthropic land cover changes, disturbances such as forest fires and storms. Hence, HS should not be understood as the actual current (or future) distribution of species. Results of our modelling approach show the changes in HS resulting from anthropogenic climate change.

A limitation of this study is that migration of tree species is not considered. Geographical shifts of HS as consequence of anthropogenic climate change can overpass the dispersal capability of tree species. For example, it is worth noting that European tree species exhibited average maximum migration rates in the order of 50 to 200 km per century during the Holocene [160]. Therefore, a “faster” shift in HS and landscape fragmentation would limit the plants’ dispersal capability. That is, new suitable areas in future scenarios could not be reachable by the species by natural processes. From the perspective of human-induced adaptation of tree species, this implies afforestation and reforestation of new suitable areas with climate adapted species. Since this is not a natural process, it is challenging to assess to which extent forest adaptation can contribute to mitigate climate effects. Nevertheless, modelling forest adaptation options is an important step to understand the potential distribution and composition of forested areas. Further modelling efforts would be required for a proper inclusion of adaptation measures that counteract the effects of a changing environment.

Results of this study are consistent with other studies in this field in Europe and other temperate regions. Iverson *et al.* [114] studied 134 US tree species and found that approximately 66 species would gain and 54 species would experience a loss of suitable habitat. In addition, most of the species habitat moved generally northeast up to 800 km in the hottest scenario. In the European context, Berry *et al.* [123] studied the potential impacts of climate change on plants in Britain and Ireland. They grouped the results in plants gaining climatic space, losing and those showing no change. The species losing climatic space show a northern shift of the suitable areas. Casalegno *et al.* [88] assessed the potential effects of climate change on *Pinus cembra* in the Alps and the Carpathian mountains finding a loss of suitable habitat between 53 % and 72 % depending on the scenario. Additionally, their results predict an upslope shift of the HS of *Pinus cembra* with no downslope shift. Benito Garzón *et al.* [143] assessed the effects of climate change on the Iberian tree species. Results show a reduction in the potential distribution of the 20 studied species under A and B family emission scenarios.

Further steps of this study look at computing HS maps of the most relevant European tree species. Whereas it is interesting seeing the potential impacts of climate change on specific species such as *Abies alba*, more robust conclusions can be drawn by assessing a consistent number of species. This would produce an overall picture of the balance of HS gains and losses as consequence of anthropogenic climate change and the potential consequences for European forests.

