Conservation Planning in Europe: Ecological, Financial, and Political Challenges

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“To waste, to destroy our natural resources, to skin and exhaust the land instead of using it so as to increase its usefulness, will result in undermining in the days of our children the very prosperity which we ought by right to hand down to them amplified and developed.”

— Theodore Roosevelt, 1907 —

Declaration of Authorship

For the thesis entitled *Conservation Planning in Europe: Ecological, Financial, and Political Challenges*, authored by Henrik Hannemann, the following contributions to the work are declared:

The work has been supervised by Professor Kathy Willis and Dr Marc Macias-Fauria. The manuscripts presented in chapters 3 to 6 of this thesis to which both supervisors are co-authors, are substantially the work of the author of this thesis and the role of the supervisors has been limited to supervisory input and comments on drafts. The same applies to chapter 5 which has a further co-author.

Chapter 1:
Entirely the work of the author of the thesis.

Chapter 2:
Entirely the work of the author of the thesis.

Chapter 3:
The chapter idea was developed under the guidance of Marc Macias-Fauria. The complete work, analysis, and writing of the manuscript was undertaken by the author of the thesis. Both supervisors commented on manuscript drafts.

Chapter 4:
The initial concept of the chapter was discussed with both supervisors who provided comments on draft versions. The required work, data mining, analysis, and writing of the manuscript was undertaken by the author of the thesis.

Chapter 5:
The palaeo-ecological analysis was developed under guidance of both supervisors. Alistair Seddon, University of Bergen, has contributed R code in order access the EPD. Additionally, Marc Macias-Fauria supported figure layout. Adaptation of the code, all analysis, and writing of the manuscript has been undertaken by the author of the thesis.

Chapter 6:
The author of the thesis collated and analysed the data and characteristics of all framework agreements incorporated and wrote the manuscript. Both supervisors provided feedback and comments on manuscript drafts.

Chapter 7:
Entirely the work of the author of the thesis.

Abstract

Conservation of biodiversity and sustainable resource use are central aims within ecology. This thesis focuses on the current data and environmental frameworks used to support these aims across different states in Europe. In particular, it examines the impact of geo-political boundaries on data-use, funding and planning for temporal movement of species in response to climate change. It also examines the current environmental framework agreements in Europe and their capacity to deal with trans-boundary aspects of biodiversity change.

Through examination of European biodiversity datasets, undertaking species distribution modelling of forest taxa, examining economic data, palaeo-ecological data, and assessing international environmental framework agreements, this thesis identifies a number of important knowledge gaps. Probably unsurprisingly, the distribution of biodiversity in Europe mostly does not match political entities, all of which have individual aims, financial resources, and biodiversity management regimes in place. All have a significant impact on biodiversity conservation planning because i) the use of geo-politically truncated data influences modelling predictions, ii) financial commitment to biodiversity conservation varies between countries influencing success outcomes, iii) biodiversity persistence in current and future climate change does not recognise geo-political boundaries, and iv) many of the key environmental frameworks are implemented within countries and do not considering trans-boundary issues.

Overall these findings significantly improve the understanding of conservation and resource management in Europe and fill a number of important knowledge gaps. They highlight the importance of appropriate trans-boundary ecological datasets and the need for more consistency across Europe in financial resources for biodiversity conservation. They also highlight the need for appreciation of areas of high-persistent biodiversity regardless of geo-political boundaries and environmental framework agreements that support cross-border conservation measures.

Preface

This thesis, submitted as partial fulfilment of the requirements for the Degree of Doctor of Philosophy at the University of Oxford, is structured in four research papers, which are designed to be or have already been submitted to relevant journals. As such the manuscripts are formatted accordingly. References are listed within the overall bibliography. Any supplementary material can be found in the relevant appendix.

Chapter 1:
General introduction

Chapter 2:
A brief review of approaches and methods

Chapter 3:
Hannemann, H., Willis, K.J., and Macias-Fauria, M. (2016) The devil is in the detail: unstable response functions in species distribution models challenge bulk ensemble modelling. *Global Ecology and Biogeography*, **25**, 26-35, DOI: 10.1111/geb.12381

Chapter 4:
Hannemann, H., Macias-Fauria, M., and Willis, K.J. (2017) Money well spent? National expenditure on protected areas in Europe over time. *In prep.*

Chapter 5:
Hannemann, H., Seddon, A., Willis, K.J., and Macias-Fauria, M., (2017) Lessons from the past - Hotspots of forest taxa persistence across Europe informed by palaeo-ecology. *In prep.*

Chapter 6:
Hannemann, H., Macias-Fauria, M., and Willis, K.J. (2017) Trans-boundary conservation and environmental framework agreements in Europe. *In prep.*

Chapter 7:
Concluding remarks

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List of Abbreviations

ANN . . . . . . Artificial Neural Networks

AUC . . . . . . Area Under the Curve of the Receiver Operating Characteristic

BRIDGE . . . Bristol Research Initiative for the Dynamic Global Environment

CBD . . . . . . Convention of Biological Diversity

CMS . . . . . . Convention on the Conservation of Migratory Species of Wild Animals

CRU . . . . . . Climate Research Unit, University of East Anglia

CTA . . . . . . Classification Tree Analysis

EC . . . . European Commission

ECB . . . . . . European Central Bank

EPD . . . . . . European Pollen Database

EU . . . . European Union

EUFORGEN . European Forest Genetic Resource Programme

GAM . . . . . Generalised Additive Model

GBM . . . . . Generalised Boosted Model

GLM . . . . . . Generalised Linear Model

IUCN . . . . . International Union for Conservation of Nature

MARS . . . . . Multiple Adaptive Regression Spline

OECD . . . . . Organisation for Economic Co-operation and Development

PADDD . . . . Protected area downgrading, downsizing, and degazettment

PCA . . . . . . Principal component analysis

PPP . . . . . . purchasing power parity

RF . . . . Random Forest

ROC . . . . . . *see* AUC

SDM . . . . . . Species Distribution Modelling

SLOSS . . . . . Single Large Or Several Small protected areas

TSS . . . . . . True Skill Statistic

USD . . . . . . United States Dollar

VarImp . . . . Variable importance

WB . . . . . . World Bank

WDPA . . . . World Database on Protected Areas

yr BP . . . . . years before present

1
Introduction

Conservation science and methods to determine the persistence of biodiversity have been prominent and long-established research fields within ecology (Chapin et al., 2010; Pinchot, 1910). These research fields span aspects such as protected area planning, identifying important habitats and mechanisms for protection beyond reserves, as well as modelling approaches e.g. species distribution modelling (SDM) (Feranec, 2016; Guisan and Thuiller, 2005; Hannah, 2008; Kareksela et al., 2013; Petchey and Gaston, 2006). Biodiversity conservation research has always been interdisciplinary with subjects encompassing resource use, ecological requirements for species persistence, modelling, and policies for underpinning protected area planning. All have been recognised as central components for developing conservation strategies for the 21st century and beyond.

Biodiversity in Europe (and globally) is currently threatened by widespread land-use change and climate change (Royal Botanic Gardens, 2016; Thomas et al., 2004; Thuiller et al., 2005). Biodiversity persistence is especially under pressure within areas of high human development and resulting fragmentation of landscape (Henle et al., 2008; Kuussaari et al., 2009). This is further exacerbated by changing climatic conditions and their impact on these fragmented ecosystems (Araújo et al., 2011; Harrison et al., 2006; Milad et al., 2011).

Current conservation regimes in Europe are based on a plurality of approaches, and there is no agreed best-practice approach to identifying areas or species in need of protection (Adams et al., 2010; Cabeza and Moilanen, 2001; Carvalho et al., 2010). There has also been some criticism concerning spatial focus of present-day conservation actions. It is argued they often concentrate on low-impact land areas which hold low opportunity costs (Adams et al., 2010) with limited cross-border integration and lack of joint management of protected areas (Kark et al., 2015). Additionally, researchers tend to use political entities as cut-off points in their modelling of species which results in biodiversity distributions being artificially truncated (e.g. Broadmeadow, 2005; Edman et al., 2011; Keenan et al., 2011; Raes, 2012). The impact of this on full understanding of current and future responses of species to climate change is, as yet, unknown. Poor understanding of temporal dynamics is also an issue. There is a wealth of data in palaeo-ecological studies indicating much wider natural distributions than are currently observed on our cultural landscape (Williams and Jackson, 2007). Such records hold distinctive potential to inform conservation under change (Cabeza and Moilanen, 2001; Macdonald and Willis, 2013; Visconti et al., 2010; Willis et al., 2010).

The direction and success of conservation action plans across Europe also depend on both political and economic frameworks. Within Europe, two core groups of political frameworks affect conservation. They are not mutually exclusive and, in most cases, interdependent: i) directives of the European Union (EU, e.g. Habitats Directive) and ii) international conventions (e.g. Convention on Biological Diversity). These agreements have far-reaching consequences on various spatial and temporal scales for biodiversity conservation – now and in the future. The economic aspects that influence conservation actions include co-financing from the EU and international specialist funding from government and non-government organisations, for example, the World Bank, World Wide Fund for Nature, Conservation International (Kark et al., 2015; Waldron et al., 2013). Not surprisingly, studies have indicated that conservation effectiveness may be limited due to lack of overarching funding approaches (Iftekhar et al., 2017).

Biodiversity conservation research is therefore positioned between natural and social sciences. It spans questions of prioritisation under scarcity, economic and political considerations, and temporal dynamics of the resource (Adams et al., 2010; Arponen et al., 2010; Fuller et al., 2010; Moilanen and Arponen, 2011*b*).

The following sections consider these issues in more detail and highlights current knowledge gaps:

1.1 Impact of political boundaries in Europe

Europe is classified into numerous biogeographic zones and there is extensive data available on species' ranges and their dispersal patterns. Europe is also dissected by numerous political boundaries. Since the late 1940s, the number of protected areas has been increasing across the region (Chapin et al., 2010). Protected area categorisation schemes have tended to prioritise political boundaries over biogeographic zones. This has created a number of issues namely i) the boundaries do not reflect ecology; ii) the boundaries are often used for conservation planning which involves the use of truncated datasets; and iii) false ecological 'islands' are created. Each will be discussed briefly in turn.

First, ecological zones and habitat types routinely cross political borders. As a consequence conservation research in Europe, more often than not, is focused on habitats or species within a single political entity (e.g. Broadmeadow, 2005; Edman et al., 2011; Keenan et al., 2011; Raes, 2012). The problem with this approach is that the output does not represent the true ecological situation of species or habitat under consideration.

Second, the use of truncated datasets in conservation planning, whilst seeming quite sensible at face value because it enables the stakeholder to assess the effectiveness and efficiency of a conservation regime within the area specified, neglects important ecological considerations such as edge effects (Venter et al., 2016) and/or spill-over (Andam et al., 2008). It also tends to ignore positive benefits, for example, obtained from a neighbouring country hosting an adjacent protected area thus providing a larger-scale protected region (Ring et al., 2010).

Third, by only considering in-country conservation approaches, individual countries are viewing their biodiversity equivalent to ecological islands. This is ecologically incorrect and can result in prioritisation of species and communities as 'rare' when in fact they may be ubiquitous elsewhere (Kukkala et al., 2016). This is showcased by e.g. *Betula nana* being classified as 'least concern' across Europe but as 'critically endangered' in the United Kingdom (IUCN, 2013; Stroh et al., 2014).

The stark difference between ecological reach and political entities is therefore an issue when it comes to conservation planning (Kark et al., 2015). There are still considerable knowledge gaps surrounding the impact of geo-political boundaries on conservation protection in Europe.

1.2 Impact of national funding regimes on conservation

Economic support for conservation is a key aspect to its success (Iftekhar et al., 2017). Similar to the issues of truncation of ecological data by political borders, public spending regimes on biodiversity protection are politically restricted within Europe. Biodiversity conservation funding should ideally align with conservation strategies, which, under ideal circumstances, in turn align with ecological distributions (Devictor et al., 2010; Miller et al., 2013; Waldron et al., 2013). Due to political devolution and budgetary constraints, cross-border funding is only an option under the auspices of supra-national entities or the binding obligations of environmental framework agreements setting up e.g. specialists funds. Thus the domestic budgetary priorities of each nation become a vital component of regional conservation.

A key knowledge gap, therefore, is how this in-country funding situation impacts conservation strategies that are set at a European and global level. In particular, there is a lack of cross-disciplinary use of available data by conservationists to understand the full consequences of varying levels of economic commitment to biodiversity conservation. This means that there may well be a misalignment of priorities and resources (Rands et al., 2010).

1.3 Temporal dynamics of biodiversity through time

Biodiversity and its persistence are currently under duress due to continued fragmentation and change in environmental conditions (Krauss et al., 2010; Milad et al., 2011; Thuiller et al., 2005). Throughout Earth's history, biodiversity has always shifted in response to climate change (Willis et al., 2010). Research has indicated compositional change being the norm rather than a fixed assemblage in a certain location. Therefore, the adaption to an ever-changing world and varying ecological baselines is central for dynamic conservation in the 21st century (Gillson and Willis, 2004; Pressey et al., 2007). There is no reason to suggest that with current climate change shifts will not happen again, nonetheless most conservation assessments and planning are based on static inventories and are constrained by political boundaries. This is particularly the case for national biodiversity strategies and assessments.

What kind of biodiversity can be found where, under which conditions, and what is required to support its temporal persistence under stress are key aspects for effective conservation planning (Bellard et al., 2012; Bini et al., 2006). This specifically highlights the importance of assessing current presences and dynamic responses in order to support long-term viability (Venter et al., 2016; Visconti et al., 2010). Currently biodiversity conservation and identification of resource use are predominantly based on snap-shot present-day assessments. They do not incorporate available palaeo-ecological data which would enable clear identification of areas of long-term persistence. A key knowledge gap, therefore, exists in identifying persistence of genera through time to highlight ecologically sensible locations of resource deployment.

1.4 Suitability of current environmental framework agreements

It has been suggested many times that the dynamic effects of climate change and underlying anthropogenic influence on the landscape will threaten current protected area networks across Europe (Araújo et al., 2011; Gillson and Willis, 2004). Biodiversity conservation across the region is governed by numerous environmental framework agreements which have been drawn up independently of each other but work as an interlinking safety net. Each framework agreement provides a different focus, different instruments and implementation, and divergent approaches for facilitating biodiversity conservation. Implementation of strategies is mainly left to individual member states (Bennett and Ligthart, 2001; Erasmus et al., 1999; Kukkala et al., 2016). While baselines for conservation provisions are established through international agreements and EU directives, their applicability is questioned in a dynamic situation requiring a reassessment of static inventories for protected area designation (Trouwborst, 2009). Current research is not reflected within the environmental framework agreements. A re-assessment of these agreements affecting the conservation strategies across Europe enables targeted revisions. In order to allow an efficient cross-disciplinary use of resources and sustained levels of biodiversity presence (Chapin et al., 2010), it is of key importance to examine all agreements with respect to their applicability of their aims under dynamic changes to support successful future conservation.

Therefore, an emergent knowledge gap within biodiversity conservation is the applicability of current environmental framework agreements under dynamic change. Whether their scope, established funding mechanisms, or ecologically necessary trans-boundary cooperation is sufficient – now and in the future – is debated.

1.5 Aims and Objectives

This thesis aims to address the knowledge gaps outlined above by 1) assessing the impact of political boundaries on biodiversity data and the associated conservation spending, 2) highlighting the dynamic nature of biodiversity persistence throughout time, and 3) assessing current environmental frameworks within Europe in the light of predicted changes in the future. This is achieved by four inter-linking objectives:

i. Determining the potential consequences of using truncated training data in species distribution modelling and its impact on predictions. (Chapter 3; Hannemann et al., 2016)

ii. Assessing the status of current state-based conservation spending patterns both across Europe and within individual states by using a long-term data set of economic variables to determine the differences in consistency and priority of conservation between countries and across time. (Chapter 4)

iii. Examining the effects of expanding the temporal dynamic of SDM on genera persistence by incorporating palaeo-ecological data to detect the effects of past climate changes on distributions of forest taxa within Europe throughout the Holocene to the present-day (from c. 8,000 years before present). (Chapter 5)

iv. Examining key international and regional environmental framework agreements to identify both potential and shortfalls in the obligations across Europe with respect to the insights from the previous chapters. (Chapter 6)

1.6 Thesis outline

The structure of the thesis follows the aims and objectives highlighted above. The four core areas identified are preceded by a brief review of approaches of conservation strategies and species distribution modelling based on the ecological niche concept (Chapter 2).

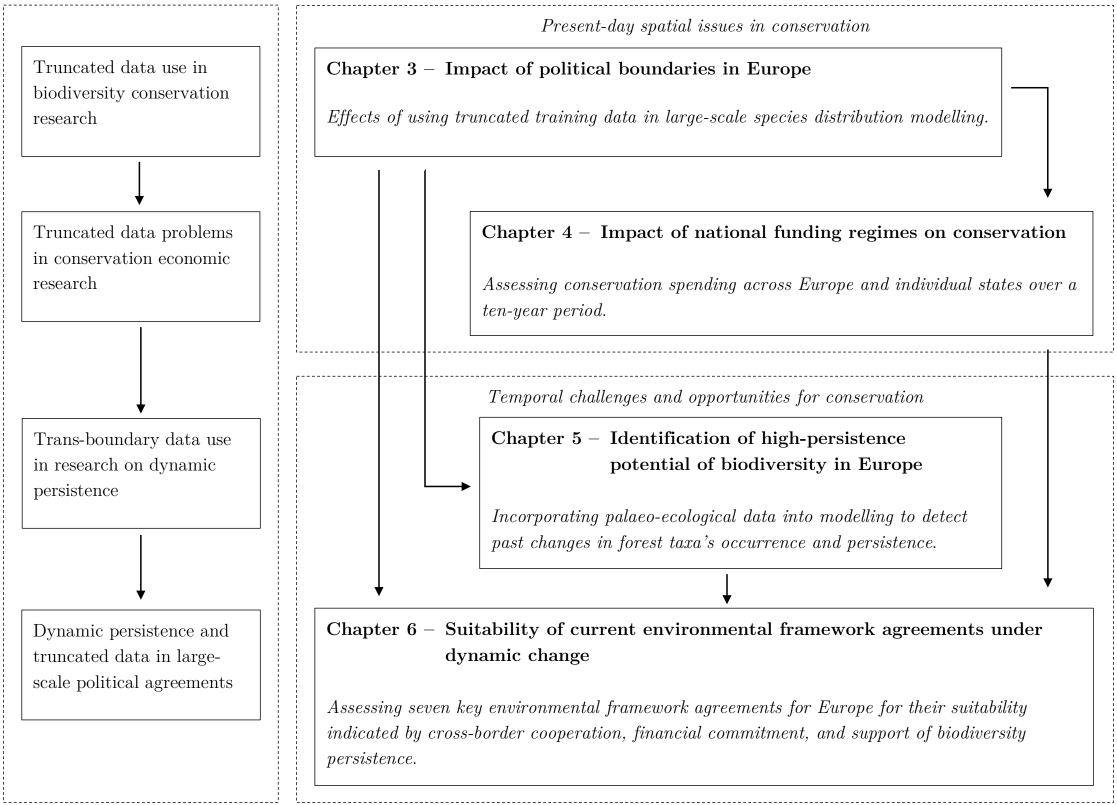

Figure 1.1: Thesis structure. Conceptual overview of the interlinking structure of the four research chapters and how they align with overarching concepts assessed in this thesis.

Chapter 3 assesses the use of (politically) truncated ecological data sets in SDM and the consequential errors resulting from it in contrast to the use of regional data sets. Seven forest tree species with a natural occurrence across Europe showcase the issue at hand by using Germany as political entity to truncate distributions in Central Europe.

Chapter 4 examines the economic framework of conservation by utilising government expenditure data and numbers of designated protected area as a proxy for commitment to conservation. Assessing the financial components over a ten-year time frame (2004 to 2013) allows for identifying prioritisation and consistency across time as well as highlighting the differences in expenditure despite the countries i) being subject to the same international and regional conservation agreements and ii) differing a lot in biodiversity richness, irreplaceability, and status.

Chapter 5 uses palaeo-ecological data to inform the potential for the use of SDM approaches in identifying suitable long-term persistence of biodiversity, focusing on forest taxa for e.g. conservation areas or forestry use, which is found to consistently span across several political boundaries. The use of large-scale sets of bioclimatic variables and palaeo-ecological data within an SDM framework supports a more grounded and informed approach to resource use, both in conservation and economic contexts (e.g. Fuller et al., 2010; Thuiller et al., 2008).

Chapter 6 reviews the political background to current conservation within Europe and highlights the potential of current environmental framework agreements under dynamic changes. A close review of five international conventions and two EU directives, all of which are influencing the conservation agenda across the region, is undertaken. Special attention is directed to institutionalised cross-border cooperation and to mechanisms identifying and facilitating persistence of biodiversity under changing climatic and environmental conditions, financial commitment and funding mechanisms, and the potential for degazettment of protected areas. A qualitative assessment is made as to whether, due to the factors listed, the agreements are suitable for the current situation and hold potential for future-orientated conservation planning.

1.7 Study area

Europe provides a diverse background for both ecological and economic research. As such it is an ideal study area for the interdisciplinary aspects of conservation. The European Union includes 28 member states with a combined land area of c. 4.5 million km^2 and an aggregated gross domestic product of 16.5 trillion United States Dollar (USD) as of 2016. A wider geographical extent of Europe (considered as 11°W – 32°E and 34° – 72°N) is used for ecological analysis and SDM in Chapters 3 and 5 of this thesis.

Eight biogeographical regions can be identified throughout Europe: Alpine, Atlantic, Black Sea, Boreal, Continental, Mediterranean, Pannonian, and Steppic (European Environment Agency, 2012). Data availability for species occurrence (including palaeo-ecological records), climate projections, and bioclimatic variables in both spatial density and temporal continuity support Europe as a choice for SDM-based research on conservation.

1.8 Data and methods

All chapters are designed to incorporate publicly available data wherever possible in order to provide a replicable and transparent research approach which can be utilised for conservation assessments in other countries and regions as well.

Forest taxa are used as proxy for biodiversity. Their longevity and near ubiquitous distribution across Europe allows to encapsulate numerous habitat types and the entailing ecosystems by utilising trees as umbrella taxa (Andelman and Fagan, 2000; Fleishman et al., 2000). Only those taxa with natural occurrences within the study area are considered. A few cases of species or genera with ranges beyond the study area are considered, but occurrences outside the European extent are discounted.

The thesis is methodologically based in the interdisciplinary cross-over between bioclimatic envelope modelling, economic data, and literature-based research on international conservation agreements. Each chapter focuses on a separate aspect and all contribute to chapter 6 and the general discussion. The varying data requirements for each chapter, its research question, and the research approaches are briefly outlined:

Chapter 3 used occurrence data for the selected tree species from the European Forest Genetic Resource Programme (EUFORGEN; euforgen.org). Bioclimatic variables were used from the Climate Research Unit (CRU; cru.uea.ac.uk). SDM and all subsequent assessment were undertaken using R.