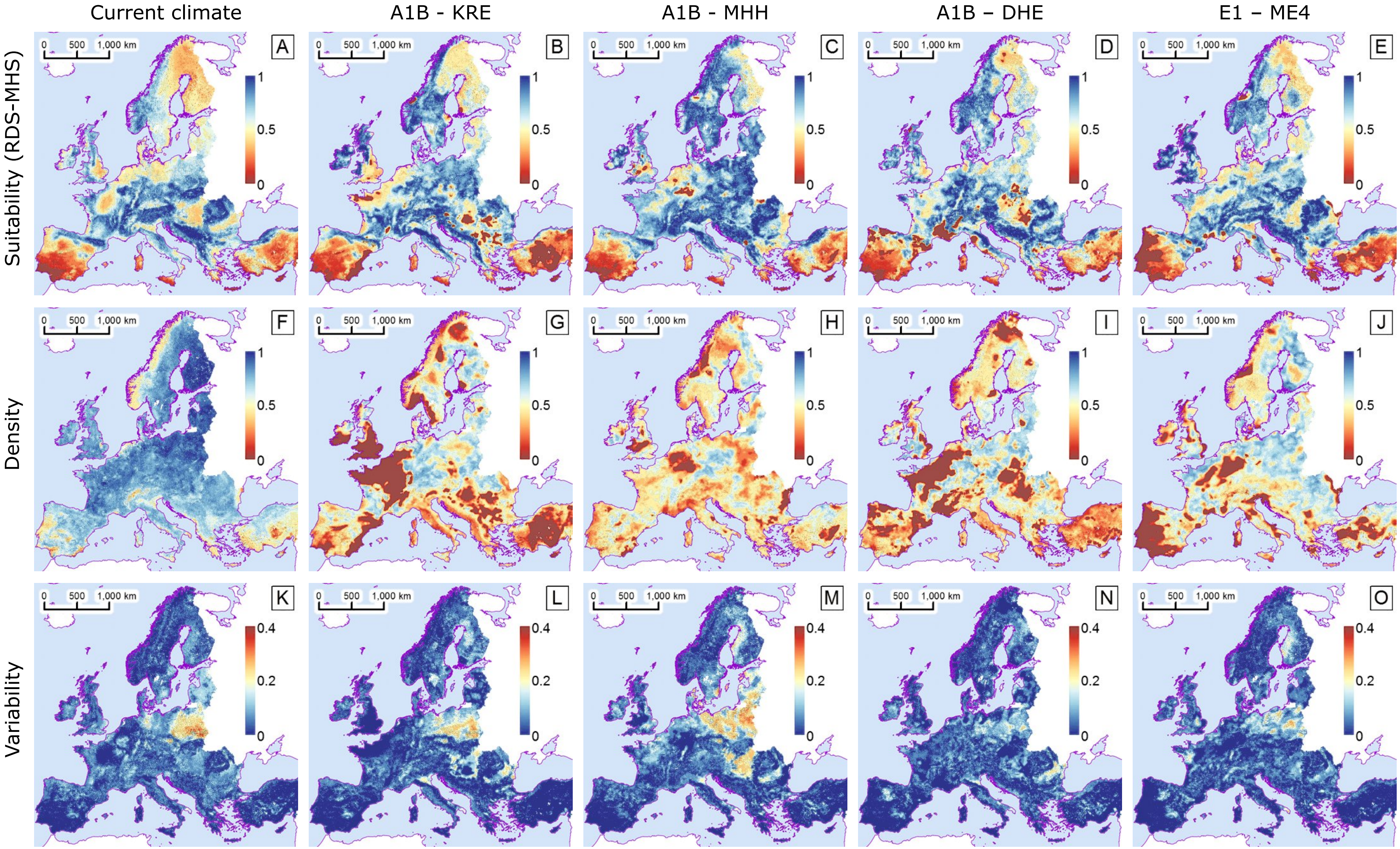

Figure 12: *Abies alba* habitat suitability, density and variability for current climate and future scenarios A1B (KRE, MHH and DHE models) and E1 (ME4 model). Colour scheme derived from Harrower and Brewer [157] (see http://colorbrewer2.org/?type=diverging&scheme=RdYlBu).

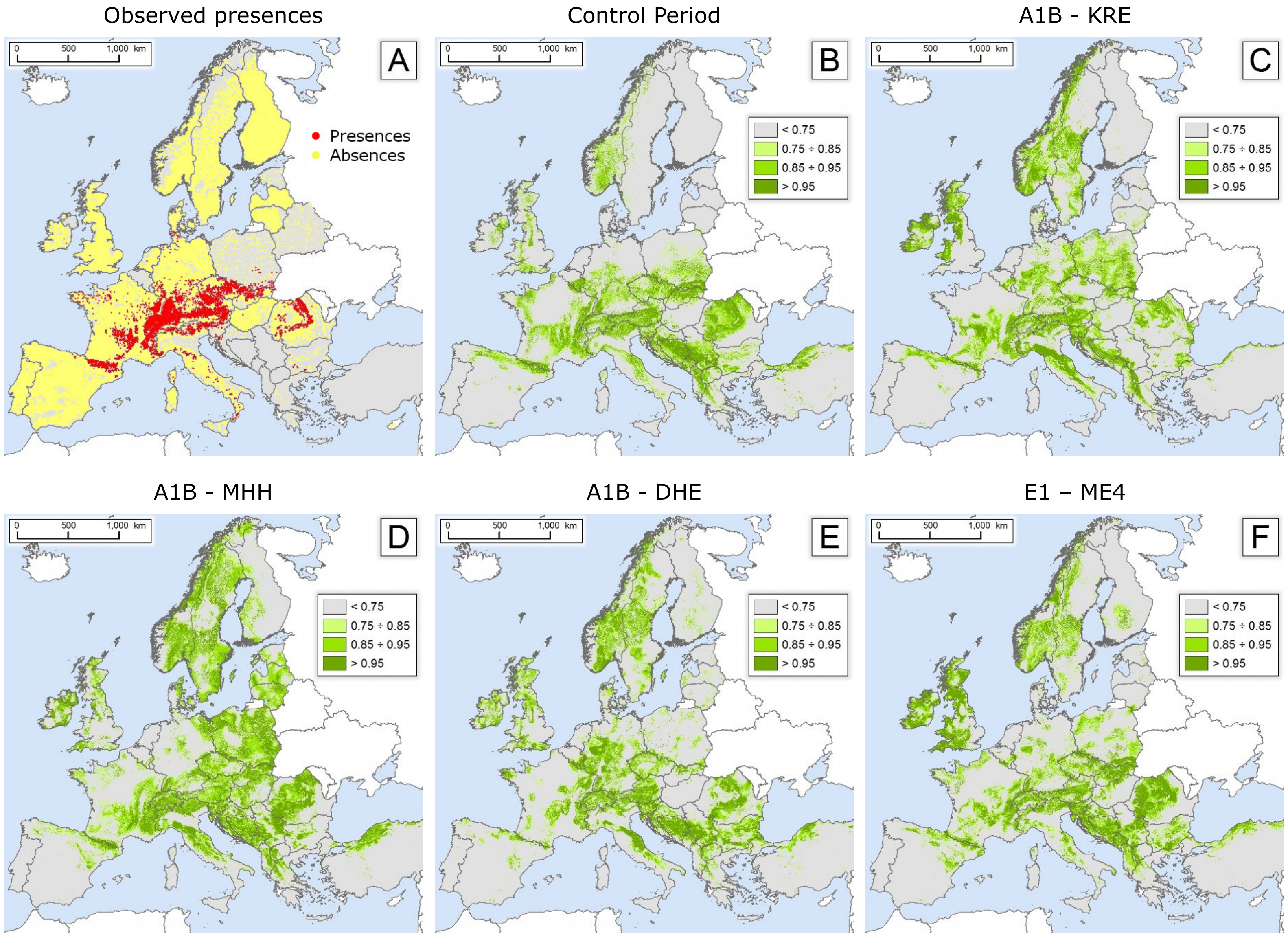

Figure 13: *Abies alba* observed presence (A) and areas of high habitat suitability (>= 0.75) under current climate (B) and future scenarios A1B: KRE, MHH and DHE models (C, D and E) and E1: ME4 model (F). While all available observations are reported in (A), the remaining prototype maps have been generated using a significantly reduced subset of training data. Nevertheless, (A) and (B) are in good agreement.

Box 2. Assessing accuracy and specificity of maximum habitat suitability estimates for the current climate: the case for limited training sets

As already discussed, MHS can only be validated by comparing estimated suitability versus observed presences. At the 1 km^2 spatial resolution, reported absences refer to small plot areas within the spatial cell and not to the entire spatial cell - hence a tree species absent in a given plot does not imply the species to be absent in the corresponding entire spatial cell. Furthermore, absences may occur for many reasons in bioclimatically suitable areas (see the section of the Foreword on the robust modelling of tree species habitat suitability). Table 4 summarises a quantile-based assessment of accuracy and specificity (for the current climate) for the case study on *Abies alba* with and extensive validation and a reduced training set.