Chapter 4 is based on publicly available socio-economic data and inventories of protected areas. The sources utilised are: World Development Indicators by the World Bank (WB; data.worldbank.org), Country Indicators from the Organisation for Economic Cooperation and Development (OECD; data.oecd.org, stats.oecd.org), public exchange rates from the European Central Bank (ECB; ecb.europe.eu), and details of countries' protected area networks from the World Database on Protected Areas (WDPA; protectedplanet.net).

Chapter 5 uses palaeo-ecological data on genera occurrence data from the European Pollen Database (EPD; europeanpollendatabase.net) in combination with present-day occurrence for the respective genera's species as listed by EUFORGEN. Palaeo climate data obtained from the downscaled climate model simulation outputs throughout the Holocene from Bristol Research Initiative for the Dynamic Global Environment (BRIDGE; bridge.bristol.ac.uk) were used in the SDM.

Chapter 6 reviews the conventions' and directives' texts as publicly available from their respective depositories and secretariats at: Convention on Biological Diversity (cbd.int/convention/text/), World Heritage Convention (whc.unesco.org/en/conventiontext/), Ramsar Convention (ramsar.org), Convention on Migratory Species (cms.int), Bern Convention (coe.int/en/web/bern-convention), and the Habitats (Council of the European Communities, 1992) and Birds Directive (European Parliament and Council of the European Union, 2009).

2
Review of approaches and methods

This thesis and the knowledge gaps highlighted above are based on biodiversity conservation approaches depending on trade-off decisions between resource use, overarching concepts such as protected area designations, and prior use of these approaches in biodiversity conservation planning. Additionally, ecological niche concepts are playing a key part in the data used and in informing the methods applied, such as species distribution modelling.

2.1 Conservation

2.1.1 Resource scarcity and trade-offs

Natural resources, including biodiversity, continue to decline, and as such, scarcity management is needed in order to stabilise the current inventories wherever and whenever possible. The overuse of common resources[1] in the recent past is pressuring

[1] The *Tragedy of the Commons* was the title of Hardin's seminal paper which, building on William Forster Lloyd (1833), highlighted the risks of common-use resources. The central point of diverging personal (maximum gain/yield) and public interest (long-term sustaining of the resource) is especially eminent in non-exclusionable goods such as environmental benefits. While it is advantageous for the community to retain the resource, the individual can increase personal gain through increased extraction. This freeriding imposes the social cost of the resource on all other parties while the freerider is still profiting from the communal action. Relaying the economic notion to biodiversity as a common-good resource certain social costs are incurred and since it is economically advantageous for the individual actor to go against the common good, further exploitation would be rational unless costs through e.g. fines are imposed on the actors (Coase, 1960; Hardin, 1968)

the resilience of natural systems and threatening persistence of biodiversity (Davies and Rangeley, 2010; Hardin, 1968). Conservation decisions are twofold: ecological and socio-economic. Whereas the former prioritises preservation (or restoration) of environmental conditions from a functional ecosystem perspective, coupled with the ideal of retaining all or most biodiversity present (Mace et al., 2012; Margules and Pressey, 2000; Wilson et al., 2009), the latter focuses on maximum yields and viable resource extraction regardless of the consequences beyond the anticipated extraction time frame (Greenstreet et al., 2011). To date "biodiversity planning is still rarely viewed as a political and economic process in which hard decisions are to be made on resource allocation and use" (Prip et al., 2010, p. 3). The current background to the conservation debate is marked by a lack of interlinking of viewpoints from science, economics, and politics (Holmes et al., 2017). Therefore, creating clearly defined areas in which management practices can be established to ensure persistence of common-good biodiversity is essential.

Gazetting land for conservation competes with e.g. agricultural land use or infrastructure development (Henle et al., 2008; Kiesecker et al., 2010; Moilanen and Arponen, 2011*b*). This resource scarcity forces the decision to either preserve an exact ecosystem (compositional approach) or preserve its functionality (functional approach), potentially with a varying species assemblage. Additionally, trade-off decisions need to be considered between the various options of land use: whether to spare, i.e. strictly delineating protected and non-protected land parcels, or to share, i.e. utilising a less restrictive matrix of both agriculture and conservation (Phalan et al., 2011). Considering Europe, land scarcity is driven by a combination of agricultural and infrastructural demands, as well as urbanisation (Henle et al., 2008; Mcdonald et al., 2008; Young et al., 2005). Encroachment on biodiverse land is highlighted by the increase of protected area downgrading, downsizing, and degazettement (PADDD) (Fuller et al., 2010; Mascia and Pailler, 2011). Placing conservation demands of land resources in the context of highly fragmented and industrialised landscapes, as is the case in Europe, marginal land is the choice with the lowest opportunity cost[2] for conservation. The choice of location and spatial requirements of conservation combined with the key notion of resource limitation and the economic consequences of choice scarcity not only embeds conservation firmly as a scientific, but also as a socio-economic question (Holmes et al., 2017).

2.1.2 Conservation concepts

The mismatch of species, habitats, and ecosystems distributions on the one hand and political entities on the other is both a continued challenge and opportunity. Biodiversity conservation approaches and requirements differ since they are based on land available for conservation and species of concern. In general terms, conservation is considered to be "a series of measures required to maintain or restore the natural habitats and the populations of species of wild fauna and flora at a favourable status" (Council of the European Communities, 1992, Article 1). A wide variety of measures and tools are utilised for conservation which act both as transient measures and within designated spatial boundaries. Protected areas, which are defined as a "geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (Dudley, 2008, p. 9) are a cornerstone within conservation (Cabeza and Moilanen, 2001; Mascia and Pailler, 2011).

Many of the current areas are based on traditional notions such as 'wise use' of natural resources, or creating areas to preserve 'natural beauty' or 'wilderness' formed in the 19th century (Pinchot, 1910). The current, skewed distribution of protected areas stemming from these traditional notions is to be regarded as a historic relic with the increased designation of formally protected areas since the late 1940s and early 1950s (Chapin et al., 2010; Mascia and Pailler, 2011). The progression of conservation priorities from aesthetic to socio-economic ones highlights

[2] If several, mutually exclusive, options are available, the opportunity cost is the highest-yielding potential option foregone. Choice scarcity dictates that even if more than two alternatives are available, only the second most yielding option rather than the sum of the foregone yields is taken into account. For biodiversity conservation agricultural use/yield of the land or infrastructure development of the area are often considered as opportunity costs (Adams et al., 2010; Balmford, 2002; Carwardine et al., 2008)

the predominant structured approach, though the lack of consistent large datasets can seriously undermine conservation assessments (Ladle and Whittaker, 2011).

2.1.3 Protected area planning

Initial conservation designations supported a patchy set of protected areas which focused on specific but individual and independent arguments for protection. A continuation of such a conservation regime does not necessarily contribute to biodiversity persistence (Pimm et al., 2014). Historically protected sites can be seen as initial network nodes which need to be reassessed to ask whether the original designation is still warranted and if their current locations still support the persistence of biodiversity when accounting for dynamic shifts (Araújo et al., 2005*b*; Fuller et al., 2010; Rose and Burton, 2009; Thuiller, 2004). The background to the current network reflects the lack of overarching planning and incorporation of large-scale data and knowledge of ecological processes (Araújo et al., 2011; Hannah, 2008). Designation procedures vary between authorities, and the considerations for gazetting depend on various environmental framework agreements or existing conservation regimes (Araújo et al., 2011; Battisti, 2013; Battisti and Fanelli, 2015). The devolution of political powers impacts the implementation of large-scale conservation planning (Erasmus et al., 1999; Kark et al., 2015). Given the shortcomings of current knowledge of species' distribution, performance within their ranges, potential shifts thereof, and vulnerability through time, the precautionary principle is adopted to avoid negative impacts on the environment (Cameron and Abouchar, 1991).

Different approaches have been used in order to identify specific highly-biodiverse areas across the globe (Kreft and Jetz, 2010; Myers et al., 2000). The imbalance between threatened habitat type and location of protected areas in conservation is increasingly visible when assessing the current networks at large spatial scales. Identification of areas of high biodiversity allows efforts to be concentrated, but also showcases the imbalance of so-called mega-diverse countries and their respective socio-economic abilities to protect such biodiversity (Brooks et al., 2006; McDonald et al., 2015; O'Connor et al., 2003). Overall, a *status quo* of targeting areas for protection based on current species and habitat inventories rather than accounting for current and future contribution of the area under shifting climatic conditions is apparent (Lindner et al., 2010; McCarthy et al., 2011). Such an approach follows the notion of creating a representative sample of the current distribution of biodiversity with no regard for spatial and temporal fluidity (Schloss et al., 2011). Therefore, the effectiveness and efficiency of the current protected area network in light of changing climate has been questioned (e.g. Araújo et al., 2011) since little is known generally about the success and effectiveness of networks around the world in terms of preserving biodiversity (Rodrigues et al., 2004; Rose and Burton, 2009). It is noted that a conservation area can serve as an extinction avoidance refuge (Naidoo et al., 2008; Ricketts et al., 2005).

Spatial requirements of protected areas are based on ecological necessities: certain species or populations (or assemblages of them) require a distinctive minimum size in order to persist (Cabeza and Moilanen, 2001). The Single Large Or Several Small (SLOSS) debate covers arguments for and against a single large protected area versus a network of several small ones (Diamond, 1975; McCarthy et al., 2011). Key arguments in the debate are species retention within a given area, the species' dispersal capacity, local extinctions, or migration to new areas, as well as the assessment of meta-population dynamics (Cabeza et al., 2004; McCarthy et al., 2011). While the overall aim of preserving biodiversity does not change, the individual target species' dynamics have a significant impact. Species at risk of extinction in small or fragmented habitat patches are favoured in a network with few but significantly-sized protected areas. Others with a more dispersed range are better supported by a larger network with numerous sites. As such, the ideal number of protected areas in a network can vary greatly as both large patches and smaller stepping-stones are needed to facilitate dispersal, migration, and habitat support (Ladle and Whittaker, 2011). Spatial needs can be represented through proxy as indicated in concepts such as umbrella, keystone, or flagship species (Edman et al., 2011; Fleishman et al., 2000). The underlying assumption in these approaches is that habitat for species not explicitly protected will be provided by the protection of the flagship species' provisions (Andelman and Fagan, 2000; Rodrigues et al., 2004). Arguably protecting e.g. certain forest taxa or habitat types in general will support a potentially large number of other species. Furthermore, this allows utilising more readily available data for e.g. conservation planning tools such as trans-boundary distribution modelling (Chapter 3 and Chapter 5). Currently conservation decisions tend to be made in political fora, taking little account of the value of ecologically consistent approaches which use natural delineations rather than political borders. The latter, in most cases, only represents a subset of the ecological reality (e.g. Keenan et al., 2011; Raes, 2012; Serra-Diaz et al., 2012). This sub-optimal procedure leads to restricted planning opportunities, inefficient resource use, and potentially unsuitable protected area selection heavily based on political requirements (Moilanen and Arponen, 2011*b*). In addition to the *status quo* issues posed for conservation, climate change and its induced range shifts add further stress to the existing system. Furthermore, selected protected areas are seldom considered on grounds of long-term economic viability. These issues highlight the current short-termism and disjunction of the individual academic disciplines involved in conservation research. A dynamic and less politically opportunistic conservation approach is necessary to support more effective conservation. A triage of conservation concepts in order to establish whether they are still applicable to the available knowledge, financial resources, and ongoing changes in climatic conditions and entailing land use requirements is needed. Overall, current conservation research output has the potential to be more successfully used in an interdisciplinary context incorporating economic paradigms and politics (Brooks et al., 2006; Gorenflo and Brandon, 2006; Henle et al., 2008).

2.2 Niche concept

The natural environment can be conceptualised as a multifaceted and multi-dimensional space which incorporates innumerable interactions. The environmental conditions required by a species are considered a species' niche termed by Hutchinson as "the sum of all the environmental factors acting on the organism; [. . . which] is a region of an n-dimensional hyper-space" (Hutchinson, 1944, p. 20). The *Hutchinsonian* niche, which is delineated by environmental conditions and resources, stems from Grinnell's niche concept (Grinnell, 1917*a*,*b*). Additionally, functional adaption of an organism to its position within the ecosystem and conditions present is known as the *Eltonian* niche (Elton, 1927; Soberón, 2007; Soberón and Nakamura, 2009).

Abiotic factors are considered to underpin biodiversity as resources facilitating and affecting life, including growth, maintenance, and reproduction (Chapin et al., 2011). They depend on and influence each other to a greater or lesser degree based upon both their temporal and spatial association as well as their modification by other factors, e.g. anthropogenic involvement. Modifications of abiotic factors can only be identified in respect of current understanding of the environment or with hindsight judgement of resulting past changes to e.g. persistence of species or assemblages. The availability of data on abiotic factors is thus key to establishing consistent knowledge of species' distribution potential. Biotic factors are not commonly considered owing to a general lack of large-scale data (Araújo and Guisan, 2006; Pearman et al., 2008*b*; Pressey et al., 2007).

The concept of the niche, as described by Hutchinson (1944), contains a dichotomy of fundamental and realised niche: in its strictest interpretation, a species' niche is limited only by the abiotic conditions and thus contains all environmental and physical tolerances. Competition for resources such as light and space, presence and absence of grazing etc. lead to a restricted realised niche of the species' fundamental niche (Araújo and Guisan, 2006; Hutchinson, 1957; Kearney, 2006; Pearman et al., 2008*b*; Soberón and Nakamura, 2009; Wiens, 2011). In addition to observed biotic competition, current occurrence data may also exclude previous climatic conditions which no longer exist and as such the species' current range may not represent its full distributional potential. Furthermore, biogeographic factors such as location and natural dispersal limitation influence occurrence, too (Soberón and Peterson, 2005). Consistent and large-scale niche data supports biodiversity research as it allows detailed and robust assessment of changes in species distribution.

2.3 Distribution modelling

The fundamental concepts of *Grinnellian* or *Hutchinsonian* ecological niches, i.e. conditions preferred or habitat occupied by certain taxa which may even outcompete others with similar preferences, form the base principles of species distribution or environmental niche modelling (Grinnell, 1917*a*,*b*; Hardin, 1960; Hutchinson, 1944, 1957; Soberón, 2007, SDM;). SDM operates by estimating the probability of presence of a species based on the correlation between known species' occurrences and corresponding bioclimatic variables (Guisan and Zimmermann, 2000; Pearman et al., 2008*b*). SDM acts as an informed alternative to large-scale consensus data (Austin, 2002). Computer-based modelling techniques can support re-assessment and re-design of conservation networks in Europe. During the last decade, SDM has both been further developed and utilised as a prominent tool for environmental research (Araújo and New, 2007; Broennimann et al., 2012; Guisan and Thuiller, 2005; Pearman et al., 2008*b*).

An identified range of relevant and preferential climate conditions for a species is commonly termed 'climate space' in modelling. Once the initial correlation has been established, the model's result can be used to project or predict the species' occurrence in other bioclimatic datasets, as it is done in e.g. forecasting future distributions (Carvalho et al., 2011; Thuiller et al., 2008). This also allows utilising SDM to provide insight into large-scale ecological patterns and shifts thereof (Thuiller et al., 2009). Therefore, these natural interactions throughout time can be represented by computer-based modelling techniques in order to contribute to conservation research and management. Because SDM largely utilises current occurrences it is argued that it predominantly encompasses realised niche space (Araújo and Guisan, 2006; Sillero, 2011).

Furthermore, modelling is based on environmental equilibrium, i.e. that every species present has reached its full potential in dispersal and is occupying its maximum range (Kearney, 2006; Sillero, 2011; Williams et al., 2013). Both distribution ranges and bioclimatic conditions vary over time. Tolerable or preferred habitat space may temporarily or permanently disappear or geographical space with favourable conditions may be restricted through physical barriers which prevent dispersal into suitable areas (Soberón and Peterson, 2005). Therefore, current occurrence data only outlines a truncated portion of the species' fundamental niche and creates potential shortfalls due to restricted data (Beale and Lennon, 2011; Veloz et al., 2012). Environmental equilibria are subject to change due to fluctuating bioclimatic conditions which in turn influence the persistence of the species in its full environmental range. Adaptive capacities indicated by past distributions and entailed resistance to change in environmental conditions expand the climate space incorporated into the model itself and partially alleviate e.g. the shortfall of stable niche assumptions (Martinez-Meyer et al., 2004). Therefore, multi-temporal data allows assessment of dispersal regimes throughout time and can validate equilibrium assumptions between species occurrence and environmental conditions (Broennimann et al., 2012; Pearman et al., 2008*b*). Utilising SDM also enables species persistence through time to be highlighted regardless of current occurrence and assumptions about vulnerability (Aitken et al., 2008; Thomas et al., 2004).

The models employed are heavily dependent on initial assumptions of niche availability, competition, and habitat retention over time. Any data used for SDM needs to represent bioclimatic factors and ecological gradients or thresholds sufficiently in order to support a robust predictive capacity (Araújo and New, 2007; Beale and Lennon, 2011; Veloz et al., 2012). Spatial and temporal data allows for minimising niche truncation thus supporting a more robust modelling approach. Within conservation strategies under climate change scenarios, it is paramount to consider distributions of species and their ability to retain habitat space or their migration capacity to future ranges (Araújo and Guisan, 2006; Pressey et al., 2007). Niches through time may highlight the likelihood that bioclimatic conditions appearing to be threatening or novel to species have in fact been present throughout different periods of time, e.g. the Holocene, and can therefore be accounted for. Therefore, any progress in understanding niche dynamics and providing more consistent and coherent large-scale datasets are essential to the ongoing success of

SDM.

2.4 Conservation data

The availability of data throughout Europe is variously layered. Large-scale data sources independent of political borders allow for ecological assessment of data without resolution or sampling relicts due to geo-political restrictions (Kark et al., 2015). Nonetheless, present-day data is the most used option and is assembled by both international networks and national inventories. Successful regional co-operation in data gathering for conservation is highlighted by e.g. EUFORGEN. Furthermore, national inventories allow detailed assessment with rich local knowledge for spatially analogous questions. Multi-temporal data availability for conservation questions is based upon either modelled assessments or, in case of past distributions, palaeo-ecological analysis of e.g. fossil pollen.

Databases such as EUFORGEN are set up as cross-border resources in order to facilitate protection of species throughout their range by retaining key genetic variance as well as persistence throughout their current range. The database was chosen to provide background data for the work at hand due to its direct embedding in the scope of the Ministerial Conference on the Protection of Forests in Europe and thus reflecting both scientific and politically overarching conservation background. The restricted number of species currently held in the database (107 entries, 47 with distributional data attached) is dependent on their respective exposure to threats both at species as well as individual population level (Koskela, 2013). Databases do not necessarily incorporate all species of a genus nor is the data provided suitable for all research undertakings. The species set represented by EUFORGEN is a broad cross-section covering multiple bioclimatic areas, habitat preferences, both deciduous and coniferous taxa, and various levels of conservation necessity.

While palynological data can provide insights into past distribution patterns, fossil pollen availability is limited by its preservation, the availability of suitable geographic features for sedimentation (e.g. lakes, wetlands, swamps) (Birks and

Birks, 1980), and research sampling bias. Furthermore, palaeo-ecological pollen data provides a coarser taxonomic resolution compared to present-day data due to the inability to identify pollen spores to consistently to species level. Therefore, analyses based on genus-level taxonomic resolution due to incorporation of palaeo-ecological data incorporate a wider variety of niche representation and potential inflation of traits due to a more generic approach (Hendricks et al., 2014).

Thus the following research on effects of truncated data use in SDM, issues of national budgets for biodiversity conservation, temporal dynamics of biodiversity using palaeo-ecological data, and the long-term suitability of environmental framework is embedded in the approaches outlined above.

3
Unstable response functions in SDMs

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3.1 Abstract

Aim: Species distribution models (SDMs) are commonly used to determine biodiversity threats and opportunities under climate change. Despite SDMs being based on the assumption of complete knowledge of the climate space of the modelled species, truncated occurrence datasets (and hence truncated climate spaces) such as national inventories are often employed. This may lead to prediction errors, which have been proposed to stem from 1) the degree of climate space truncation and/or 2) instability of modelling algorithms. Our aim was to explore potential causes of prediction errors in SDMs based on using truncated training data sets.

Location: Europe 11°W – 32°E, 34° – 72°N

Methods: SDMs were applied to seven forest tree species employing commonly used bioclimatic variables. We created two model training data sets covering 1) Germany only (significantly truncated climate space) and 2) Europe (minimally truncated climate space). Differences between the climate space represented by Germany-only and European data were measured on two-dimensional climate spaces obtained through principal component analysis of the bioclimatic variables. Seven SDM algorithms were run, and response function stability and variable selection for each species and model type were analysed.

Results: The degree of climate space truncation was less important for model performance than the instability of model algorithms and indiscriminate variable selection. The latter led to irrelevant relationships of species occurrence with bioclimatic variables. These instabilities caused pronounced prediction errors.

Main conclusions: Our results strongly suggest that erroneous model predictions stem from instability and ecological irrelevance of the statistical functions relating species probability of occurrence with bioclimatic variables, compounded with a lack of consistency in variable selection. Models displaying these characteristics

showed lower overall performance when trained with truncated data sets. Further, commonly used ensemble approaches do not compensate the shortfalls of individual models. Detailed model-by-model, species-by-species analysis of response functions and variable importance is recommended.

3.2 Introduction

In order to successfully conserve biodiversity, the potential impact of climatic change on species needs to be accounted for, and both current and future distributions assessed (Araújo and Rahbek, 2006). Species distribution modelling (SDM, a.k.a. environmental niche modelling or bioclimatic modelling) is frequently employed to determine changes in species' distribution patterns in response to climate change and to assess potential threats – or resilience – in the light of loss of suitable climate space (Araújo et al., 2011; Milad et al., 2011; Thomas et al., 2004). Such models are routinely used to provide insight into large-scale ecological patterns and niche behaviour under environmental or climatic change (Thuiller et al., 2009).

Due to their comparatively easy implementation and low data requirements, SDMs are often utilised in 'bulk' modelling of vast numbers of species (Araújo et al., 2011; Thuiller et al., 2014). They are based on the notion of environmental niche as conceptualised by Hutchinson (1957) and are built by statistically linking species occurrence and environmental (most often bioclimatic) data, identifying an n-dimensional space contained within a set of relevant and preferential climate conditions commonly termed as the 'climate space' of the species. Once fitted (or calibrated, or trained), models can be projected onto other datasets comprising environmental/bioclimatic parameters for future or spatially different scenarios in order to study potential spatial and/or temporal distributional changes (e.g. in case of future distribution projections or invasive species acquiring new ranges; Carvalho et al., 2011; Pearman et al., 2008*a*; Spangenberg et al., 2012; Thuiller et al., 2008).

A basic assumption in setting up SDMs is that the full climate space of the modelled species is observed and incorporated into the training dataset. Yet, in many cases SDMs are constructed using data derived from reduced datasets (e.g. individual countries) that may not coincide with their full present geographical ranges, and/or occurrence data may be incomplete. As a consequence, conservation recommendations stemming from their use are often based on a truncated bioclimatic niche space, which is used to infer current and future distribution areas regardless

(Bertrand et al., 2012; Broadmeadow, 2005; Bálint et al., 2011; Edman et al., 2011; Keenan et al., 2011; Raes, 2012; Serra-Diaz et al., 2012). The extent to which the use of these truncated datasets may influence conservation recommendations is, as yet, unknown.

Palaeo-ecological studies on past distributions of several taxa highlight the very distinct possibility that even in the case where the full present geographical range of a given species is known, its full bioclimatic space might remain unknown (e.g. Veloz et al., 2012). This might be due to anthropogenic activities (Willis and Birks, 2006), insufficient post-refugial dispersal time, physical dispersal barriers (Soberón, 2007), or to the ability of the species to tolerate climatic conditions that are not observed now but that occurred in the past (non-analogous climate; Williams and Jackson, 2007). Thus, even in best-case scenarios, we are left with uncertainty as to this basic assumption in SDMs, making it a more general problem than is often realised.

Poor model performance stemming from the use of training data sets where the full bioclimatic range of the species is not included is thought to result from 1) the inability of statistical SDMs' to forecast species occurrence probabilities into non-analogous climate space (e.g. Harrison et al., 2006; Rodríguez-Castañeda et al., 2012; Williams and Jackson, 2007) and/or 2) the instability of model algorithms, as seen in unstable response functions – where the true relationship between the probability of species occurrence and climate is not properly captured – and in arbitrary variable selection (Araújo et al., 2005*b*; Barbet-Massin et al., 2010; Thuiller, 2004; Thuiller et al., 2004). In the former, maximizing as much as possible the climate space used in the training data would reduce the chance of SDM errors, whereas in the latter the reasons for response function instability and arbitrary variable selection – and whether they are at all related to truncation of the species climate space in the training data – would need to be established. Thus, although being widely discussed (e.g. Soberón, 2007), the statistical causes of such errors have not been extensively studied, especially when using (as often is the case) truncated datasets (e.g. Keenan et al., 2011; Serra-Diaz et al., 2012; Thuiller et al., 2014).

Ensemble modelling has been proposed as a compromise in order to encompass some of these issues (Araújo and New, 2007). This approach consists of combining output from multiple models – by e.g. averaging predicted occurrence probabilities – to provide more robust projections or forecasts of distributions, and stems from the ensemble methods employed in climate modelling (Araújo and New, 2007; Thuiller et al., 2009). The ensemble modelling approach assumes that individual model errors are minimised in favour of a common inter-model signal, and that averaging potentially very different response functions will result in clearer model predictions. However, this is based on the assumption that the response functions in each individual model are broadly correct and reflect the relationship between species and bioclimatic variables. If this were not the case, ensemble averaging of models with unstable response functions could potentially result in an addition of noise.

The aim of this study was thus to understand the shortfalls of species distribution modelling when using truncated training datasets. We evaluated two explanations for prediction errors in SDMs, namely (1) the effect of climate space – i.e. how well do the models perform outside of the bioclimatic niche space represented in a truncated dataset on which they were trained and (2) the effect of model algorithm choice – affecting variable selection and response function stability i.e. how does the use of a truncated dataset influence the description of the relationship between the individual species probability of occurrence and its bioclimatic variables. We then discuss the implications of our results for use of ensemble modelling approaches.

3.3 Data

Continental Europe (EUR, 11°W – 32°E, 34° – 72°N) provides an ideal study area as it contains eight biogeographic regions (Alpine, Atlantic, Black Sea, Boreal, Continental, Mediterranean, Pannonian, and Steppic regions) and thus a strong gradient of bioclimatic factors and a concurrent spatial turnover in species distributions. This diversity of bioclimatic factors is an important requirement for SDMs if they are to be a useful tool for e.g. future-oriented conservation planning in the face of climate change (e.g. Carvalho et al., 2011; Margules and Pressey, 2000; McMahon et al., 2011; Moilanen et al., 2009; Pearson and Dawson, 2005; Wilson et al., 2005). Germany was chosen as a political entity to truncate occurrence data (GER). This is because Germany contains coverage from the Atlantic biogeographic region in the northwest, the Continental region mainly throughout, and the Alpine region at its southern end, and it therefore covers several bioclimatic zones.

Occurrence data from seven forest tree species with a distribution within Europe and including presence in Germany was obtained from the European Forest Genetic Resources Programme (EUFORGEN, http://www.euforgen.org/). The use of international distribution data such as provided by EUFORGEN is key in order to be able to sufficiently manipulate the dataset into truncated and non-truncated modelling data. Since the data is provided across the ecological range disregarding political entities, potential sampling legacies which may be the case within national datasets, are not an issue. Additionally, use of national inventory data would depend on consistent sampling efforts, consistent methodology applied to all sampling, and availability throughout the range in order not to incur artificial truncation due to political borders. These were: silver fir (*Abies alba* Mill.), sycamore (*Acer pseudoplatanus* L.), beech (*Fagus sylvatica* L.), European larch (*Larix decidua* Mill.), pedunculate oak (*Quercus robur* L.), service tree (*Sorbus domestica* L.), and European white elm (*Ulmus laevis* Pall.). The selection of these species was chosen in order to encapsulate both deciduous and coniferous species with the combined ranges covering as much of Europe as possible. Highly competitive and far reaching species such as *F. sylvatica* and *U. laevis* were complemented by alpine species and those reaching further into southern Europe (*A. alba* and *L. decidua*), while *S. domestica* represented a weaker competitor species with high light demands and distribution in a more open landscape matrix. If covering a larger area than Europe (as in the case of *A. pseudoplatanus* that has a disjointed population in the Caucasus), *Q. robur* (fragmented population in Western Russia and the Caucasus),

	Dataset		EUR training data			GER training data		
	Presences	Absences	GDD	Pre	Presu	GDD	Pre	Presu
A. alba	2215	28,215	0.269	0.292	0.937	0.171	0.343	1.017
A. pseudoplatanus	7967	22,463	0.637	0.328	0.635	0.311	0.410	0.614
F. sylvatica	5871	24,559	0.577	0.440	0.350	0.316	0.899	0.195
L. decidua	1237	29,193	0.191	0.322	0.985	0.013	0.034	1.014
Q. robur	13,871	16,559	0.681	0.152	0.448	0.984	0.367	0.437
S. domestica	5579	24,851	0.630	0.392	0.371	0.491	0.645	0.608
U. laevis	10,753	19,677	0.621	0.228	0.658	0.578	0.406	0.769

Table 3.1: SDM Variable Importance. Presence and absence data within the dataset for each species are shown in the first two columns. The following columns depict the importance of each individual variable within the ensemble species distribution models for each of the seven species modelled. The importance of each variable was calculated as 1 – [the correlation between the predicted probability of presence made by (1) a model including all variables except for a randomised target variable, and (2) a model employing all variables]. Note that for some species (e.g. *Acer pseudoplatanus*, *Fagus sylvatica*, *Sorbus domestica*) no clear indication of consistent variable selection can be identified, whereas for some others (e.g. *Larix decidua*, *Abies alba*) variable importance is consistent across the training datasets. GDD, growing degree days; Pre, annual precipitation; Presu, summer precipitation.

and *U. laevis* (continuous distribution in Western Russia), the distribution was minimally clipped according to the designated extent of Europe. EUFORGEN supplies presence and absence data as high-resolution shapefiles which were gridded according to the 10’ spatial grid used by the bioclimatic variables. This created a presence/absence matrix throughout Europe for each individual species (Table 3.1; 30,430 presence and absence data points).

Bioclimatic data for 1901 – 2000 was obtained from the Climate Research Unit (CRU, http://www.cru.uea.ac.uk/). Widely used bioclimatic variables reflecting ecological requirements for forest tree species were employed in the modelling exercise (Prentice et al., 1992). These were: annual precipitation (mm), summer precipitation (mm; June, July, August), winter precipitation (mm; December, January, February), mean annual temperature (°C), minimum temperature (°C), mean summer temperature (°C; June, July, August), growing degree days (GDD; days above 5°C), and equilibrium evapotranspiration (mm).

3.4 Methods

Seven statistical algorithms commonly used in SDM were employed in this study. These were: artificial neural networks (ANN), classification tree analysis (CTA), generalised additive model (GAM), generalised boosted model (GBM), generalised linear model (GLM), multiple adaptive regression spline (MARS), and random forest (RF). In these models, each species is represented by its n-dimensional climate space delineated by the bioclimatic variables. Models were run separately using non-truncated (EUR) and truncated (GER) training data sets. The Biomod R package (Thuiller et al., 2009) was used to run the model algorithms.

In order to avoid collinearity between the model covariates, only growing degree days, annual precipitation, and summer precipitation were used (Elith and Leathwick, 2009; Prentice et al., 1992) after a correlation matrix of all the bioclimatic variables was used to exclude highly correlated pairs of bioclimatic variables (r^2>0.65). Each model run was repeated three times for each species: all models were run using a 70% random sample as calibration and a 30% random sample as validation data (cross-validation) (Breiman, 1993). These random splits differed for each of the iterative runs. These iterative runs are common practice and are designed to provide the best possible insights given the limited data available. Predicted probabilities of occurrence were transformed into presence-absence predictions by selecting a cut-off probability value for each model type and species that would maximise model performance. Area Under the Curve of the Receiver Operating Characteristic statistic (AUC), Cohen's Kappa, and True Skill Statistic (TSS) were evaluated (Allouche et al., 2006; Hanley and McNeil, 1982; Monserud and Leemans, 1992).

3.4.1 The effect of climate space

We hypothesised that models for species whose climate space had been severely truncated by the choice of Germany as a training data set (that is, species with a total climate space encompassing conditions far from those observed in Germany only) would perform worse than models for species whose climate space was more similar to the conditions experience in Germany only. For example, the climate space of a species with a range restricted to central Europe will suffer from a smaller loss of information if only the climatic conditions observed in Germany are considered than that of a species with a range encompassing central and southern Europe, and this loss of information should result in poorer model performance. The association between the degree of truncation in the training data set and model performance was thus tested by comparing the performance of SDMs trained with truncated (GER) and non-truncated (EUR) data sets with the degree of climate space truncation in the training data.

A principal component analysis was computed on all the bioclimatic variables (EUR extent) to reduce the dimensions of the bioclimatic dataset and simplify the calculation of climate space extent and truncation. The two largest principal components were temperature and water availability – accounting respectively for 62.41% and 27.95% of the total variance (i.e. 90.36% of the total variance combined). These two variables were then used to compute climate spaces for both the EUR and the GER datasets (Barbet-Massin et al., 2010) (Supplementary Materials Figures A.1 and A.2).

For each species, occurrences were projected onto the two-dimensional climate space. We applied the following measurements: percentage overlap between EUR and GER climate space areas (defined as the convex hull of the climate space), percentage overlap between EUR and GER occurrence points, distance between the EUR and GER climate space centres of density, and distance between the EUR and GER geometric centroids (Table 3.2). Measurements were then repeated with rarefied datasets in order to exclude potential bias in natural climate space availability of the occurrence data (Broennimann et al., 2012).

3.4.2 The effect of model algorithm choice

The choice of the modelling algorithm has been shown to affect model performance and predicted distributions (Araújo et al., 2005*a*). Model algorithms determine the characteristics of the response functions, which attribute values of probability of

	AUC	KAPPA	TSS	Climate space		Overlap (%)	
				Gravity	Geometric	Area	Points
L. decidua	0.884	0.518	0.704	0.585	1.226	15,608	16,087
S. domestica	0.715	0.257	0.398	1.262	2.212	7093	5180
A. alba	0.659	0.117	0.332	0.308	1.751	10,598	19,233
Q. robur	0.641	0.301	0.326	0.253	3.498	6994	11,391
F. sylvatica	0.629	0.158	0.266	0.097	1.840	12,874	21,240
A. pseudoplatanus	0.597	0.194	0.230	0.242	1.782	11,392	14,924
U. laevis	0.554	0.226	0.257	0.429	1.332	11,169	9,328

Table 3.2: SDM Model performance. Measurements of model performance and climate space for all species. AUC, Cohen's Kappa, and TSS are given for comparison of the ensemble models for GER training data (Germany only) projected onto Europe (see Data 3.3 and Methods 3.4). Geometric distance between the centre points of the convex hulls of each species' training data sets has been calculated. The same convex hull delineation was used to calculate the climate space area. Note that there is no clear relationship between measurements of climate space and model performance.

species presence within the climate space. Likewise, model algorithms determine the selection of and the weight given to the bioclimatic variables used as predictors for species occurrence. Poorly performing models may show erratic response curves and variable selection. We thus assessed response curves and variable selection for each individual model and species for three scenarios: GER projected onto GER (significantly truncated, analogous); GER onto EUR (significantly truncated, non-analogous); and EUR on EUR (minimally truncated, analogous).

Response functions were examined for each individual model and for each species and scenario respectively as well as averaged for the species on the whole in an ensemble approach (Araújo and New, 2007). They consist of functions that estimate, for each species and bioclimatic variable, probabilities of occurrence along the climatic gradients defined by the range of climatic conditions observed in the training data sets. The ensemble projection consisted of a weighted average of model outputs according to model performance statistics. In order to maximise sensitivity-specificity sums and minimise their difference, the ensemble models were weighted according to AUC (Hanley and McNeil, 1982).

Variable selection and weighting can be assessed by the statistic 'variable importance', which is calculated as "1-(*the correlation between the estimated probability* *of presence made by a model including all variables except for a randomised target variable, and a model employing all variables*)" (Thuiller et al., 2009). According to this, low variable importance scores (e.g. <0.3) indicate high degrees of correlation between the two model predictions – that is, the inclusion or exclusion of the target variable does not affect the overall model forecast, indicating low variable importance, and vice versa. Variables showing low importance typically have very low weight/loadings and hence do not contribute to SDM predictive ability.

The joint analysis of response functions and variable importance provides information on the effects of the choice of model algorithm. In the worst case scenario, a model algorithm might produce response functions not reflecting any real relationship between a bioclimatic variable and the probability of occurrence of a species (e.g. overfitting), and at the same time attribute a large importance to this bioclimatic variable, magnifying the biased response function and resulting into completely erroneous predicted species distributions.

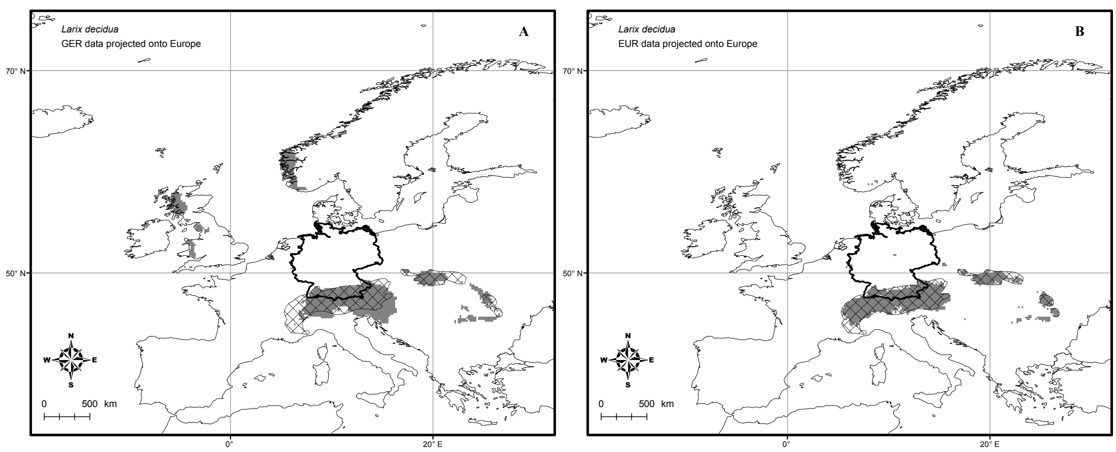

Figure 3.1: *Larix decidua* distribution. Predicted distributions over Europe (grey) for *Larix decidua* yielded by modelling according to the two distinct training data sets of Germany-only (GER) (**A**) and full European area (EUR; see Data 3.3 and Methods 3.4) (**B**). A bold black line highlights the political boundaries of Germany. The probability of occurrence was converted to binary presence/absence by choosing a threshold which optimises the model's AUC statistic. **A** highlights a small degree of overpredictions in case of truncated training data (GER) being extrapolated on continental scale. **B** shows the predicted distribution if a more complete spatial data set is used (EUR) for continental scale predictions. The observed current occurrence of *L. decidua* is indicated by the crosshatched area.

3.5 Results

3.5.1 The effect of climate space

Model performance statistics did not show any consistent relationship with the proportion of climate space occupied by the truncated GER vs. the non-truncated EUR data sets, as measured by distances between centres of gravity, geometric centroids, or area or presence overlap (Table 3.2). This suggests that the degree of climatic truncation in the model training data was not a decisive factor to explain prediction uncertainties.

3.5.2 The effect of model algorithm choice

Response function instability and variable importance were shown to contribute to important differences in model performance for all seven species used and thus to influence final predictions of species occurrence, especially when using a truncated data set. Examples highlighting these findings are illustrated in the output for the following species:

i. *L. decidua* displayed consistent results with largely accurate predictions both under truncated (GER) and full-scale (analogous – EUR-trained projected on EUR – and non-analogous – GER-trained projected on EUR) bioclimatic training data (Figure 3.3, Table 3.2). Each of the individual models suggested robust variable selection identifying summer precipitation as key in both truncated and non-truncated projections (Figure 3.2A). Although the spread of predictions increased in wetter summer conditions, all models agreed in assigning a zero probability of *L. decidua* presence in dry summer locations, and suggested a threshold along the summer precipitation gradient (Figure 3.2A, C and Supplementary Materials A). Although the response functions of the remaining model bioclimatic variables portrayed erratic behaviour, variable importance for these variables has very low (e.g. 0.013 for GDD, 0.034 for annual precipitation, *vs.* 1.014 for summer precipitation in GER training data, Table 3.1 and Figure 3.2A). This implied that the importance of summer precipitation and its stable response functions was able to override the influence of erratic response functions for unimportant variables in the final model prediction.

ii. The distribution of *A. pseudoplatanus* was largely successfully predicted in its current occurrence range throughout Europe when models were trained over EUR (analogous). However, large-scale false-positive forecasts were observed when a non-analogous projection was used (i.e. GER-trained projected onto Europe; Figure 3.3A, Table 3.2). Both individual and ensemble response functions showed erratic behaviour (best seen in Figure 3.2B, D, and Supplementary Materials A). Variable importance was also inconsistent between each of the separate model runs and types. No variable was identified as particularly important (Table 3.1). The standard error of the ensemble functions remained large, and the overall importance of variables with response functions that might contribute to good predictive ability was too low to mask the noisy predictive ability of the other bioclimatic variables (Figure 3.2B).

Importantly, the response functions for the individual algorithms demonstrated varying patterns even for the same species and the same training data. For example, when comparing models trained on GER and projected on EUR with those both trained and projected on GER, no stability of the response function was observed, even in the climate range area of GER (Figure 3.2 and Supplementary Material A).

3.6 Discussion

Species distribution modelling is based on the combined understanding of species occurrence data and its relationship to ecologically relevant climatic/environmental conditions in which it exists (its bioclimatic envelope). Whereas the truncation of the climate space – potentially restricting its true bioclimatic envelope – resulted in worse model performance under non-analogue conditions, a surprising result from this study was that poor model performance did not depend on the degree of truncation (i.e. we did not observe a positive or meaningful relationship between the degree of truncation and model performance) (Table 3.2). Instead, it was the combined effect of the response functions (i.e. the shape of the predicted relationship between the probability of species occurrence and its bioclimatic variables) and variable selection by the model algorithms that showed different behaviour in individual model runs, and this was the main factor responsible for poor SDM performance. Within this modelling exercise, the instability of response functions

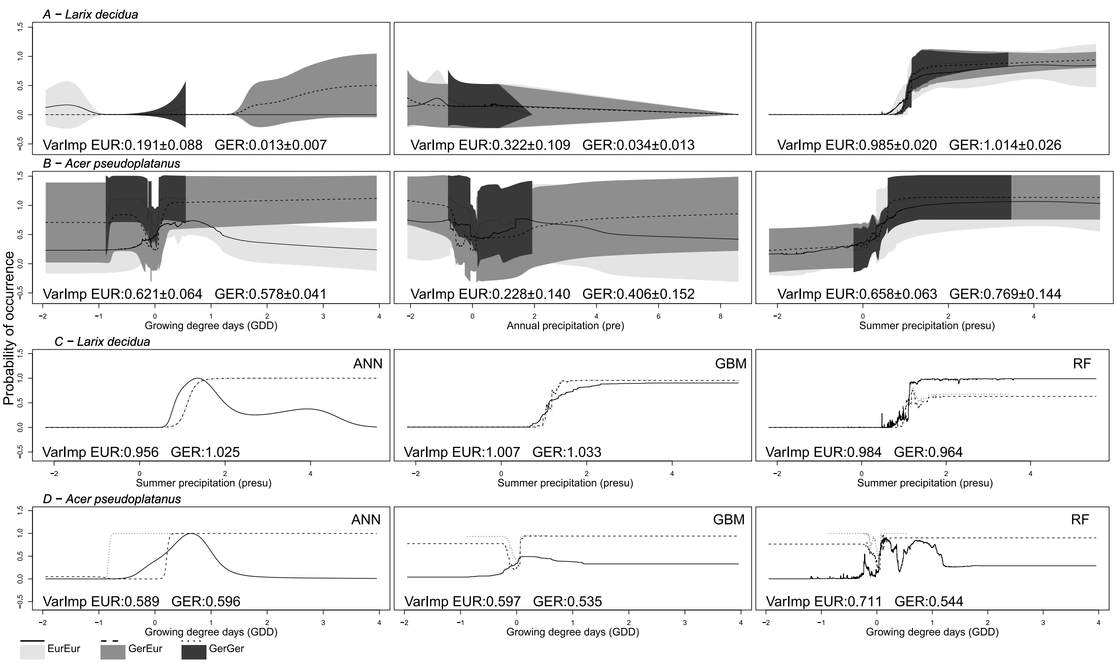

Figure 3.2: Response functions of *Larix decidua* and *Acer pseudoplatanus*. Ensemble and individual modelled response functions for *Larix decidua* and *Acer pseudoplatanus*. GER denotes Germany-only training data whereas EUR indicates training data over the full European area. For all figures the continuous line indicates EUR training data and prediction (EurEur), the dashed line shows GER training data and European prediction (GerEur), and the dotted line indicates GER training data and Germany prediction (GerGer). The variable importance (VarImp) is shown at the bottom of each panel. All variable units have been standardised. **A** shows the ensemble response functions for *L. decidua* for all three variables included in the models, their standard deviation (shaded areas: light grey for EUR predicted on EUR, dark grey for GER predicted on GER, grey for GER predicted on EUR), and the variable importance according to the training data used. **B** shows the same for *A. pseudoplatanus*. Note that in the latter case, large standard deviations and evenly spread values of averaged variable importance lead to over-fitting and largely ecologically unsound model predictions. **C** shows three individual algorithm response functions (artificial neural network - ANN, generalised boosted model - GBM, and random forest - RF) for summer precipitation for *L. decidua*, highlighting the overall consistency of function shapes and high variable weighting leading to consistent model predictions. **D** indicates the equivalent response functions for growing degree days for *A. pseudoplatanus*, showcasing erratic behaviour and irregular variable importance.

was therefore shown to contribute to significant errors in SDMs and to influence final predictions when using truncated data sets. Thus, the usefulness of SDMs dramatically dropped when the shapes of the functions describing the probability of presence along bioclimatic gradients changed depending on the training datasets used (Figure 3.2). Models showing these characteristics showed the worst predictive performance when trained with truncated datasets.