Table 4: Assessment of accuracy and specificity (current climate) of the case study on *Abies alba* with more than 370000 harmonised plot observations and a reduced training set to stress the learning ability of the model. Training set based on less than 2 % of the total available observations. Ensemble based on 100 bootstrap runs (see Figure 9) aggregated via weighted median (Figure 10) – weights proportional to the corresponding *density* estimations of each run (see Figure 12). This simplistic assessment (see in particular the heterogeneous spatial density of the available plots in Figure 6) offers a qualitative overview of the performance which may be easily achieved by the model – here under a simple unsupervised covariate-weighting and a reduced training set.

Accuracy of modelled maximum HS vs. observed presences:	
Observed presences where MHS > 95 %:	49.9 %
Observed presences where MHS > 90 %:	65.5 %
Observed presences where MHS > 85 %:	78 %
Observed presences where MHS < 70 %:	4.6 %
Observed presences where MHS < 50 %:	0.41 %

Specificity of the modelled maximum HS:	
1 km^2 spatial cells where HS > 95 %:	6.03 %
1 km^2 spatial cells where HS > 90 %:	10.2 %
1 km^2 spatial cells where HS > 85 %:	15.3 %
1 km^2 spatial cells where HS < 70 %:	65.9 %

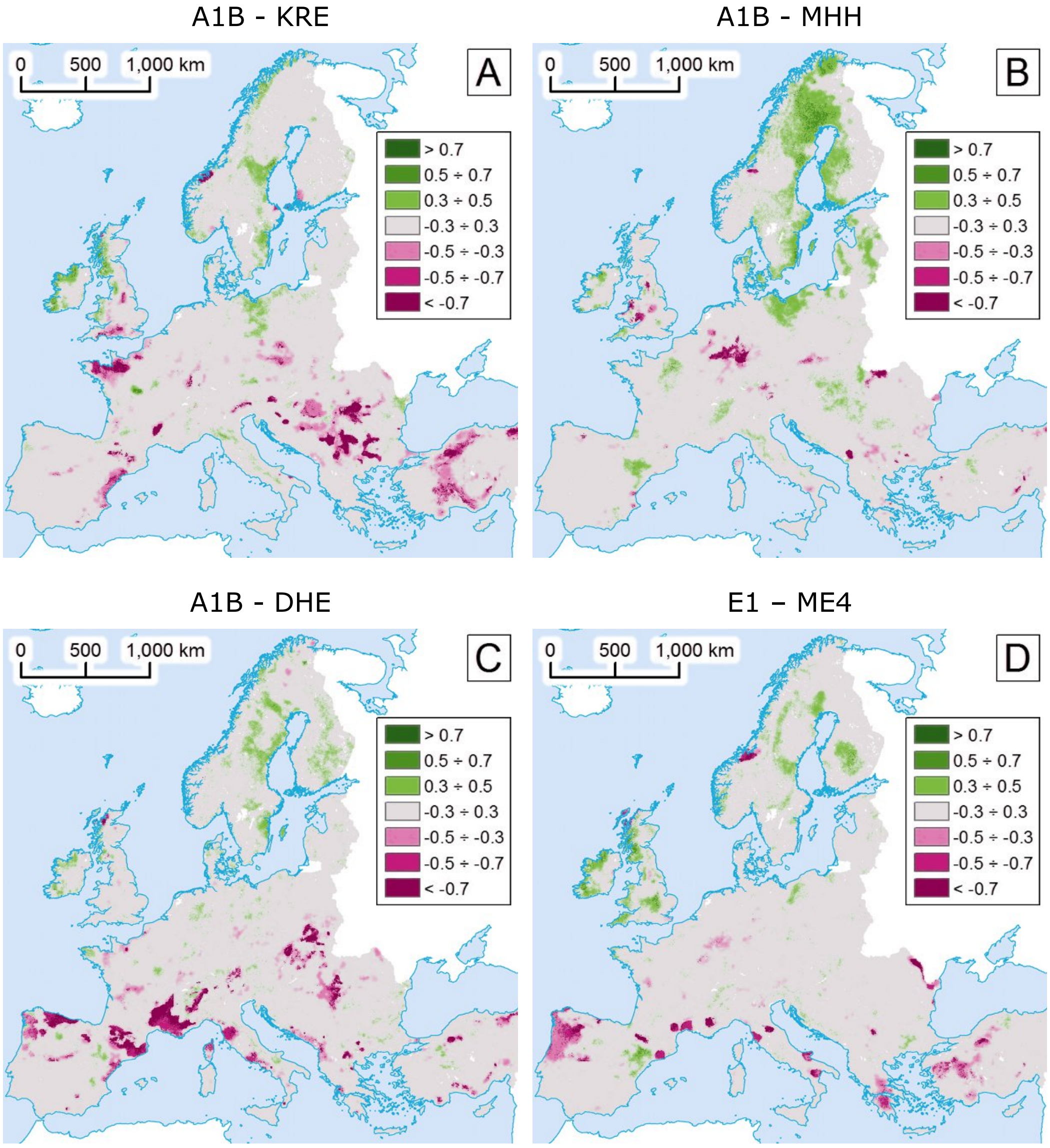

Figure 14: Changes in the maximum habitat suitability of *Abies alba* between current climate and future scenarios A1B (KRE, MHH and DHE models) and E1 (ME4 model). Colour scheme derived from Harrower and Brewer [157] (see http://colorbrewer2.org/?type=diverging&scheme=PiYG).

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List of abbreviations and definitions

FISE	*Forest Information System for Europe*. Hosted by the JRC is a focal point for the European Union policy relevant forest data and information [109, 1, 2]. See http://fise.jrc.ec.europa.eu/.
HS	*Habitat suitability*: potential suitability for a certain organism (e.g. a tree species) to live in a given local habitat. Although there is no agreement in defining *habitat* within the ecological literature, a working definition for operational purposes has been proposed as "description of a physical place, at a particular scale of space and time, where an organism either actually or potentially lives" [48]. HS It is generally a quantity varying from 0 (0 %, unsuitable habitat) to 1 (100 %, potentially highly suitable habitat).