The characteristics of individual model algorithms can be clearly seen when the response functions are analysed (e.g. whereas algorithms based on smoothing functions will show smooth response functions, decision tree–based algorithms will tend to present step-like response functions). This not only allows the identification of common statistical fit, but also the assessment of ecologically sound threshold changes or optimums (Figure 3.2). Ecological soundness might ideally be assessed on the light of prior knowledge of the species ecology (e.g. Oksanen and Minchin, 2002), however identifying unsound response functions does not necessarily require this: an ecologically sound function depicting the probability of occurrence for a given species

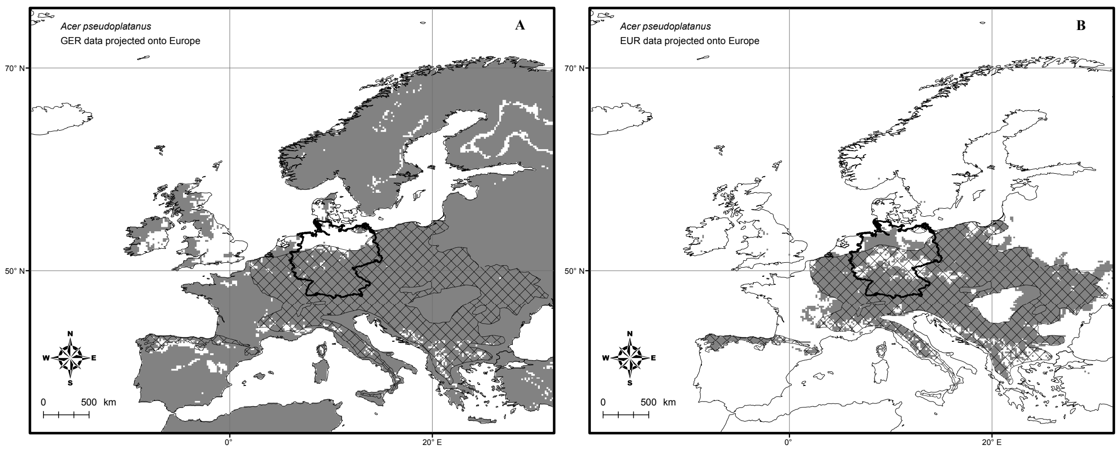

Figure 3.3: *Acer pseudoplatanus* distribution. Predicted distributions over Europe (grey) for *Acer pseudoplatanus* yielded by modelling according to the two distinct training data sets Germany-only (GER) (**A**) and full European area (EUR; see Data 3.3 and Methods 3.4) (**B**). A bold black line highlights the political boundaries of Germany. The probability of occurrence was converted to binary presence/absence by choosing a threshold which optimises the model's AUC statistic. **A** highlights the vast overprediction in case of truncated training data (GER) being extrapolated on continental scale. **B** shows the predicted distribution if a more complete spatial data set is used (EUR) for continental scale predictions. Both maps indicate the observed current occurrence of *A. pseudoplatanus* as crosshatched.

across a bioclimatic gradient should not consist of several optima and minima, nor show strongly irregular shapes. This should be a warning against overfitting, or at least for model fitting of underlying processes beyond the explanatory reach of the bioclimatic variable being used (Austin, 2007; Oksanen and Minchin, 2002; Townsend Peterson, 2011). Overall, the shape and structure of the response functions allow an initial assessment of ecologically sound statistical model fit.

Although no clear cause for the erratic behaviour of the response functions was identified, response function stability (Figure 3.2A, B) coincided with variable selection; i.e. variables identified as important had more consistent response functions throughout all training data regimes and model types as shown by e.g. *L. decidua*. This would therefore suggest that a process to identify important variables can help to suppress erratic variable responses and allow successful prediction as in the case of *L. decidua*, for which summer precipitation (Figure 3.2A) has by far the highest influence and thus the irregular response functions of other variables are proportionally of no importance.

We also found that aggregation into ensemble predictions (see Figure 3.2A, B, Supplementary Materials A; Araújo and New, 2007; Thuiller et al., 2009) did not necessarily results in improved predictive ability. We examined all three available statistics (AUC, Cohen's Kappa, TSS; Table 3.2) as threshold values to optimise model performance. Regardless of the use of truncated or non-truncated occurrence data, all ensemble models indicated shortfalls. In many cases, there was no clear constraining or promoting signal for any of the species; instead an overall noisy prediction resulted due to the averaging of a series of data fitting exercises. Further noise was added to the ensemble models prediction through inclusion of models with indiscriminate variable importance. Ensemble averaging does not therefore necessarily provide more reliable predictions, and especially under non-analogous conditions, meaningless values of variable importance may lead to erroneous predictions. In this respect, the main limitation in the analogy between ensemble projections of physically-based climate models and those of statistical SDMs relies on the blindness of SDMs to capture ecological processes linking climate and species occurrence: in order to determine whether a given SDM might be capturing an ecological process and thus can be incorporated in an ensemble averaging, a close and critical inspection of its characteristics is needed.

Our results suggest that an optimal approach to robust SDM use lies in the assessment of the across-model consistency and a good understanding of the response functions, paired with the appropriate weighting of variables used within the modelling process. Given that SDM modelling is still the choice method used among other things to assess the threat potential to biodiversity (Araújo et al., 2011; Thomas et al., 2004), it is essential that the relationship between the bioclimatic variables and the probability of species occurrence is captured in consistent response functions, and that these factors are taken into consideration, especially before truncated datasets or projections into non-analogue climate spaces are employed.

Our results strongly support the idea of conservation planning schemes based on robust model results paired with the ecological necessity to move away from restricted planning scopes (e.g. political boundaries as represented by the GER data set). We have shown that prediction errors stem from the individual algorithms used and are readily identifiable within single predictions. Overall we suggest that more stringent principles need to be applied in order to supply more reliable and ecologically realistic modelling results. The large-scale prediction errors shown in this study highlight the importance of an integrated research approach in order to connect conservation tools with ecological realities.

4

National expenditures on protected areas in Europe over time

In preparation as Hannemann, H.[1], Macias-Fauria, M.[2], and Willis, K.J.[1,3] (2017) Money well spent? - National expenditures on protected areas over time.

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4.1 Abstract

Conflicts between conservation and anthropogenic activities lead to a continued loss of biodiverse land in Europe. The management of the trade-off between various land-use options is central to this problem. Thus, financial investment in biodiversity conservation and research is key to counterbalance loss of biodiverse land. This research aims to examine recent trends in the public expenditure on protected areas across Europe, and whether ecological or economic factors are the driving forces for

designating, i.e. gazetting, of new protected areas.

Within Europe, a ten-year data set from 2004 to 2013 containing multiple socio-economic and protected area-related variables was obtained of 18 countries which are member states of both the EU and OECD. The status and change of protected areas and conservation finances in all countries was assessed. Multiple linear regressions were run to identify key gazettement contributors.

Results indicated that the number of protected areas has increased by 26%, the area covered by 67% during the ten-year period. Yet despite this increase, the average expenditure per protected area has declined by 3%. A maximum of 0.35% of a countries' GDP, equivalent to 1.04% of total government expenditure, has been provided for conservation measures. The decisions for the creation of new protected areas appear to be based on economic rather than ecological factors and driven by prior expenditure on conservation and the countries' GDP and not based on ecological need. This could have detrimental impacts on European efforts towards persistence of biodiversity in Europe and create a shortfall in Europe's collective international responsibility of conservation.

4.2 Introduction

The more constrained a resource or its available supply, the more value is attached to the accessible stock of said resource (Barbier, 2013; Hotelling, 1931). Natural resources, especially those provided by biodiverse land which contribute to clear societal benefits (e.g. ecosystem services that provide food, energy, clean water, clean air, recreation, hazard protection, wildlife conservation, and equitable climates), have been under continuous, exhaustive use; a factor that is now being recognised as being both of scientific and socio-economic concern (de Groot, 2006; Moilanen and Arponen, 2011*b*; Schliep and Stoll-Kleemann, 2010).

The situation in many parts of Europe showcases the complexity of conservation planning and economic development. While conservation strategies are in place, large areas of biodiverse land are unprotected and readily available for conversion to other uses and the current protected area system is lacking ecologically representativeness (Rodrigues et al., 2004). One of the key issues Europe currently has to address is the level of expenditure for conservation measures that is considered adequate for international, regional, and national aims and obligations, alongside competing demands for land use in Europe's highly fragmented landscape (Araújo et al., 2011; Harrison et al., 2006; Henle et al., 2008; Kuussaari et al., 2009; Milad et al., 2011; Young et al., 2005). Or, considered from a different viewpoint, a country's weighing of biodiversity protection and retention compared to other governmental expenses over time. Socio-economic and political dimensions of conservation have been recognised in the policy context (Butchart et al., 2015; Fuller et al., 2010; Harrison et al., 2006; Kujala et al., 2013; Thuiller et al., 2008), however, to date there has been little attempt to estimate Europe-wide conservation expenditure and to assess the suitability of the current levels of public expenditure in the respective countries.

Europe provides a model case for comparing the budget allocations that individual countries are prepared to undertake for conserving biodiverse land. The region as a whole is covered by multiple political entities, and both national and supra-national conservation planning regimes are in place. Protected areas as a conservation strategy (Chape et al., 2005) is still considered a cornerstone of conservation in Europe (Cabeza and Moilanen, 2001; Mascia and Pailler, 2011).

Europe spans various definitions and political entities, showcasing a fragmented landscape on both political and ecological scales. Within Europe, large-scale agricultural use of the landscape, dense population, and high economic potential can be considered the norm (Hodge et al., 2015). Both international treaties and Directives of the European Union (EU) are seen as key to consistent monitoring and protection of biodiversity (Epstein et al., 2016; Pullin et al., 2009) in Europe as a whole, whereas individual national governments provide the necessary financial resources for doing so.

As early as 1973 the EU (the European Economic Community until 1993) started to integrate environmental policy with the first Environmental Action Programme (Hodge et al., 2015), but a consistent cross-border approach did not emerge until the adoption of the Habitats Directive 92/43/EEC (Council of the European Communities, 1992) and the resulting establishment of the Natura 2000 network. As of 2011, the EU considers that c. 6,300 € per km^2 per annum (European Commission, 2011) are needed to maintain the Natura 2000 network. While other designations are in place across Europe (e.g. local nature reserves or in-country national parks), they do not have a specific sum attributed to them. Currently, despite available data, there still appears to be a knowledge gap of detailed analyses of conservation expenditure relative to a country's economic power or in relative terms to neighbouring nations.

In order to examine the current economic *status quo* of biodiversity and its conservation across Europe, this study therefore examined a subset of eighteen countries both being members of the EU and the Organisation for Economic Co-Operation and Development (OECD) covering the time interval 2004 to 2013 (Figure 4.1). In this study we examined i) the differences in governmental budgets and the relative placement of conservation area expenditure within them, ii) the change in numbers of protected areas and overall area under conservation management, iii) the relative expenditure in relation to the Gross Domestic Product (GDP) in

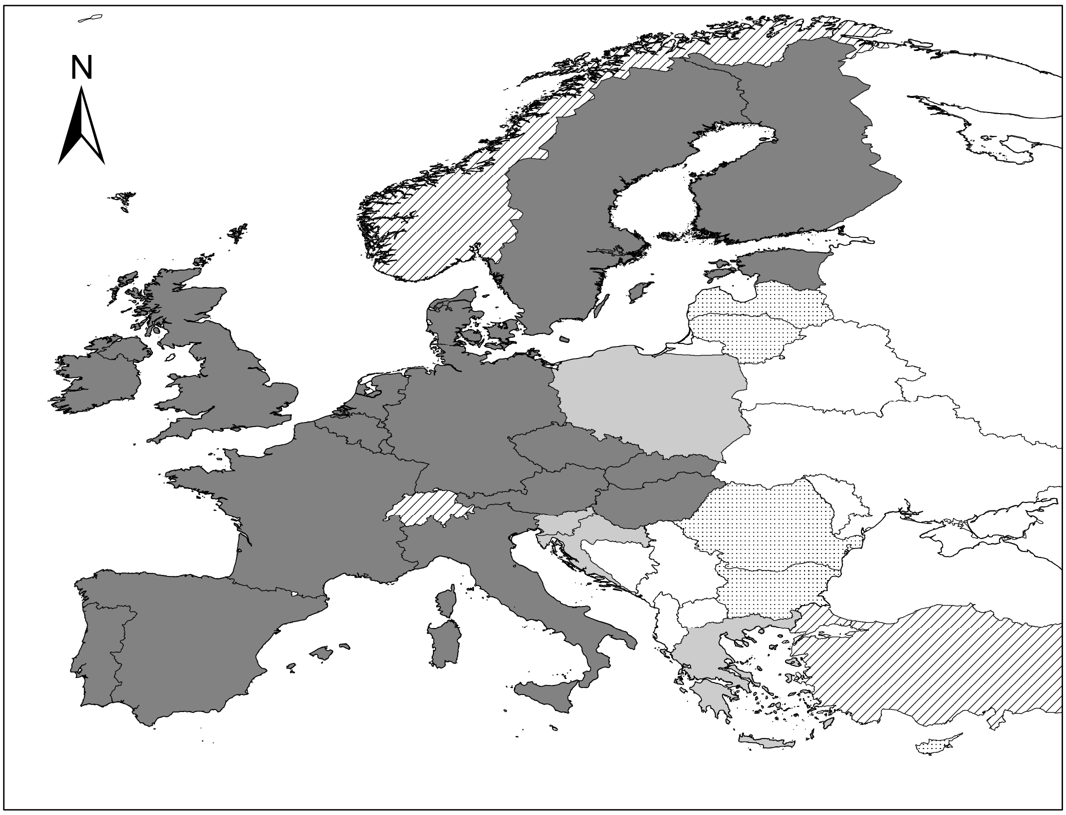


Figure 4.1: EU and OECD countries. Map showing the countries which are member states of both the European Union and the Organisation of Economic Co-operation and Development examined in this research (dark grey), those not included due to lack of data (light grey), countries being only member of the EU (scatter), or only of the OECD (hatched). Other countries do not hold membership in either organisation.

each country for biodiversity protection as seen in conservation areas comparatively across all 18 countries, and iv) the factors contributing to the designation of a new protected area, i.e. its gazettement. The research is based on the assumption that increases in protected areas (both their overall number and the area covered) should be at least synchronous with increased expenditure and that across Europe public expenditure on conservation areas should be proportional to the land area protected.

The assessment was focused on comparison between countries rather than as an overarching European conservation expense thus showcasing the financial commitment by individual states to conservation in a large part of Europe.

4.3 Materials and Methods

4.3.1 Data

The valuation assessment is focused on the following 18 European countries, which have been selected because of consistent data availability over the ten-year timeframe (2004 to 2013): Austria (AUT), Belgium (BEL), Czech Republic (CZE), Denmark (DNK), Estonia (EST), Finland (FIN), France (FRA), Germany (DEU), Hungary (HUN), Ireland (IRL), Italy (ITA), Luxemburg (LUX), the Netherlands (NLD), Portugal (PRT), Slovakia (SVK), Spain (ESP), Sweden (SWE), and the United Kingdom (GBR).

In order to i) assess the public expenditure on conservation and ii) highlight country-specific stressors, the following variables were considered for each country: total land area (km^2), agricultural area (km^2), total population, population density (people/km^2), GDP, absolute expenditure for environmental protection, and the government's spending quota. Additionally, the number of protected areas per country and the cumulative area of land under conservation management (km^2), i.e. including all official protection statuses such as e.g. Natura 2000, national parks, Special Sites of Scientific Interest, etc., for each respective year were also considered. Exchange rates and purchasing power parity (PPP) were used to compile the dataset.

The dataset was compiled from publicly available resources: GDP, PPP, environmental protection expenses, government spending quota, and total population were taken from the OECD (data.oecd.org, stats.oecd.org); total land area, agricultural area, and population density were taken from the World Bank (data.worldbank.org); annual average exchange rates (1st January – 31st December) were taken from the foreign exchange reference rates from the European Central Bank (ECB; ecb.europa.eu); the number of gazetted areas per country and their respective area was taken from the World Database on Protected Areas (WDPA; protectedplanet.net).

4.3.2 Data handling

All monetary values for GDP and environmental expenses were adjusted to 2010 United States Dollar (USD) using PPP in order to allow between-country and across-time comparison. OECD data was provided in USD and national currencies, therefore annual average exchange rates by the ECB were used for converting these currency values. All financial values used in the analysis are given in Euro.

The OECD data on environmental protection expenditure per country is examined jointly with the information on protected areas provided by the WDPA. Therefore, both the absolute number of protected areas present within a country and across all 18 countries, as well as the area covered, i.e. the area under conservation management (km^2), are used to provide a two-fold assessment of financial commitment to environmental protection. The listings provided by the WDPA include in some cases multiple designations on the same parcel of land. Thus, both the total number of protected areas and the area und conservation management will be an overestimation.

Government spending quota was used to i) scale the relative spending on environmental expenditure and ii) identify the average actual expenditure per conservation area (paired with the absolute number of protected areas within each country). All areas without a noted designation date (2,841 areas in total, 3% of the total number) were deemed to have existed by 2004. The range and consistency of environmental protection expenses, the corresponding GDP proportion, the number of protected areas newly designated in that year, and the annual average expenditure on both protected areas as well as the area under conservation management were assessed using the full data range.

A multiple linear regression was run in order to identify factors determining designating a further protected area, i.e. using number of protected areas as dependent variable portraying a binary decision for or against gazettement. This does not account for location or size of the protected area, purely whether or not it will be created. Potential correlation between the explanatory variables was assessed prior to computing the regression. Environmental expenditure, population, and agricultural land area were excluded on grounds of being highly correlated (r^2>0.65) with both each other as well as some of the remaining variables. A backwards stepwise regression with a threshold for removal of $p<0.1$ and a threshold of entry of $p<0.05$ was run.

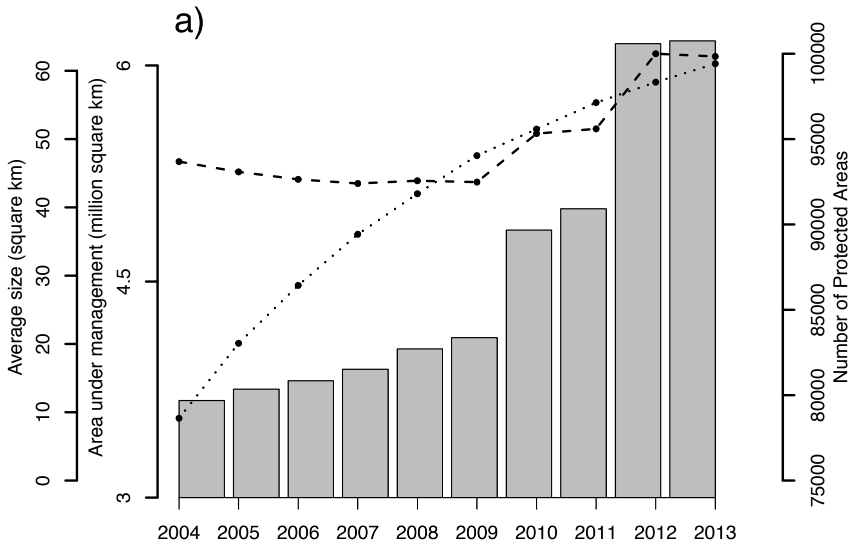
4.4 Results

The number of gazetted protected areas across all 18 countries rose by 26%, from c. 79,000 to c. 100,000, throughout the ten-year time span. The total area under conservation management increased by 68% to 6.17 million km^2, as did the average size of a protected area averaged across all 18 countries from 46.7 km^2 to 62.1 km^2 (33% increase; Figure 4.2a). However, over the same interval in time the average expenditure per km^2 under conservation management decreased from c. 1,800 € to c. 1,330 € in 2013. Concurrently, the average expenditure per protected area across all 18 countries declined by 3% from c. 84,000 € to c. 82,000 € (Figure 4.2b).

Consistency in expenses per km^2 varied drastically: while the United Kingdom's expenditure sank in 2013 to 10% of its 2004 funding per km^2, countries such as Belgium or Slovakia spent 216% and 255% respectively in 2013 compared to their 2004 expenditure. Per protected area rather than per km^2, the average expenditure ranged from Estonia spending c. 4,600 € per area to Portugal spending c. 953,400 € (largest inter-country disparity, year 2006).

Conservation expenses as percentage of government expenses ranged from 0.038% (Ireland, 2010) to 1.039% (Estonia, 2005) (Table 4.1). While the cumulative conservation expenses from 2004 to 2013 increased significantly ($p<0.01$), the median conservation expense did not show a significant change ($p=0.636$) across the same time span. Contrasting to this, the percentage of conservation expenditure within government expenses showed no significant change in its total ($p=0.058$), mean ($p=0.334$), or median ($p=0.116$).

A multiple linear regression was run with the number of protected areas as dependent variable. When utilising GDP, government spending, average spending per protected area, population density, land area, and total area protected per



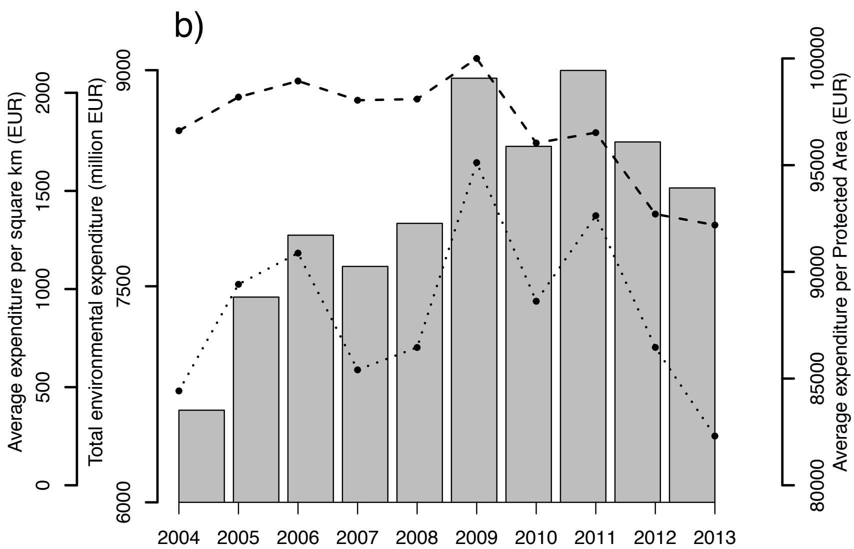


Figure 4.2: Change in protected areas and environmental expenses. a) change of protected areas across all 18 countries for the 2004 to 2013 timeframe. The barplot shows the area under conservation management in million square kilometres showing a distinctive increase 2009-10 and 2012-13. The dotted line indicates the, gradually increasing, cumulative number of protected areas, whereas the dashed line highlights the average size of a protected area in each corresponding year. **b)** the overall financial expenditure for protected areas in 2010 USD is indicated by the barplot. The dotted line shows the average expenditure per protected area and the dashed line the average expenditure per km^2 under protection.

country as independent variables, only GDP and average expenditure per protected area were highlighted as significant factors ($p<0.1$; adjusted $R^2=0.389$) when iteratively excluding the least significant variable.

4.5 Discussion

4.5.1 Funding attributed to protected areas in government budgets over the past decade

Financial resources put towards conservation – as measured through average expenditure per protected area per country – appear from our work to have remained proportionally level across the examined 10-year time period. The national accounting figures from the OECD allow the most clear-cut and transparent assessment of conservation expenditure possible due to their consistent enquiry across countries and years, despite not encompassing every finance mechanism,

Country	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
Austria	0.144	0.147	0.140	0.155	0.144	0.116	0.120	0.111	0.111	0.107
Belgium	0.217	0.210	0.204	0.245	0.253	0.274	0.280	0.284	0.279	0.290
Czech Republic	0.131	0.128	0.134	0.131	0.145	-	-	0.197	0.125	0.143
Denmark	0.288	0.331	0.333	0.260	0.251	0.216	0.225	0.198	0.192	0.218
Estonia	0.670	1.039	0.513	0.904	0.788	0.336	0.507	0.539	0.622	0.471
Finland	0.191	0.185	0.181	0.169	0.169	0.185	0.177	0.131	0.126	0.117
France	0.218	0.196	0.214	0.173	0.158	0.160	0.153	0.138	0.134	0.134
Germany	0.120	0.114	0.112	0.100	0.103	0.103	0.097	0.103	0.103	0.105
Hungary	0.142	0.148	0.085	0.097	0.197	0.299	0.087	0.227	0.250	0.170
Ireland	0.044	0.045	0.049	0.058	0.066	0.061	0.038	0.057	0.059	0.060
Italy	0.119	0.127	0.125	0.121	0.119	0.134	0.124	0.125	0.119	0.119
Luxembourg	0.087	0.104	0.080	0.077	0.070	0.068	0.084	0.071	0.068	0.066
Netherlands	0.078	0.061	0.060	0.065	0.059	0.080	0.057	0.058	0.056	0.042
Portugal	0.247	0.230	0.270	0.215	0.265	0.134	0.209	0.218	0.149	0.142
Slovak Republic	0.271	0.272	0.353	0.282	0.260	0.258	0.349	0.454	0.355	0.378
Spain	0.141	0.140	0.158	0.131	0.150	0.149	0.138	0.201	0.119	0.114
Sweden	0.314	0.502	0.520	0.355	0.327	0.362	0.387	0.436	0.443	0.302
United Kingdom	0.203	0.276	0.242	0.262	0.221	0.290	0.262	0.242	0.235	0.196

Table 4.1: Scaled conservation expenditure. Conservation expenditure as percentage of the total government expenditure per year. The results are calculated using GDP and government expenditure in parity across all countries. The data for the Czech Republic in 2009 and 2010 is non-comparable as the national accounts include profits from carbon trading.

such as EU funding linked in with agricultural subsidies (therefore, the overall expenditure does not indicate a progressive economic buy-in into conservation).

Neither increased funding in order to facilitate achievement of conservation goals, nor an increase in efficient conservation expenditure can be identified in the financial documents examined. From this finding it would therefore appear that the marginal cost of an additional conservation area has, to all intents and purposes, remained static when accounting for financial parity across the examined time. This highlights that the addition of protected areas has not changed the administrative systems, and that the budgetary items have only increased proportional to the average expenditure of a further protected area. While this has allowed countries to claim that they are not negating on conservation responsibilities, in relative terms the insignificant change in budget allocation across all 18 countries indicates conservation being regarded as a necessity which needs to be stabilised in financial terms, but does not warrant budgetary increase in line with identified threats to biodiversity persistence from both land-use change and climate change (Wätzold and Schwerdtner, 2005).

Thus, the interlinking between conservation and budgetary decisions seems to be on a constant expense approach needed to maintain *status quo* rather than on a proactive management of biodiversity as a constrained resource. It has to be argued that the close look at conservation in budgetary terms supports a stronger case for cross-country and regional cooperation in conservation: currently the EU-level mechanisms of co-funding initiatives do not account for the heterogeneous distribution of biodiversity across countries and, more importantly, the stark difference in absolute investment into conservation.

4.5.2 Number of new conservation areas set-up in Europe over the past decade

The general increase in number of protected areas does not incorporate re-assessment of currently gazetted areas and potentially replacing ones with new designations supporting conservation goals better than previous areas (Fuller et al., 2010; Mascia and Pailler, 2011; Wiersma and Nudds, 2009).

The results indicate that in all countries studied there has been an increase in the number of protected areas but wider variations in how and what is being protected occur between countries. Therefore, overall area under conservation management, as proxies for conservation effort indicates the differences in conservation scale between European countries, but also allows for an assessment regardless of country or habitat type concerned.

The presence of protected area and the area covered by conservation designations across all 18 countries as well as within each country is the best available measurement of effect of financial input. A potential issue is that the type of gazettement within the database is not assessed against its strictness. The varying degrees of protection across the protected areas analysed do not account for differences in e.g. allowed use or modification of the landscape as reflected in the IUCN protected area categories. In the case of Germany low-level protection such as IUCN category V covers 27.9% of the total land area whereas strict protection equivalent to IUCN category II or above only accounts for 0.6% (Macke et al., 2016). This discrepancy in protection consistency may indicate a varying need in financial support and therefore may influence whether a new protected area is being gazetted due to the constraints entailed by each designation. With a median value of 53 new protected areas are designated annually across each of the countries assessed, countries like Sweden and Finland, gazetting on average c. 550 and c. 620 new protected areas annually, adding to their already large networks of protected areas, need to be considered outliers. Especially smaller countries, limited by their available land area, gazette very few or none at all. Financially, the entailing expenses for new protected areas have been level in relative and absolute terms per protected area despite the significant increase in numbers.

It is important to indicate the potential lag in decision making and execution. As the WDPA only provides dates of initial gazettement of the protected area, it cannot be assessed when proposals for further protected areas were made. Thus, it is possible that planned new protected area designation are shifted outside of the assessed timeframe.

4.5.3 Relative difference in conservation expenditure between countries

The direct comparison of expenditure on conservation between countries allowed the assessment of relative differences. Utilising both the number of protected areas as well as the total area under conservation management as proxies for conservation contrasts the relative expenditure per area, including all managerial obligations, and the more generically applicable measure of per km^2. While the disparity in expenditure per protected area between countries is highlighted distinctively and showcases up to 200-fold disparity in actual expenditure, the relative provisions both per km^2 and per protected area are relatively stable within each country across the ten-year timeframe (Table 4.1).

The more severe decrease in expenditure per km^2 (-27%) than per protected area (-3%) can be attributed to the marked differences in number of areas gazetted (+26%), the total area covered (+68%) as well as the increase in average size (+33%), and the respectively varied increase in government expenditure on conservation in each country. The minimal reduction in expenditure per protected area suggests that the increase in funding has not quite kept up with the increase in number of areas, though indicates a consistent adjustment of budgetary terms to keep environmental funding level in relative terms. Nonetheless, the c. 1,330 € spent on average per km^2 in 2013 and the EU-recommended 6,300 € per km^2 for Natura 2000 still highlight a gap between reality and planning. Ownership is a key factor for implementation of efficient funding mechanisms for conservation. The assessment of utilised public funds has to be regarded as conservative and the decline of funding in countries with additional charitable contributions to conservation, such as the United Kingdom, will be less drastic than indicated by these overarching results. The focus on public spending allows for like-for-like comparison, though it does not encapsulate every funding method used in every country assessed.

4.5.4 Factors contributing to determining new protected areas in Europe

Our results showed that designating protected areas is dependent on overall GDP and average expenditure per protected area. While the available land area or the anthropogenic stress, such as through agricultural use and population density, which indicate a high opportunity cost of land, are not indicated to be significant for gazettement, the monetary aspect was highlighted as significant in conservation decisions. As such new areas are not necessarily considered on grounds of economic feasibility or ecological necessity, but purely due to international commitments and available resources. Differences in budgetary capacities of the countries (Table 4.1), national conservation priorities, and requirements of e.g. EU Directive and international treaties can lead to a yet further fragmentation of conservation and network structures within Europe.

The use of designation (rather than the size of area or similar variables) was chosen as dependent variable due to the available data resources, since presence of designated conservation areas is more readily available than precise sizing and in combination with the assumption that protected areas are initially created or not, whereas the exact location and the resulting size do not directly contribute to the decision process of whether a further protected area is ecologically necessary and financially possible. The indication that gazettements are decided on economic grounds, which is supported by the relative stability of budgetary expenses for conservation to the increase in number of protected areas, warrants a closer interlinking of budgetary realities, economic research, and ecological decision-making. Furthermore, the debate about desired network size, structure, and number of protected areas, indicates the handling of designating conservation areas as binary decision rather than including further information on ecological necessity and current conservation gaps (Rodrigues et al., 2004).

While more land area is being protected across all 18 countries throughout the 2004 to 2013 period, funding mechanisms and overall funding of area conservation within Europe has been very heterogenic and disparate between countries. Overall the funding has risen in absolute terms, matching the increase in area under protection, though in relative terms conservation still occupies a low budgetary priority on national scale (Table 4.1). Funding for biodiversity conservation needs to be leading rather than following as it is currently indicated that more conservation merely increases the budgetary items by the marginal increase in expenditure. Especially in light of new gazettements, the economic factors need to be supported by ecological factors in order to utilise funding effectively on both ecological and economic grounds.

4.6 Conclusion

The overall expenditure in Europe for nature protection measures in the examined countries has been held constant and on a very low level over the past decade. The aligned budgetary increase mirroring the number of protected areas indicates the economically undifferentiated conservation approach due to the constant marginal cost despite progress in research and available conservation tools.

Further research should focus not only on the ecological importance of new protected areas, complementing existing sites within a network, but on the economic potential currently contained within the national budgets. Any new addition to an existing conservation network needs to not only target ecological, but also economic potential on the scale of the individual protected area as well as the marginal benefit to the network and conservation in the region on the whole.

The increase in number of areas as well as size across all 18 countries gives valuable indication of conservation currently being treated as a retention of *status quo*, though further research should also consider the effect of multiple designations placed upon the same area and their economic implications. Both of these aspects would warrant a detailed, small-scale analysis of individual protected areas and types and their entailing budgetary constraints and potential identifying differences in financial necessities in terms of set-up of conservation areas and their operating costs.

5
Temporal dynamics of biodiversity through time

In preparation as Hannemann, H.[1], Seddon, A.[2],Willis, K.J.[1,3], and Macias-Fauria, M.[4] (2017) Lessons from the past – Hotspots of forest taxa persistence across Europe informed by palaeo-ecology.

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5.1 Abstract

Species' ranges change over time and are largely shaped by environmental conditions. Especially on large scales, climatic changes are one of the main drivers of

distinctive distributional shifts. Species distribution models hold the potential to support identification of viable geographic space for taxa in order to establish e.g. conservation areas or forestry use. Palaeo-ecological occurrences allow the inference of taxa's past responses to climatic shifts and may highlight previously occupied but currently abandoned range or niche space.

We applied an ensemble of bioclimatic niche models using palaeo-ecological occurrence data to 11 forest genera covering the last 8,000 years at 1,000 year intervals, which provided information on the probability of occurrence for each taxon in each time interval across Europe. All genera showed distinctive areas of high persistence potential, which did not generally overlap with present-day occurrences. Furthermore, all taxa occurrences – modelled past and present – spanned multiple modern-day countries, highlighting the cross-border effect any decisions about conservation or extractive resource use can have.

The results indicate a consistent trans-boundary persistence of all genera across all time slices. The incorporation of multi-temporal data enhances the robustness of the modelling approach and supports key conservation and resource use decisions. Utilising palaeo-ecological data to identify trans-boundary persistence of taxa and potential range areas allows for a more targeted approach to land use and natural resource planning.

5.2 Introduction

Occurrence of a species is dependent on a variety of factors. Biotic, abiotic, and historic distribution affect presence or absence of a taxon at present day (Di Marco and Santini, 2015; Guisan and Thuiller, 2005). The geographical range of a taxon's occurrence shifts through time depending on the degree of change of the facilitating bioclimatic conditions. In order to support conservation and use of natural resources, it is key to identify how ranges of forest taxa have changed through time and where the hotspots of long-term persistence are. The combined use of present-day and past biotic data to identify suitable range areas and persistence hold the potential to provide informed decisions on conservation and economic matters. Effective trans-boundary conservation planning or sustainable extractive use of natural resources (e.g. forestry) is necessary due to rapidly changing landscape matrices driven by climate change and a high degree of scattered regionalism in political entities in Europe.

Species distribution models (SDMs) are a widely used tool to assess potential changes in distribution patterns given changes to bioclimatic variables (Anderson, 2013; Araújo and New, 2007). Recently, their use has rapidly increased in many areas of ecological and conservation research in order to assess conservation opportunities and to apply inferred niche spaces to future distributions and ecological assemblages (Araújo and New, 2007; Di Marco and Santini, 2015; Maguire et al., 2015; Svenning et al., 2011). SDMs employ species occurrences (and absences if available) and environmental data to generate probabilistic estimates of habitat/environmental/bioclimatic suitability (Guisan and Thuiller, 2005). The environmental space estimated by this approach cannot exclude the influence of non-climatic interactions – e.g. biotic interactions or dispersal limitation (Maiorano et al., 2013; Soberón and Nakamura, 2009), and hence it is positioned in the continuum from the fundamental to the realised niche.

A multi-temporal approach to niche identification through the use of palaeo-ecological data allows for an improved niche and potential range estimation (Nogués-Bravo, 2009), since varying climate and biotic conditions for each time period can be incorporated (Veloz et al., 2012). Moreover, palaeo-ecological data allows the identification of persistence in geographic terms, as current species' ranges may be in a transient state due to underlying shifts of climate variables. In addition to these variables, ecological factors such as competition and dispersal and use and management of the taxa affect current occurrence data. The competitive advantage of other species will restrict the occurrence to represent the realised niche (Hutchinson, 1944). Management such as clearing of woodlands and general disturbance allows for both *in situ* expansion of present taxa but also of *ex situ* settlement of different taxa (Bradshaw, 2004). Furthermore, the climatic changes of the past (Davies et al., 2009) have created disparate distributions at various stages, and the current occurrence data does not yet reflect equilibrium distribution for some species or may not account for refugia throughout glacial periods (Maiorano et al., 2013; Meier et al., 2012; Svenning and Skov, 2007). Palaeo-ecological persistence of taxa has also enabled the identification of climatically stable regions across temporal gradients acting as important refugia under climate change (Blois et al., 2013; Maiorano et al., 2013; Svenning and Skov, 2007) as well as the study of sources and persistence of endemism which can be better protected with targeted and informed measures (Carnaval et al., 2009). Hence, identifying the variation between current occurrence and the suitable range space as indicated through prior distribution provides extremely useful information for conservation and habitat provisions across Europe, including the identification of regions suitable to extractive use of natural resources such as sustainable forestry. In this respect, cross-border distributions of economically relevant forest taxa highlight the importance of large-scale approaches in identifying range areas to facilitate both ecological persistence and sustainable maximum yields from natural resources.

Irrespective of a taxa's current level of threat (perceived or measured), combining SDM approaches with palaeo-ecological data can provide information on a given taxa's persistence through time. Since the spatial realisation of a niche is expected to shift within the current global context of change (Guisan et al., 2014; Zhu et al., 2012), the opportunities given by large-scale multi-temporal data to assess range shifts within SDM frameworks is becoming ever more applicable. This approach can identify species displaying high and low tolerances to changing environmental factors, and locations with long-term favourable conditions *vs.* much less stable ones. Present-day occurrence of a taxon is influenced by past climatic changes (Davies et al., 2009), whereas its persistence, i.e. continued presence in the same location, is indicated as being driven by current climate (Pearson and Dawson, 2003). As such, the use of available data sources, as it can be done through existing palaeo-ecological data, can contribute to model robustness, providing a better alternative to the use of data limited to the present (Broennimann and Guisan, 2008; Guisan et al., 2014). Palaeo-ecological data on forest taxa is widely available throughout Europe: circa 2,000 sites with records of fossil pollen are registered in the European Pollen Database (EPD, www.europeanpollendatabase.net) across the region (Figure 5.1).

Employing palaeo-ecological data and present-day distributions within an SDM framework, this research aims to identify the geographical distribution of persistence over the last 8,000 years for a selected subset of European forest taxa: we used 11 genera across Europe, incorporating in only three cases data from more than two species. The ensemble aggregation across all time slices provides a better approximation to the total range occupancy when compared with utilising single-time modelling. A focus on forest taxa allows to highlight the importance of persistence through time for overarching habitat provisions as well as economic use such as forestry.

5.3 Materials and Methods

The study was geographically restricted to 11°W – 32°E and 34° – 72°N and to the extent of the European continent (Figure 5.1).

5.3.1 Taxonomic data

Records of presence and absence for 11 genera across Europe from 8,000 to 1,000 years before present (yr BP) were obtained from the EPD. Present-day distribution of the selected genera was created by merging current distribution data of species belonging in the respective genus from the European Forest Genetic Resource Programme (EUFORGEN, www.euforgen.org). The taxonomic resolution of present-day data from EUFORGEN exceeds the fossil pollen resolution, as the former provides occurrence data at species level whereas the latter only provides genus-level data. The selected genera, and respective number of tree species used, are the following: Fir (*Abies* Mill., 6 species), maple (*Acer* Mill., 2 species), Alder (*Alnus* L., 1 species), birch (*Betula* L., 2 species), beech (*Fagus* L., 2 species), ash (*Fraxinus* L., 1 species), spruce (*Picea* Mill., 1 species), pine (*Pinus* L., 6 species), oak (*Quercus* L., 3 species), lime (*Tilia* L., 1 species), and elm (*Ulmus* L., 1 species) (Table 5.1). We assumed phylogenetic niche conservatism, i.e. the pattern where close relatives occupy similar niches, in our modelling exercise (Wiens, 2011). Accordingly, we assumed that a genus-wide niche existed within a recognisable environmental space. Whereas the geographic areas occupied by the seven European *Abies* species suggest a similar, constrained niche owed to the genus being subjected to isolation events rather than adaptive speciation, the six European *Pinus* species show a wide variety of niches due to the disparate locations of occurrence (Hendricks et al., 2014). Hence the estimated genus-wide niche for the latter will be less constrained. Finally, we only pooled the available tree species ranges per genus, excluding shrub species such as *Betula nana* L. or *Quercus coccifera* L.

The EPD was searched for records across the study area and the resulting 1,988 sites were matched against age-depth model availability (Giesecke et al., 2014), which reduced the suitable number to 760 sites. The dataset was further

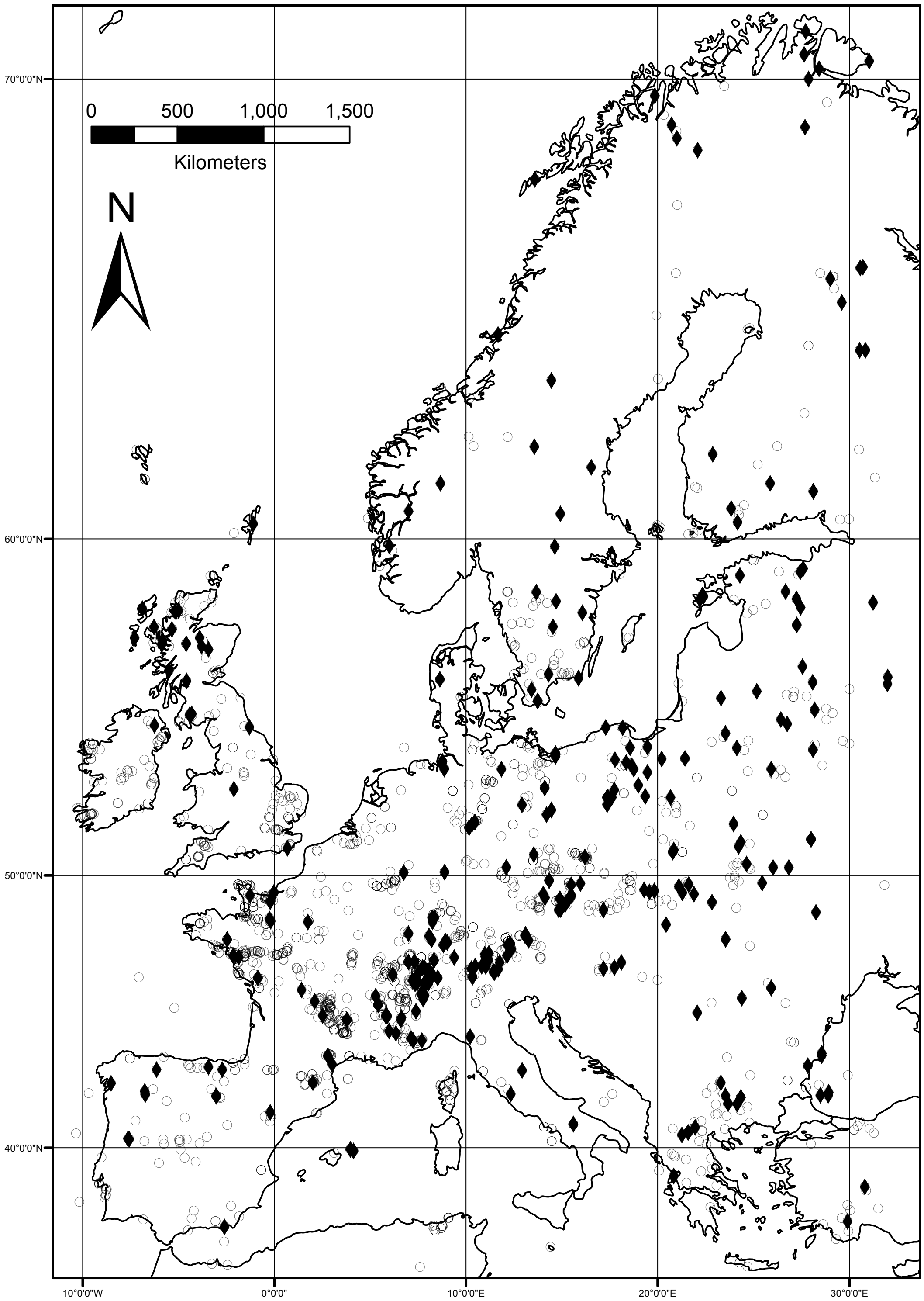

Figure 5.1: Fossil pollen record locations. Map of the study area showing all fossil pollen locations deposited in the EPD within the study area. Unfilled circles identify locations which were not used, filled diamonds are cores which were included in the analysis. Some locations may have contributed more than one core to the EPD and both circle and diamond may occur.