IPCC	*Intergovernmental Panel on Climate Change*. See http://www.ipcc.ch.
JRC	*Joint Research Centre* of the European Commission. See https://ec.europa.eu/jrc/en/about/jrc-in-brief.
MHS	*Maximum habitat suitability* (or *survivability*): a dimensionless index based on RDS to estimate e.g. where a certain tree species could potentially occur if climatic conditions and ecological conditions are met.
NFI	*National Forest Inventory*. Information systems at country level to collect information about national forests. While the NFI systems are different in most countries, they collect forest ground data and information suitable to be processed to obtain harmonised European-wide forest information [50].
NFIs	*National Forest Inventories* (see NFI).
PESETA	Series of cross-disciplinary projects mainly developed within the JRC. The acronym is for *Projection of Economic impacts of climate change in Sectors of the European Union based on bottom-up Analysis*. See https://ec.europa.eu/jrc/en/peseta.
RDS	*Relative distance similarity*: the similarity between two patterns of information based on their relative distance. For example, for a nonnegative quantity the relative distance between two measures/estimates of it is the dimensionless ratio between their numeric values – which does not depend on the particular units in which the values are expressed. Multi-dimensional arrays of information are associated with an aggregated dimensionless RDS. For example, the maximum habitat suitability of a given tree species in a certain area, based on how similar are the bioclimatic conditions of the area with the ones found where the available field observations indicate the presence of the species.
RPP	*Relative probability of presence*: probability of finding a certain organism or entity (for example, a certain tree species) in a given area, irrespective of the probability of finding other entities (e.g. without taking into account other tree species). Concerning tree species, the sum of the RPP associated with different taxa in the same area is not constrained to be 100 %. For example, in a forest with two co-dominant tree species which are homogeneously mixed, the RPP of both may be 100 %.
SRES	IPCC *Special Report on Emissions Scenarios* [107].

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KJ-04-17-260-EN-N

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Publications Office

doi:10.2760/296501

ISBN 978-92-79-66704-6