Table 5.1: Genera and pollen thresholds. All respective species are incorporated into the 11 genera in order to create genus-wide distribution maps and calibrate the algorithms for modelling. The threshold indicates what percentage of pollen in the EPD was considered a presence (Brewer et al., 2016).

Genus	Species included	threshold
Abies	*A. alba*	0.5%
	A. borisii-regis	
	A. cephalonica	
	A. cilicica	
	A. nebrodensis	
	A. nordmania	
Acer	*A. campestre*	0.1%
	A. pseudoplatanus	
Alnus	*A. glutinosa*	2.5%
Betula	*B. pendula*	5.0%
	B. pubescens	
Fagus	*F. orientalis*	1.0%
	F. sylvatica	
Fraxinus	*F. excelsior*	0.5%
Picea	*P. abies*	1.0%
Pinus	*P. brutia*	10.0%
	P. halepensis	
	P. nigra	
	P. pinaster	
	P. pinea	
	P. sylvestris	
Quercus	*Q. petraea*	1.5%
	Q. robur	
	Q. suber	
Tilia	*T. cordata*	0.5%
Ulmus	*U. laevis*	0.5%

reduced to 300 fossil pollen chronologies which had continuous records across the timeframe (at least 500 yr BP to 8,000 yr BP), and calibrated ^{14}C dating. Data for all locations was extracted at single time point at 1,000 year intervals. We included occurrences within 250 yr from each 1,000 yr time step. The resulting fossil pollen percentages were transferred to presence-absence data using threshold values for presence predetermined as a function of the relative pollen productivity of each taxon (Table 5.1, Brewer et al., 2016). All data analysis was undertaken in R (R Core Team, 2016).

5.3.2 Bioclimatic variables

Bioclimatic data concurrent to the taxa occurrence from 8,000 yr BP until present-day was obtained from the Bristol Research Initiative for the Dynamic Global Environment (BRIDGE, www.bridge.bris.ac.uk) in 1,000-year time slices. All climate data is based on the Hadley Centre Climate Model (HadCM3) as provided in the dynamic TRIFFID model (Cox et al., 2000). Each 1,000-year interval provided data for each variable at a 0.5° by 0.5° resolution.

We considered a set of seven bioclimatic variables which have been identified to be of importance for the distribution of the genera selected (Prentice et al., 1992): annual precipitation (mm), summer precipitation (June, July, August; mm), winter precipitation (December, January, February; mm), annual mean temperature (°C), summer mean temperature (June, July, August; °C), annual mean evaporation (mm), and growing degree days (sum of the days with temperatures > 5°C). Accounting for high correlation ($r^2>0.7$) between pairs of the seven variables, only annual precipitation, summer precipitation, evaporation, and annual temperature were used for model calibration.

5.3.3 Genus distribution modelling

All modelling was carried out using biomod2 (Thuiller et al., 2016, 2009). Each 1,000-year time slice was treated equally and models were calibrated using the presence/absence data of the palaeo-record from the EPD or the corresponding EUFORGEN data at the locations of the fossil pollen points for present-day. For each taxon and time slice, eight different SDM algorithms were employed: Artificial neural networks (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalised additive models (GAM), generalised boosted models (GBM), generalised linear models (GLM), the multiple adaptive regression spline (MARS) and random forest (RF).

All algorithms were run three times with random 70% data sample without replacement to calibrate and a 30% data sample to validate the models (Breiman, 1993). Variable importance within each model was determined by five-fold permutation. The responses were evenly weighted across all algorithms. Models were assessed using the Area Under the Curve of the Receiver Operating Characteristic statistic (AUC of ROC), Cohen's Kappa, and the True Skill Statistic (TSS) (Allouche et al., 2006; Hanley and McNeil, 1982; Monserud and Leemans, 1992).

Detailed response-curve analysis in biomod2 was used to identify the taxon-specific response to bioclimatic conditions within individual genera. In accordance with the potential shortfalls of ensemble modelling, each individual genus' response curve for each model was assessed for its ecological consistency and excluded from the ensemble in case of ecologically unsound behaviour (Hannemann et al., 2016). The top-performing four algorithms across all time slices for each genus were chosen. An ensemble model was then created for each genus at each time slice maximised as per AUC and additionally excluding any models falling below a 0.7 quality threshold from this ensemble. Additionally, the probability of presence was transformed into a binary format (presence/absence) by selecting a cut-off probability value that maximized the percentage of presences and absences correctly predicted using the AUC of the ROC (Thuiller et al., 2009).

In order to establish potential habitat of the genus in question within each time slice, the occurrence based on the location of available fossil pollen was projected into the bioclimatic envelope of the corresponding 1,000-year time slice. The calibration and modelling is happening in concurrent time slices. This does not force the correlative model outside of its calibrated conditions, which would entail more risks the further the models are forced outside their base conditions. Both potential of presence and the persistence through time of each genus were identified by equal-weighting aggregation of all nine 1,000-year time slices into a heat map showcasing the degree of suitable bioclimatic conditions through time.

5.3.4 Range occupancy

For each of the studied genera, all cells indicating presence in the EUFORGEN data (i.e. present day, 0 yr BP) were summed, and compared to all cells indicating presence as modelled for the present-day time slice, thus establishing the degree of potential range being occupied at present. Next, presence-absence data for all time slices for each genus were summed, and for each cell within the study region counts were made indicating ≥50%, ≥75%, and 100% of predictions of presence throughout all time slices. Finally, a third measurement of persistence was computed which aimed at identifying the degree of equilibrium between high-persistence and current

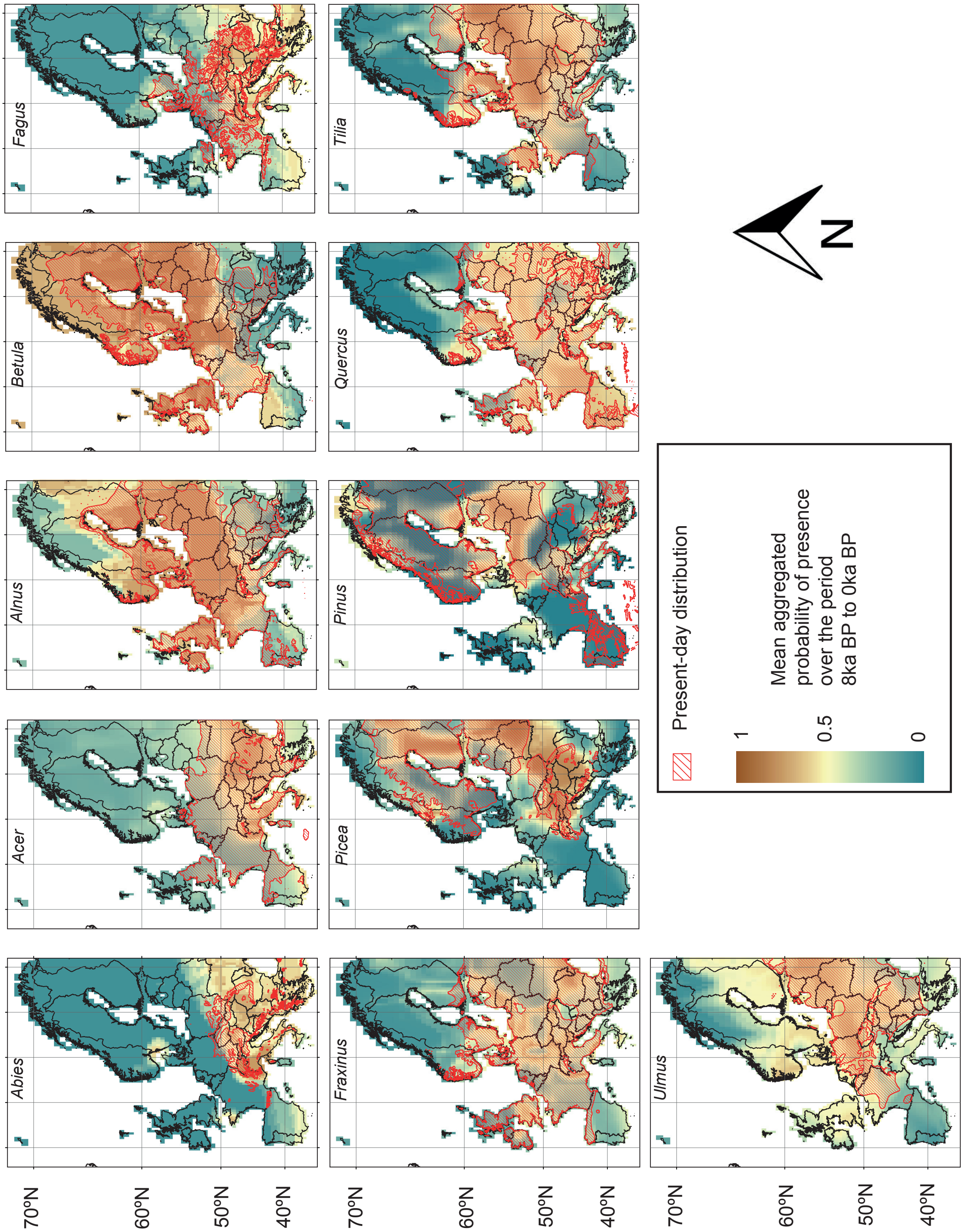

Figure 5.2: Probability distribution maps for all studied genera. All eleven genera showing the predicted presence of the genus according to the modelling results of aggregated probability occurrence across all time periods summed and proportionally scaled. The red hatched areas indicate present-day distribution of the respective genus according to EUFORGEN.

occurrence: all cells predicting presence in ≥50%, ≥75%, and 100% of cases across all time periods and having present-day occurrence were summed. The resulting percentages are used as rate of geographic range occupancy when utilising long-term paleo-ecological data versus using a single time frame, in this case present-day.

5.4 Results

5.4.1 Genus distribution modelling

Close examination of all algorithm's response curves for each genus showed ecologically meaningless statistical fit in a number of them (Hannemann et al., 2016). Across all taxa, GAM was excluded most often (84%) due to this. Both GBM and RF best reflected the underlying ecological potential, resulting in being excluded in only 1% of the cases. The following four algorithms were selected for each genus: *Abies*, *Alnus*, *Betula*, and *Fagus* – CTA, GBM, GLM, RF; *Acer* – FDA, GBM, GLM, RF; *Fraxinus* and *Picea* – GBM, GLM, MARS, RF; *Pinus*, *Quercus*, *Tilia*, and *Ulmus* – FDA, GBM, GLM, RF.

Modelled probability of presence highlighted some genera, such as *Alnus* or *Betula*, with very dynamic range shifts and modifications throughout the examined time periods, which might indicate their ability to closely track their niche across space and time. Others, such as *Quercus* or *Tilia*, showed a more consolidated range of potential presence, with consistent and smaller border zones (Figure 5.2; Supplementary Materials B).

The models indicate areas of continued persistence throughout all time periods for all taxa. Current occurrences were in previously occupied geographic areas. Aside from *Alnus*, which has past presence in the northwest of the Iberian Peninsula, and *Betula*, which is indicated to occur in the Balkans and South-Eastern Europe in present-day as well, none of the other genera show any novel range space occupied at present in relation to the last 8,000 yr BP (Supplementary Materials B). The size and location of high-presence probability varied for all taxa, and does not fully coincide with present-day occurrence (Figure 5.2, Table 5.2).

	present day 0 yr BP			predicted presence						high persistence					
	EUFORGEN	modelled	overlap	1.00	overlap	0.75	overlap	0.50	overlap	1.00	overlap	0.75	overlap	0.50	overlap
Abies	266	499	53.3%	98	17.2%	816	143.4%	1406	247.1%	32	12.0%	121	45.5%	227	85.3%
Acer	767	2021	38.0%	238	8.4%	971	34.3%	1687	59.5%	124	16.2%	469	16.6%	632	82.4%
Alnus	1940	1959	99.0%	1230	42.7%	1905	66.2%	2293	79.6%	901	46.4%	1274	44.3%	1478	76.2%
Betula	2041	2828	72.2.%	895	21.6%	1949	47.1%	2510	60.7%	665	32.6%	1271	30.7%	1612	79.0%
Fagus	679	1908	35.6%	180	6.4%	1192	42.3%	1634	58.0%	63	9.3%	289	10.3%	391	57.6%
Fraxinus	1977	2369	83.5%	111	3.1%	735	203%	1690	46.8%	96	4,9%	609	16.9%	1212	61.3%
Picea	1113	1194	93.2%	226	13.9%	814	50.0%	1139	69.9%	131	11.8%	460	28.2%	605	54.4%
Pinus	1804	1788	100.9%	283	12.3%	992	42.9%	1727	74.8%	252	14.0%	567	24.5%	892	49.4%
Quercus	1790	2356	76.0%	820	22.1%	2329	62.7%	2860	77.0%	543	30.3%	1469	39.6%	1702	95.1%
Tilia	1933	1681	115.0%	674	32.0%	1260	59.8%	1657	78.7%	594	30.7%	1059	50.3%	1350	69.8%
Ulmus	1183	1466	80.7%	230	11.3%	995	49.0%	1855	91.4%	152	12.8%	522	25.7%	760	64.2%

Table 5.2: Range occupancy and genera persistence. All counts refer to individual cells (0.5° by 0.5°) across the whole projected area. Occurrences at present-day are taken from rasterised distributions as provided by EUFORGEN data sets. Predicted distribution at present-day is taken from the modelling result for each genus as produced by the binary conversion maximising the AUC of the ROC. Long-term persistence stems from cumulative individual time period model outputs which are summed and scaled accordingly. High persistence is classified as both threshold-predicted presence and current occurrence in the same cell (see Methods 5.3). Thresholds of 0.5, 0.75, and 1 of all time periods' models indicating presence.

5.4.2 Range occupancy

As expected, none of the 11 genera examined display a current geographic distribution (0 yr BP) equivalent to the range space indicated by the summed predicted occurrence across all time slices (Figure 5.2, Table 5.2). Comparing present-day observed and modelled occurrences, *Tilia* occupies equivalently 115% of its potential range space. Contrastingly, present-day *Fagus* only occupies 36.5% of area size what models predict as suitable range space. The latter implies that 1) climatic variables not used in our modelling exercise and/or 2) processes other than climate (e.g. biotic interactions, land use) largely affect the distribution of *Fagus*. On average, genera occupy an equivalent of 77% of the area predicted as presently suitable range.

Predicted presence throughout all time slices at 0.5, 0.75, and 1 thresholds (see Section 5.3.4) showed that all genera – aside from *Abies*, which indicated a modelled range area of 143.4% (0.75 threshold) and 247.1% (0.5 threshold) of its 0 yr BP modelled area, fall short of their modelled potential. In the case of *Abies*, this indicates a strong reduction in range occupancy at present with respect to its long-term persistence – i.e. a genus in clear geographic decline throughout Europe. At the other extreme, permanent predicted presence (1 threshold) of *Alnus* occupies only an equivalent of 42.7% of its present-day modelled potential, indicating a genus in clear recent expansion. In general, high long-term persistence areas showed to be small and limited in their distribution as compared with present-day values (Figure 5.3). Only four genera (*Alnus*, *Betula*, *Quercus*, and *Tilia*) show a permanent core long-term persistence area (defined as all pixels with predicted presence in all – 100% - time slices) >30% of its present-day occurrence. On average, all genera showcased only a 20% overlap between long-term persistence and their current occurrence. With decreasing thresholds, high persistence areas showed *Tilia* (50.3% at 0.75 threshold) and *Quercus* (95.1% at 0.5 threshold) to be the most consistent genera. *Fagus* (10.3% at 0.75 threshold and 57.6% at 0.5 threshold) had one of the lowest degrees of overlap between long-term persistence areas and current occurrence (Figure 5.3, Table 5.2).

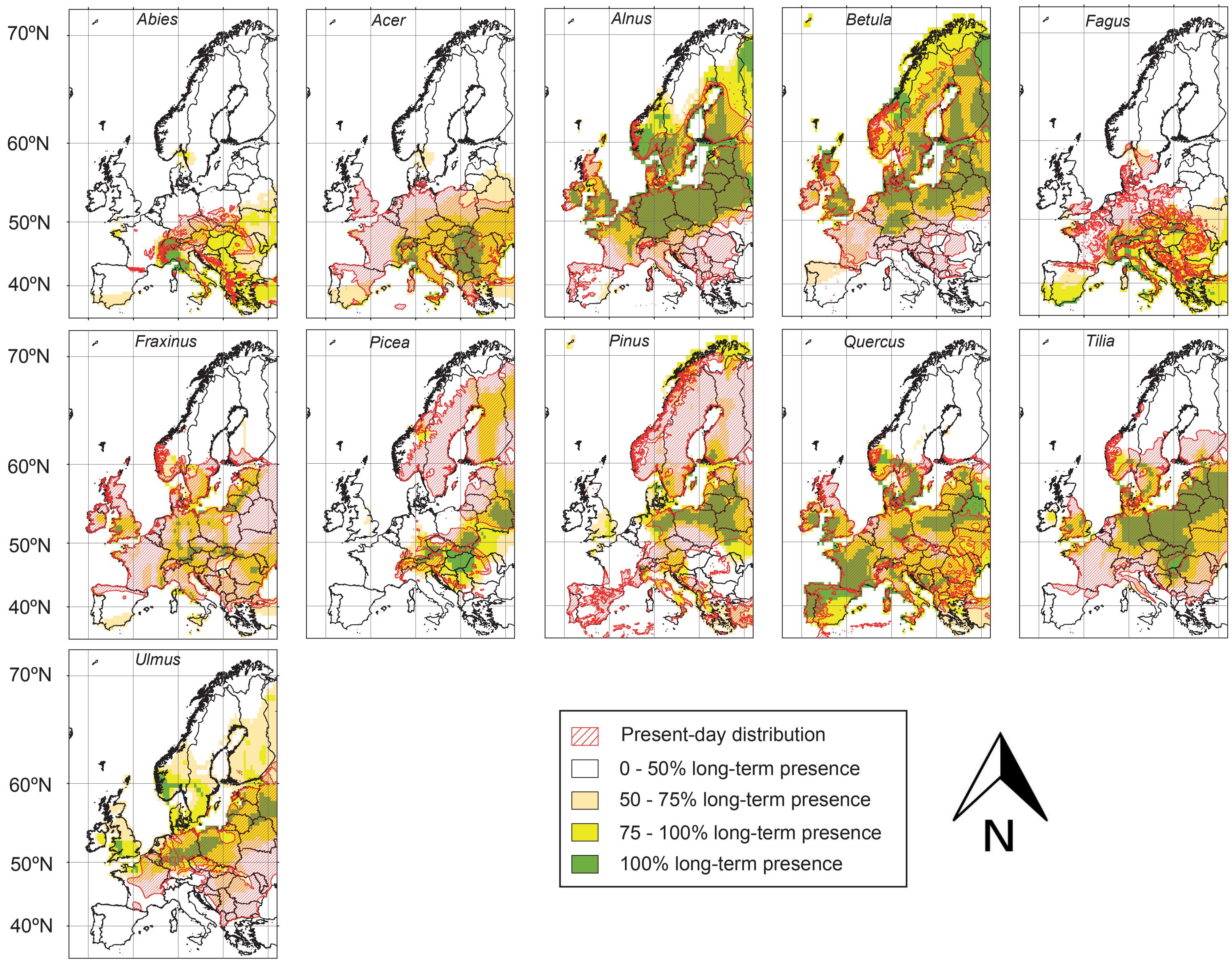

Figure 5.3: Persistence distribution maps for all studied genera. All eleven genera's persistence as maximised by AUC. Thresholds indicating presence in at least 50% (beige), 75% (yellow), and 100% (green) of time slices. The red hatched areas indicate present-day distribution of the respective genus according to EUFORGEN.

5.5 Discussion

5.5.1 Variation in current occurrence and long-term persistence areas

The differences between present-day taxa's distribution and modelled long-term persistence (Figure 5.3, Table 5.2) indicate potential land areas which can be utilised for e.g. conservation habitat, timber production, or a mixed-used forest. The fact that no genus – except for *Betula* and *Alnus* – show any novel range space occupied at present in relation to the last 8,000 yr BP suggests that most taxa are not currently expanding. Further, apart from *Abies*, which is predicted to occur in spatially disjoint patches, in part due to a) its occurrence on southern and central European mountain ranges and b) the fact that is it the most species-rich genus studied, all genera show contiguous and trans-national distribution across Europe, with particularly strong areas of long-term persistence. In general, current distributions across multiple countries only slightly match up in area with long-term persistence areas, which in turn are shown to span a significant number of present-day countries across Europe (Figure 5.3, Supplementary Materials B). In particular, *Fagus* and *Fraxinus* only align in <10% of their current range with past continuous persistence. In the cases of *Betula*, *Quercus*, and *Ulmus*, long-term persistence areas were found at the periphery or away from the geographical centres of their current ranges (Figure 5.3, Supplementary Materials B). Thus, the probability of occurrence and the entailing potential range areas (Figure 5.2, Table 5.2) indicate clear spatio-temporal shifts in bioclimatic conditions showing the discrepancy between long-term and present-day realised range area. This finding is especially relevant, since the studied genera are key taxa in forestry throughout the continent: many of these genera's currently exploited species show long-term high persistence in countries other than where they occur – and are intensively used – now.

The use of palaeo-ecological data included within distribution models allowed for a detailed assessment of geographic ranges through time (Table 5.2). While all genera show geographic range shifts throughout the examined time frame, differences can be identified between genera. Both *Betula* and *Tilia* (Supplementary Materials B) show distinctive changes in geographical distribution across the time frame, but the aggregated persistence (Figure 5.3) indicates a more geographically confined area for *Tilia*, which closely matches its present-day distribution (Table 5.2). All genera show an indicative tracing of their bioclimatic envelopes, clearly crossing the current political borders of various countries, both within the past and persisting into present-day distributions. Both *Alnus* and *Betula* show large-scale past distribution shifts across most of Europe. This may be indicative of adaptive traits or high susceptibility of changing climatic variables to which other taxa are less responsive.

5.5.2 Informing resource use

The selected research taxa are all economically contributing forest taxa across Europe. Their persistence is of economic importance and no conservation measure, except for broad-spanned habitat approaches, will specifically encompass them. While some subspecies or endemic species within the studied genera may be considered under threat, e.g. Sicilian fir (*Abies nebrodensis* (Lojac.) Mattei) or Spanish fir (*Abies pinsapo* Boiss.) which are listed as critically endangered and endangered respectively (IUCN, 2009, 2010), the main argument for supporting the persistence in these 11 taxa is in their roles of wide-spread landscape matrix and economic forestry (Estreguil et al., 2013).

Robust use of available data aimed at establishing key areas for forestry and conservation is of importance to both activities. Persistence of biodiversity allows for adequate use of financial conservation resources which are already very varied between countries in Europe (Chapter 4), but also identifies sustainable levels of industrial use. With 52.7 € billion output and employment of over five hundred thousand people, forestry and logging industry are important sectors across the European Union (Forti and Henrard, 2016). Variation and the resulting importance of presence or persistence of taxa in-country vs. trans-boundary are recognised by e.g. value added per employee, i.e. marginal profits exceeding marginal cost per employee. Sweden and Finland add over 150,000 € per employee, whereas countries like Hungary, Slovenia, and Romania only add 9,300 €, 69,500 €, and 65,300 €, respectively. These differences in productivity levels, employment rates, and stock removal among neighbouring countries stress once more the trans-boundary problem informed by large-scale data use.

Additionally, a key aspect and problem of common resource use can be identified by all examined genera spanning multiple present-day countries. Palaeo-ecological distributions and long-term genus persistence cross numerous political borders of modern-day countries across Europe. This subjects the same taxon to different treatments (e.g. timber extraction or conservation expenditure on habitat areas), and can thus question the effective persistence of the taxon across the entirety of both its currently occupied and its modelled potential range due to heterogeneous pressures or protection regimes. Both under current and future scenarios, the multi-country nature of these distributions will continue. Therefore, it is crucial to identify persistence potential in order to allocate financial, human, and land resources prudently (Moilanen and Arponen, 2011*b*) to support it in high-potential areas rather than misjudging sunk cost and allocating resources to unsustainable locations due to shifting climate or impending anthropogenic stress such as infrastructure development. Thus, the use of palaeo-ecological data can support crucial information for forest interventions and resource allocation as well as highlight already detrimental impact of anthropogenic stress due to e.g. agricultural encroachment on available range area across national borders.

5.5.3 Methodological considerations

The use of palaeo-ecological data in the present study allows stacking analogue time-slice models, preventing the propagation of non-quantified uncertainties when projecting bioclimatic envelopes into different time periods. The use of genera, owed to the taxonomic resolution of fossil pollen, needs to acknowledge the wide-spanning niche encompassed, especially in case of species-rich genera and subsequent large numbers of disparate niches (Hendricks et al., 2014). Therefore, any measure of persistence through time would need to account for genus or species specific traits in order to account for turnover or identifying lags which will be indicated by presence but low *in situ* turnover and recruitment in different locations or in only part of the present area occupied by individuals. All genera of this study show a mismatch in their potential range area, their persistent occurrence areas, and their present-day distribution (Figure 5.2 and 5.3,Table 5.1). Finally, the exclusion of shrub species in the present-day genus ranges might have contributed to some model vs. observation mismatches, such as the persistence of *Betula* in northern Fennoscandia (e.g. Figures 5.2 and 5.3).

5.6 Conclusion

Palaeo-ecological data showcases opportunities beyond individual snap-shots of short-term or single time point assessments of e.g. taxa's inventories within a landscape or their conservation status. The modelling exercise herein highlights the importance of utilising the available information of responses of various taxa to climatic varying conditions over a long-time frame, identifying the discrepancies in current occurrence and their potential range areas and genus' persistence through time.

Contrasting past and present distributions have shown current occurrence to be within range areas which have, at least at some point previously, been already occupied by the respective genus. Furthermore, all examined genera only show an average of 20% core area of persistence of their range throughout the nine time slices. Decreasing thresholds and thus more lenient high persistence interpretation highlight distributional consistency of e.g. *Tilia* or *Quercus*. The latter also showcases long-term persistence away from the centre of its present-day distribution, allowing little leading or trailing edge.

The combination of long-term data and robust modelling fill informational gaps, especially when considering geographic distribution shifts across multiple countries due to climatic change. Palaeo-ecological data as utilised in this work supports a clear focus on efficient and effective use of resources as areas of persistence can be clearly indicated. While the questions of baselines are mostly raised in a context of restorative conservation, knowing suitable geographic areas which are currently unoccupied by the taxon enables forward planning for e.g. profitable but sustainable use of land and resulting forestry resources in an ecologically sound and overarching cross-border approach for the whole region. Therefore, the use of palaeo-ecological data allows to assess both past distributions and suitable geographic areas, also supporting a forward, future-oriented outlook for the preservation and utilisation of resources.

6

Trans-boundary conservation and environmental framework agreements in Europe

In preparation as Hannemann, H.[1], Macias-Fauria, M.[2], and Willis, K.J.[1,3] (2017) Trans-boundary conservation and environmental framework agreements in Europe.

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6.1 Abstract

Biodiversity conservation in Europe is supported by numerous international and regional framework agreements. While the European Union is signatory to some, their implementation is largely dependent on individual states. Each state has

its own economic, political and biodiversity conservation objectives. Given that pressures on biodiversity are increasing due to diffuse drivers that transcend geopolitical boundaries (e.g. climate change and land-use change), a knowledge gap exists with respect to evaluating the current and future effectiveness of these frameworks and agreements. Five international conventions and two European Union directives dealing with species and habitat protection were analysed. All agreements are examined for their aims, conservation methods, the provisions made for trans-boundary conservation actions, their funding systems, and consideration of persistence and migration of ecological communities under climate change.

While biodiversity is recognised to be of international importance, the assessment highlights the shortfalls of these frameworks in terms of trans-boundary cooperation, the dominance of national-scale implementation, and large variations between states in provision of levels of funding. They also do not account for potential spatial shifts in biodiversity due to climate change. Further, the assessment also highlights the vulnerability of conservation action plans to political reach. All are key to consistent and ecological sound conservation regimes.

6.2 Introduction

Within Europe, ever-increasing agricultural intensification and increasing habitat fragmentation pose the most significant threats to persistence of biodiversity (Henle et al., 2008; Young et al., 2005). Increased land demands necessitate trade-off decisions on whether to protect land parcels or to utilise them for different purposes (de Groot et al., 2010). Despite numerous conservation agreements being in place, continued biodiversity loss is occurring (e.g. Krauss et al., 2010; Thomas et al., 2004), and both the lack of effectiveness of current legislation and the need for greater international collaboration on a political level have been highlighted a number of times (e.g. Kark et al., 2015).

Since the 1970s, increasing international cooperation has resulted in a number of environmental and conservation-orientated treaties and legal agreements. These have facilitated more consistent national and international biodiversity conservation aims. However, at the same time significant shortfalls have also been highlighted. The most obvious is an inconsistent implementation of conservation methods to achieve these aims across Europe. Currently, the capacity to select biodiverse sites and establish a representative and coherent network of protected areas is devolved to smaller political entities with many divergent interpretations and applications of approaches (Moilanen and Arponen, 2011*a*). Conservation under such direction can contribute to shortfalls due to e.g. use of truncated datasets (Hannemann et al., 2016), i.e. the small political entity does not represent the full ecological breadth of the species/habitat under consideration (Dallimer and Strange, 2015; Rodrigues et al., 2004), and funding for conservation that is dependent on local/national economic characteristics (Chapter 4; Scharks and Masuda, 2016). Given these issues, it is unclear whether the frameworks and legislation in place are capable of supporting biodiversity under current and future dynamic changes and economic priorities.

The research focuses on examining five international conventions and two European Union (EU) directives (Table 6.1 and 6.2) that represent the cornerstones of both global and European conservation in order to: i) identify their respective aims and methodologies for implementing conservation; ii) assess whether in-country or trans-boundary truncated data sets are used; iii) identify the source of funds used to implement measures and assessing issues potentially arising from it; and iv) examine the current ability of these frameworks to incorporate dynamic circumstances resulting from e.g. climate change. These are the 1) Convention on Biological Diversity (CBD), 2) Convention concerning the Protection of the World's Cultural and Natural Heritage (World Heritage Convention), 3) Convention on Wetlands of International Importance, especially as Waterfowl Habitat (Ramsar Convention), 4) Convention on the Conservation of Migratory Species of Wild Animals (CMS), 5) Convention on the Conservation of European Wildlife and Habitats (Bern Convention), 6) the EU Habitats Directive, and 7) the EU Birds Directives.

Convention/Directive	Objective	Protected areas	Designation
Convention on Biological Diversity 1992/1993/196	Conserving biodiversity Maintaining sustainable and fair use of biodiversity	not applicable	national classification
World Heritage Convention 1972/1975/192	Protecting natural areas of "universal value" (Art 2)	World Heritage List	national classification inclusion in list approved by World Heritage Committee
Ramsar Convention 1971/1975/168	Protecting waterfowl Protecting wetlands International coordination of wetland preservation	List of nationally designated protected areas in line with convention criteria	national classification international listing upon notification by state
Convention on the Conservation of Migratory Species of Wild Animals 1979/1983/120	Protecting migratory species throughout their range	none†	national classification
Convention on the Conservation of European Wildlife and Natural Habitats 1979/1982/51	*In situ* and cross-border conservation Maintaining conservation while accounting for economic and recreational use	Emerald Network‡	national classification‡
Habitats Directive	Contributing to biodiversity through habitat conservation Maintaining and restoring habitats to favourable conservation status Considering conservation in socio-economic context of the region and local characteristics	Natura2000 (Art 3.1)	national suggestion selection and approval by the EC
Birds Directive	Protecting and controlling for all bird species occurring naturally in the EU Managing exploitation of bird species Managing relevant biotopes	Protected areas (Art 3.2.a)	national classification

Table 6.1: Characteristics of environmental framework agreements. Listing of the main objectives and instruments enabled by each respective convention or directive. The characteristics of the conventions are preceded by opening for signature/entry into force/number of parties to the convention.
†Art V.5 refers to maintaining a network of suitable habitats through bi- and multilateral agreements under the Convention.
‡Emerald Network and the entailing classification are based in Recommendation No.16 from 1989

Convention/Directive	Finances	Implementation	Opt-out & degazettment
Convention on Biological Diversity	no mechanism stated	international cooperation (Art 5) national strategies (Art 6)	not applicable
World Heritage Convention	World Heritage Fund national funding (Art 15 and 25)	international cooperation (Art 7)	addition to the list may be refused de-listing
Ramsar Convention	no mechanism stated	national policies trans-boundary if species' range is in two or more signatory states (Art 5)	National/public interest (Art 2.5)
Convention on the Conservation of Migratory Species of Wild Animals	no mechanism stated	national policies regional if supranational organisation is signatory (Art I.2)	not applicable
Convention on the Conservation of European Wildlife and Natural Habitats	no mechanism stated	trans-boundary "whenever appropriate" (Art 11.1.a, Art 4.4) national policies	National/public interest (Art 9) Population management (Art 9) Territorial opt-out (Art 21.1 and 22.2)
Habitats Directive	EU/national co-financing	EU-wide "in agreement with each Member State" (Art 4.2)	National/public interest (Art 4.2)
Birds Directive	EU-wide implementation on national level	National/public interest (Art 9) Population management (Art 7)	

Table 6.2: Characteristics of environmental framework agreement - continued

6.3 Environmental framework agreements

6.3.1 Convention on Biological Diversity

The CBD and its associated protocols is a key multi-lateral treaty with an overarching framework on global biodiversity conservation. The CBD recognises the value and international importance of biodiversity along with development priorities. While species are recognised as resources individually, habitat requirements and interlinking conservation measures are highlighted as necessary to sustain them.

The convention requires the development of national strategies for conservation and sustainable use of resources (Article 6.a). International collaboration is recommended for research, knowledge sharing, and conservation practice (Article 17). It also highlights the imbalance of biodiversity hotspots as well as the heterogeneous distribution of academic and financial resources for conservation both *in situ* (Article 8) and *ex situ* (Article 9).

Additionally, the convention establishes the importance of integrating "consideration[s] of [. . .] conservation and sustainable use [. . .] into national decision-making" (Article 10.a), which establishes biodiversity as a limited and valued resource to be managed responsibly in-country. In contrast, the threat to biodiversity and potential to remedy is intensively discussed and the importance of multi-state agreements is stressed (Article 14).

6.3.2 Convention concerning the Protection of the World's Cultural and Natural Heritage

The World Heritage Convention is an international agreement dealing with protected areas across the globe. As one of the earliest framework agreements targeting conservation, this convention highlights less technical targets, but more 'traditional' conservation ideals of natural beauty, rarity, and wilderness (e.g. Article 2). Overall, the designation process is undertaken by each signatory state and is done on an inventory-based assessment of the current conservation value and potential (Articles 5 and 11). The convention highlights conservation of biodiversity for scientific purposes (i.e. incorporating snapshots of the history of the Earth, ongoing ecological and/or evolutionary processes, preserving certain habitats) and for aesthetic reasons. Furthermore, it recommends international collaboration and redistribution of financial resources in order to combat shortfalls in regions where biodiversity is most under threat.

6.3.3 Convention on Wetlands of International Importance, especially as Waterfowl Habitat

The Ramsar Convention promotes wetland habitat protection as key to species survival, aiming at preventing development on wetland areas. Individual signatory states designate suitable sites to be included in the list of internationally important wetlands (Article 2.1). Trans-boundary management options concerning neighbouring countries or other range states are not mentioned. However, in case of cross-border wetlands, consultation is required and shared wetlands or water systems are encouraged to be managed jointly (Article 5). The state has the ability to withdraw from or modify the agreements through downsizing, downgrading, or degazettement. These are subsumed under the prerogative of "urgent national interest" (Article 2.5) and can be implemented even once the wetland has been integrated into the internationally recognised list. Replacement in case of downsizing or degazettement has a two-fold demands: like-for-like replacement providing the equivalence of the original habitat, or no replacement as no further adequate or equivalent habitat can be found (Article 4.2).

6.3.4 Convention on the Conservation of Migratory Species of Wild Animals

The CMS targets ecological factors beyond political boundaries by focusing on migratory species. The incorporation of animal 'range states'[1] which are, regardless of their status to the convention itself, required to e.g. contribute to a specific species' conservation approaches, demands collaborative conservation. Agreements

[1] A range state is defined within the CMS as "in relation to a particular migratory species means any State [...] that exercises jurisdiction over any part of the range of that migratory species, or a State, flag vessels of which are engaged outside national jurisdictional limits in taking that migratory species"

concerning migratory species are required to be open for signature to all range states, regardless of a particular country being signatory to the full convention or not (Article V). The assessment of "favourable conservation status" (Article V) within the convention is determined with long-term data incorporating both the project's capacity of sustaining species' populations and utilising historic coverage as reference levels.

All agreements made under the convention are also required to take long-term perspectives to maintain favourable conservation status into account. Multi-state and multi-species agreements are encouraged (Article V.3). While providing for scientific research and species protection, this convention proposes that these agreements foster a coherent ecological approach, especially along migratory corridors (Article V.4.f).

A noteworthy characteristic of the CMS is its implementation. It is open for signatures to both individual states and supranational organisations. Should a supranational organisation be signatory, it supersedes the individual member state of that organisation in implementation of and rights within the convention (Article I.2). This allows for overarching political consistency throughout a region, and fosters ecologically sound approaches which should favour the persistence of migratory species within their natural ranges.

6.3.5 Convention on the Conservation of European Wildlife and Habitats

Similar to the CMS, the Bern Convention on the Conservation of European Wildlife and Habitats focuses on cross-border cooperation for the protection of biodiversity. The convention aims at conserving habitat and species *in situ* and as such targets ecological landscapes regardless of their political dependence. Trans-boundary and international cooperation in general is highlighted in this convention in order to maintain species and their population levels. Additionally, "[w]hile taking account of economic and recreational requirements" (Article 2) in each country, the convention links the required measures to suitable and sustainable goals. The threat to biodiversity and resource depletion over time is recognised.

The convention accounts for both current biodiversity at designated sites and potential habitat area change and deterioration. Coordinated approaches for border areas are recommended, which recognise ecological realities above political delineations and support habitat consistency and a higher potential of biodiversity persistence (Article 4, especially Article 4.4). Also, the convention specifically notes that all parties are to undertake additional and coordinated measures with respect to migratory species (Article 10.1). Interlinked approaches "whenever appropriate and in particular where this would enhance the effectiveness of measures taken under other articles of this Convention" (Article 11.1.a) further support the core principle of trans-boundary cooperation. This has been strengthened by Recommendation No. 16 (1989) establishing the Emerald Network, a set of protected areas across all parties to the convention perpetuating the conservation aims laid out.

However, while the convention specifically fosters ecological approaches transcending political boundaries, it also focuses on snapshot conservation which falls short of identifying species' dynamics. Moreover, it is stated that "in the interest of public health and safety [. . .] or other overriding public interests" parties to the convention can register exceptions to protection status (Article 9). Thus, parties can decide to exclude certain territories (e.g. Denmark has opted to not apply the convention's validity to Greenland or the Faroe Islands) or species (e.g. Finland has excluded *Canis lupus*, *Ursus arctos*, and *Accipiter gentilis*, all of which are listed as Appendix II species and as such designated as strictly protected fauna species).

6.3.6 EU Habitats Directive

The Habitats Directive classifies conservation as an "essential objective of general interest pursued by the community"[2]. The aims of this Directive are characterised

[2] The Directive refers to Article 130r of the Treaty [of Maastricht, 1992]. The most current version of the consolidated treaties of the "Treaty on the Functioning of the European Union", known as the Treaty of Lisbon, relocates the referred clauses to Part 3, Title XX – Environment, Articles 191 to 193.

by the recognition of the deterioration of the environment and threat to species due to lack of suitable habitat.

The initial definitions utilised within the directive take both the current and future status of the environment into account (Article 1). The definition of conservation status recognises the "sum of the influences acting on a natural habitat" (Article 1.e), which acknowledges it as a changing status, since these influences affect the current as well as the long-term distribution and survival of species typical for the habitat in question.

The directive establishes that "a coherent European ecological network of special areas of conservation shall be set up under the title Natura 2000" (Article 3.1). The setup is inventory-based and depending on proportional habitat cover within the member states. While the setup of protected areas is encouraged to work in an interlinking manner with already existing sites improving the ecological coherence of the network, this is not compulsory (Article 3.3). Heterogeneous distribution of ecologically valuable species and/or habitat types may place an undue burden on the respective states for which the directive establishes a co-financing programme.

The management of all sites is to be integrated into individual country's development plans (Article 6.1) and overall national land-use policy (Article 10). Sites belonging to Natura 2000 may be degazetted by "overriding public interests, including [. . .] social or economic nature" (Article 6.4). Regardless, the overall network coherence needs to be retained or re-established with compensatory measures taken. Contrastingly, priority sites can only be removed from the listing with prior approval by the European Commission (EC). Periodic review of the network also allows for declassification of sites which do no longer warrant protection under the objectives of the Habitats Directive (Article 9, Article 17.1).

Biodiversity is recognised as a communal interest, but the identification of its importance is anchored in political decision-making. The species and habitat types to be protected are listed by both the EC and the member states' relevant authorities. The member states propose relevant sites of which the EC selects appropriate network sites in liaison with the relevant state (Article 4). This mechanism of checks and balances aims to ensure a best-possible selection on an inventory basis and allows for designation by the member state once a site has been considered as important "as soon as possible and within six years at most" (Article 4.4). Taking unanimous action, the Council of the European Union can require a member state to designate a certain area (Article 5.3).

6.3.7 EU Birds Directive

The Birds Directive acts as a second pillar to the EU's terrestrial conservation approach. Having been revised in 2009, the initial directive stems from 1979. Contrasting to the Habitats Directive, this directive recognises the three-dimensional character of avian habitat and thus a more pronounced shared burden or trans-boundary challenge in protecting birds. Both the importance of residential and migratory species as well as the need for long-term protection and management is highlighted.

Congruently to the Habitats Directive, protected areas are to be set up (Article 3.2.a). Special focus is directed towards establishing and re-establishing habitats which protect species endangered due to small dependent populations or ranges (Article 4). Additionally, the recognition of habitat needs for bird species for wintering and migration stopover points especially mentions the role of wetlands, which links the directive to the Ramsar Convention as well as the CMS. An important distinction to other environmental frameworks is that while the directive allows for overriding principles of public health and safety, it also permits measures taken against wild birds for the protection of flora and fauna (Article 9).

6.4 Discussion

The features of each individual agreement are presented in Tables 6.1 and 6.2. As discussed above, the current environmental framework agreements and existing protected area networks, both in national and regional context, show challenges and opportunities in response to i) their ability to work across political boundaries; ii) their use of in-country or trans-boundary truncated data sets; iii) the source of funds used to implement measures and assessing issues potentially arising from this and iv) their ability of to incorporate dynamic circumstances resulting from e.g. climate change.

6.4.1 The trans-boundary nature of current environmental framework agreements

The analysis indicates that the aims of the conventions vary from compulsory cooperation (EU Directives) and regional implementation (Bern Convention) to encouraged bi- and multilateral agreements (Ramsar, CMS) and simple national implementation (CBD) (Tables 6.1 and 6.2).

Biodiversity is often restricted by natural barriers and abiotic factors (Soberón and Peterson, 2005), but it has been widely acknowledged that the unnatural restriction caused by political borders is detrimental to conservation (Dallimer and Strange, 2015; Kukkala et al., 2016; Opermanis et al., 2012). The evidence from this review suggests that only some of the current conservation frameworks aim at alleviating political restrictions, while others will continue to abide by political barriers. The CMS and Bern Convention create effective trans-boundary political co-operation engaging both national states on bilateral terms as well as supra-national organisations. The EU as signatory facilitates large-scale implementation across Europe.

While the CMS encourages agreements between one or more of its signatory parties, ideally covering several species and relating to a network of habitat provisions for these species (CMS, Article 5), no signatory is required to participate in ecologically important trans-boundary agreements. They operate as an opt-in approach. The fact that the EU supersedes the individual member states in their implementation of the CMS provides a trans-boundary framework and an ecologically desirable approximation of ranges (Dallimer and Strange, 2015; Kark et al., 2015).

Of the five conventions, an overarching, international network of protected areas is established only under the Bern Convention. Even then, no cross-border cooperation is given *per se*, as it is based on national designation procedures.

The EU being party to the convention supports the implementation across a wide-range of countries. The environmental directives of the EU can be seen as implementing the Bern Convention as well as establishing conservation measures in their own right. As highlighted, the matching of political decisions and ecological ranges in spatial reach is key in order to encompass ecosystems successfully and to implement a well-designed future-orientated conservation plan. Gazettement of protected areas based on local knowledge and under national auspices highlighting the sovereignty and authority of individual countries is arguably almost completely opposed to this. All the assessed conventions base conservation networks on a bottom up approach, indexing nationally gazetted areas, whereas within Natura 2000 a top down approach can be identified allowing to select necessary areas from an overarching trans-boundary viewpoint. While the former approach allows to incorporate local knowledge and national priorities, the latter can provide fewer redundancies and a more holistic approach targeting whole ranges and the ecosystems they are contained in regardless of their position on the political map.

The facilitation of trans-boundary approaches under these frameworks needs to be recognised as an applied and ecologically essential aspect of conservation. The analysis indicates that the political ownership is key to management of biodiversity regardless of ecological necessity and effectiveness.

6.4.2 Impact of truncated data on environmental framework agreements

Ecological data is widely available in political delineations, but the use of truncated data is creating shortfalls in applications e.g. ecological tools when identifying biodiversity distributions (Hannemann et al., 2016; Veloz et al., 2012) as well as imposing unnecessary costs in terms of management and legal agreements onto conservation (Dallimer and Strange, 2015). Nevertheless, the use of national inventories is the *status quo* for conservation in Europe and this is apparent on all the frameworks examined except the Habitats Directive. As demonstrated, conservation based on artificially restricted land areas which do not match, in most cases, natural occurrence (Hannemann et al., 2016), provides a far-reaching but potentially disjointed and inefficient conservation effort (Wiersma and Nudds, 2009). The international listings of the World Heritage and the Ramsar Conventions rely on national classifications. The Ramsar Convention maintains ecological integrity by obliging the relevant parties to cooperate both in the current implementation and future coordination of conservation in trans-boundary biotopes. The collaborative management across political entities is therefore a standard procedure for all signatory states and does not allow for opting-out of the mechanism. Natura 2000 is probably the best in terms of over-coming the problems of truncated datasets because designation for protected areas under both the Birds and the Habitats Directives is undertaken using national and regional data.

As previous work has shown, the detrimental use of limited data in selecting conservation priorities does not account for potential previous range areas currently unoccupied in other countries (Chapter 3, Chapter 5). In particular, the focus of the environmental frameworks assessed on national implementation or state-based conservation strategies with use of respective national biodiversity inventories is contrary to what has been identified as ecologically important. Trans-boundary conservation is only encouraged in some framework agreements and in even fewer explicitly required (Tables 6.1 and 6.2). Only the Bern Convention, and by extension the EU Habitats Directive, are actively recognising ecological reach over political one and facilitate large-scale ecologically sound conservation regimes. The large terrestrial area subjected to and the subsequent available data for the EU's environmental directives have to be considered a positive influence in the future in approximating ecological boundaries (Dallimer and Strange, 2015).

6.4.3 Conservation funding facilitated by the framework agreements

Effective biodiversity conservation is dependent on sufficient financial resources (Iftekhar et al., 2017). Europe on the whole can be considered politically stable, having a high degree of rules of law, and being a wealthy region, but it is indicated that this does not necessarily contribute to high conservation expenditure (McClanahan and Rankin, 2016). Findings from analysing conservation spending highlight the low priority of conservation for national governments as indicated by the relative budgetary item of financial commitment to conservation. OECD data from 2004 to 2013 shows a consistent low-level spending, only increasing in absolute terms relative to e.g. newly designated protected areas within the respective country (Chapter 4). The consistent increase in protected areas throughout the 20th century (Chape et al., 2005) require concurrent funding mechanism to maintain *status quo*, whereas arguably more funding should be supplied in order to combat the continued decline of biodiversity (Waldron et al., 2013).

The examined frameworks are largely based on national classification and aside from the World Heritage Convention and the Habitats Directive (Tables 6.1 and 6.2) do not name an explicit funding mechanism. The World Heritage Convention acknowledges both the common good and the heterogeneous distribution of biodiversity across the globe and a fund in order to support national efforts accordingly has been set up. Similarly, the Habitats Directive supports its regional network through co-financing conservation under its auspices. This supports the frameworks' aims in supporting biodiversity while being to some degree independent of political and budgetary constraints of the respective country. All other conventions are dependent on national designation procedures and the entailing in-country funding mechanisms. This also applies to the CMS and the Bern Convention, which work trans-boundary and target ecological rather than political scales. Previous work has shown that discrepancy in conservation spending across Europe is the norm (Chapter 4). The assessed environmental frameworks, with very few exceptions, are financially dependent on national implementation, despite contributing to uneven resource allocation throughout the range of a species. The remaining framework agreements are likely to fall financially short of their aims in tackling the requirements now and in the future due to their dependence on national economic priorities.

6.4.4 Ability of frameworks to incorporate dynamic change

Capturing significant parts of ranges or large-scale occurrence of species regardless of the underlying political map is key for biodiversity persistence (Dallimer and Strange, 2015; Kukkala et al., 2016; Opermanis et al., 2012). The international, or regional, framework agreements which approximate or even capture the full range of the biodiversity present will support a more robust persistence than individual species' protection in separate countries.

Across Europe, biodiversity indicates varying degrees of persistence in certain locations and suitable range space (Chapter 5). It is important to recognise the influence of dynamic change of bioclimatic envelopes on biodiversity occurrence throughout time (Guisan et al., 2014; Zhu et al., 2012). International cooperation is key in conservation as both past and current distributions and the resulting high likelihood occurrence areas of biodiversity span political borders (Kark et al., 2015). Biodiversity has shown mobility, persistence, and re-occurrence throughout time (Aitken et al., 2008; Svenning et al., 2008). Research has shown that long-term high-persistence areas can be clearly identified throughout the Holocene (Chapter 5). Areas of transient occurrence and less preferable range space, which are subject to potential habitat loss due to climate change (Carnaval et al., 2009), are nonetheless incorporated in current conservation networks. Key information such as the change in geographic occupancy due to dynamic changes are not accounted for in the static conservation frameworks analysed and the respective instruments proposed.

The majority of framework agreements focus on *in situ* conservation wherever possible with the exception of the CMS, Bern Convention, and the EU Directives, which explicitly highlight the importance of any site being assessed for its long-term potential to sustain its designated conservation aims. This is especially pertinent in the light of climate change affecting the current protected area systems (Araújo et al., 2011; Lung et al., 2014; Trouwborst, 2009, 2011) while also recognising the importance of consistent identification of areas with long-term persistence. Aims and focus species are listed in frameworks' appendices and are based on *status quo* threat levels to biodiversity at their current place of occurrence. Review intervals allow for adaptation of listings, which is important when taking future range shifts into account. Overall, the indices are narrowing conservation plans to present-day snapshots: fixed compositions and current ranges. Dynamic changes may be considered non-analogous to present-day occurrences, but consistent data use of available palaeo-ecological records has shown to be able to encapsulate a broader range of suitable conditions (Chapter 3; Chapter 5; Veloz et al., 2012), identifying previous response to similar changes in the taxa's bioclimatic envelopes.

Dynamic ecological shifts due to climate change also pose a further indirect threat to conservation. Both the Ramsar and the Bern Conventions exhibit challenges by allowing degazettement or rezoning of conservation sites comparatively easily. The provided degazetting mechanisms allow for "urgent national interest" or an "overriding public interest", and threaten the coherence of conservation efforts (Mascia and Pailler, 2011). Especially under increasing land demands due to climate change, it is crucial for persistence of biodiversity to adapt framework strategies to encompass such dynamic change and to be able to provide a consistent and coherent conservation set-up under current and dynamic pressures.

While all assessed framework agreements allow for adaptation of their listed target habitats or taxa, those which are based on trans-boundary collaboration are in the best position to compensate for dynamic changes of biodiversity distribution. That being said, non-ecological decision factors, e.g. economic land demands due to climate change which allow for degazettement, are a central threat to consistent conservation planning and biodiversity persistence in all of the assessed environmental agreements.

6.5 Conclusion

Europe has a large number of protected areas currently covered by a suite of international conventions, regional frameworks, and national policies. In the assessment of seven environmental framework agreements, there is evidence for diminished efficiency due to inconsistent implementation on national levels and limited cooperation due to political boundaries as well as various levels of funding across countries (Beresford et al., 2016; Kark et al., 2015). Each framework covers specific aspects, contributing in part to the increase in overall protection throughout Europe. The agreements need to be modified to support trans-boundary approaches better, decrease financial heterogeneity, and account for dynamic change.

It was found that 1) limited trans-boundary conservation, national protection designation, and the resulting funding mechanisms being by and large the norm, and 2) little opportunity to modify inventory-based conservation priorities over time to account for dynamic change. There is an urgent need for the EU to facilitate consistent and coherent strategies across the region to counterbalance Europe's political fragmentation in a positive way.

7
Conclusion

Biodiversity loss is continuing to occur at an alarming rate across Europe. This thesis looked at availability and use of data and political frameworks to stem this loss. In particular it focused on the current practice in many European states of using biodiversity data that is constrained by the country's geo-political boundaries. It also looked at the implications of varying degrees of in-country conservation expenditure and the use of temporally static biodiversity data to determine response to climate change.

The following research questions have been addressed:

i. How does use of truncated biodiversity data set constrained by geo-political boundaries influence the resulting predictions of current and future occurrence? (Chapter 3)

ii. How have in-country financial commitments to conservation in Europe changed between 2004 to 2013, and how much variance is there between countries in terms of conservation expenditure? (Chapter 4)

iii. Which areas across Europe have shown high persistence of forest taxa throughout the last 8,000 years, and how does this provide information for e.g. conservation or forestry use in the future? (Chapter 5)

iv. To what extent are the current environmental framework agreements across Europe suitable for trans-boundary cooperation, and how do they match the challenges posed by the problems associated with in-country biodiversity data use, differences in financial support, and future shocks such as climate change? (Chapter 6)

In relation to the questions above, the research has shown the following:

7.1 The implications using biodiversity datasets constrained by geo-political boundaries

The key problems identified with truncated datasets were associated with reduced number of data points and less abiotic variation reflected in the smaller datasets. It was found that the smaller/more truncated the dataset used, the more statistical errors were produced by the models and this problem exacerbated when projecting into non-analogous areas. It was also demonstrated that that models based on large-scale trans-boundary datasets encompassed more bioclimatic variation and thus produced better predictions in analogue and non-analogue situations.

Further, more stringent assessment of SDM results highlight easily identifiable prediction errors. Therefore in order to facilitate robust SDM, the instability of statistical response functions propagated under truncated calibration data or projection into non-analogue climate space need to be considered when utilising SDM in order to assess e.g. threat to biodiversity which indicates that stakeholders need to move away from politically restricted planning scopes.

7.2 Impact of in-country financial commitments on conservation

When examining in-country financial commitments for the interval 2004 to 2013, high variation both across years and between countries was shown. Specifically, no relative increase in funding could be identified. It was also found that new protected area designation was based on economic capacity of a country (as measured by

GDP) rather than ecological factors (e.g. number of threatened/rare species or agricultural land encroachment/degradation).

When new conservation designations are being considered, this work indicates that ecological factors should contribute as much as economically based factors in the decision-making process.

7.3 Identification of high-persistence potential of biodiversity through time

By examining species distributions over the past 8,000 years, this research indicated that all the taxa examined were relatively persistent through time and spanned multiple countries. However, only four of the 11 genera studied showed a high persistence of more than 30% of their potential range, indicating that future resource deployment should be in these areas, which becomes an issue if this range transcends a geo-political boundary.

Therefore, the results in this study demonstrate the use of palaeo-ecological data in supporting management of resources beyond short-term timelines or individual country snap-shots. Contrasting present-day occurrence and potential range space as indicated by the modelling throughout the last 8,000 years clearly shows areas of high-persistence. These can support resource planning by filling informational gaps about persistence under changing bioclimatic conditions.

7.4 Suitability of current environmental framework agreements under dynamic change

The assessment of seven environmental framework agreements has shown that all are providing numerous interlinking biodiversity conservation approaches focusing on various aspects of e.g. habitat types or migratory species. The framework agreements encouraged, some required, trans-boundary conservation which was particularly prominent in the CMS and Bern Convention as well as the EU Directives due to the European Union facilitating large-scale application of the agreement.

This is particularly pronounced in the creation and facilitation of the Natura 2000 network. The majority of the agreements are based on national-level biodiversity conservation designations and resultantly depend on in-country data and identified priorities. By and large the use of national data is standard which takes little account of the collaborative effort of neighbouring countries. Additionally, national-level conservation is facilitated by in-country funding mechanisms. Only the EU and the World Heritage Convention provide external co-funding mechanisms. The selection of biodiversity and implementation of approaches of the framework agreements is based on static inventories.

The assessment has shown that current environmental framework agreements are largely dependent on national conservation strategies and the resulting national-level funding. Dynamic changes are not explicitly incorporated and there are only limited options reviewing static conservation priorities. The support of consistent and coherent biodiversity conservation across large areas highlighted the urgent need for supranational entities such as the EU to take a leading role in conservation.

7.5 Concluding remarks

This thesis has shown that:

i. Using in-country truncated biodiversity data results in large-scale erroneous predictions, especially when projecting into non-analogous bioclimatic conditions.

ii. Biodiversity conservation funding is marked by significant heterogeneity between EU states and this has serious implications for parity across Europe for species and habitat conservation. Furthermore, economic variables have been identified as being the deciding factor for new conservation designations. A more prominent consideration of ecological aspects is highly desirable.

iii. Temporal dynamics of biodiversity through time are clearly identifiable through use of suitable data and tools but these are rarely used which has significant implications for trans-boundary conservation planning in response to climate change and associated sustainable resource use.

iv. Currently the environmental frameworks supposed to conserve biodiversity have shown limited effectiveness due to inconsistent, mainly national-level implementation and lack of appropriate ecological datasets in space and time. Involvement of the EU as conservation actor is identified as essential.

Overall these results contribute decisively to understanding and facilitating biodiversity conservation across Europe under dynamic shocks such as climate change. The information gathered through this research is relevant to a broad audience of scientists, conservation practitioners, and policy makers. The research approach is both interdisciplinary as well as replicable for other areas or focus taxa which supports its wide-scale applicability.

Biodiversity, while under continued threat and declining, has shown to have had large-scale persistence in the past. The crucial point for current biodiversity conservation research is to facilitate the informed use of suitable tools in order to identify the most efficient and effective opportunities to support biodiversity both now and in the future. Interdisciplinary research joining viewpoints from science, economics, and politics continues to hold the potential to provide forward-looking conservation strategies supporting the ultimate aim of halting biodiversity decline and preserve ecosystems permanently.

Appendices

A
Supplementary materials - Chapter 3

The supporting information firstly show two maps for the loadings of the two principal components across Europe. All further parts of the supporting information provide three figures for each of the seven species analysed. For all of these figures the continuous line indicates EUR training data and prediction, the dashed line shows GER training data and European prediction, and the dotted line indicates GER training data and Germany prediction.

I. **PCA maps.** Maps showing the distribution of loadings of the two main components according to the PCA across Europe. The principal component analysis was carried out using all eight bioclimatic variables (annual precipitation, summer precipitation, winter precipitation, mean temperature, minimum temperature, summer temperature, growing degree days, and equilibrium evapotranspiration), which yielded two major axes covering the thermal and hydrological spectrum and accounting for $> 90\%$ of the total variance of the variables.

II. **Ensemble model response curve for each variable and species.** The averaged response curves for the three variables (GDD, pre, presu) as well as the corresponding standard deviations and the variable weighting according to the training data used.

III. **Individual model response curves for all variables and species.** All individual model curves for each of the variables and algorithms and the variable weighting for each of these.

IV. **Occurrence maps for all seven species for both analogue and non-analogue projections.** Occurrence maps showing the study area and the current distribution data (crosshatched) overlayed with the modelled distribution according to European training data and according to Germany-only training data based on AUC threshold.

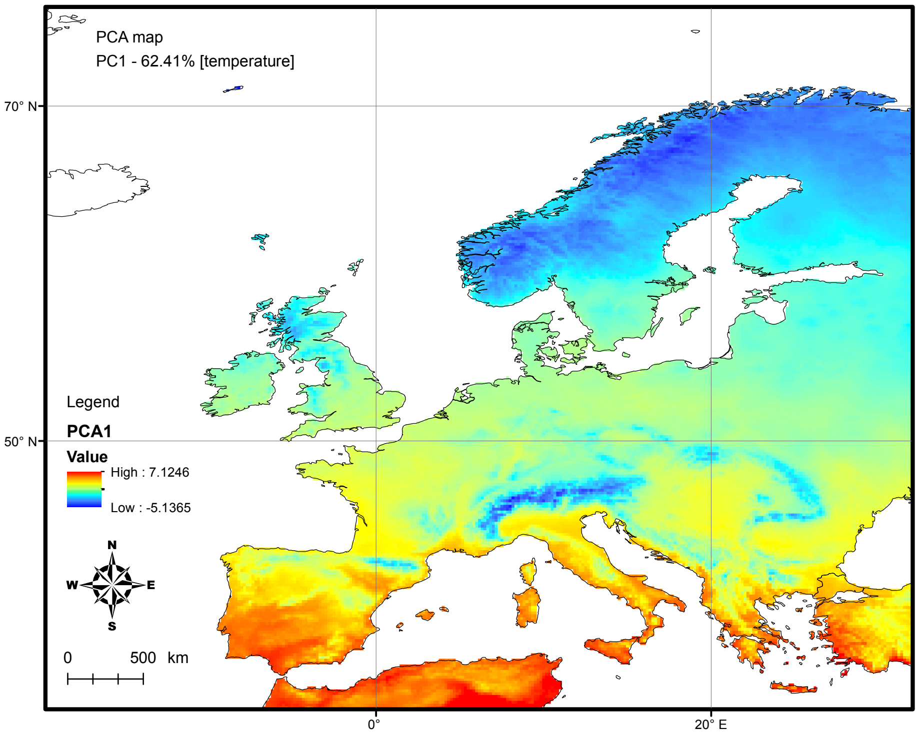


Figure A.1: Map for the loading of the thermal axis of the PCA

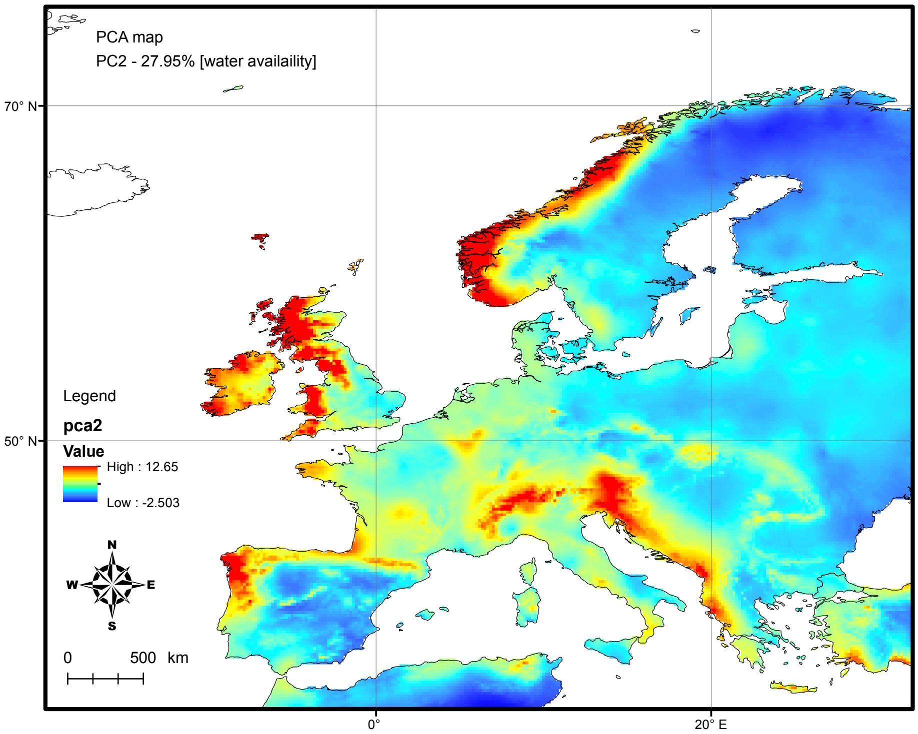


Figure A.2: Map for the loading of the hydrological axis of the PCA

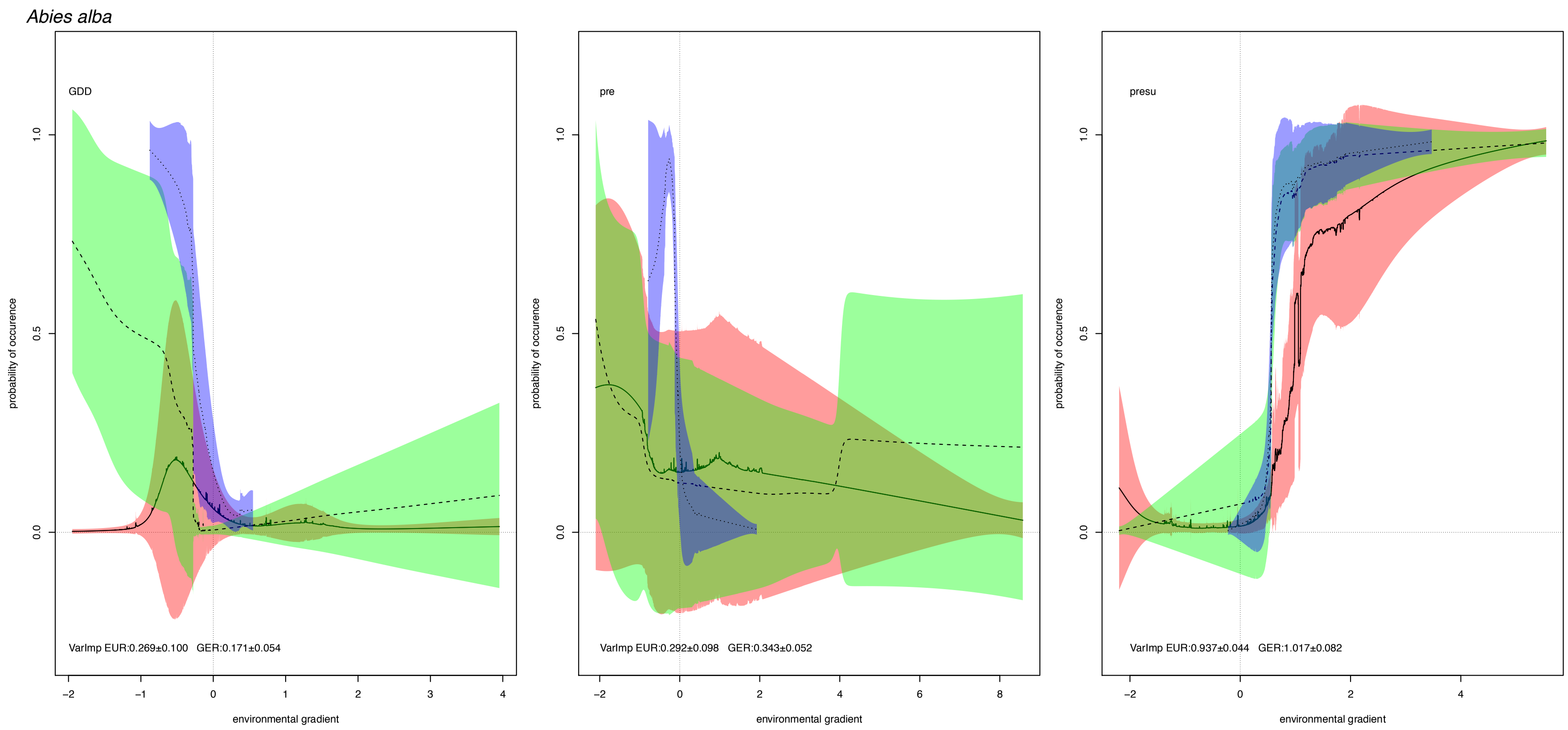


Figure A.3: Figure showing the averaged response curves for *Abies alba* and their corresponding standard deviations as well the weighting of variables according to the training data used (red: EUR training and prediction; green: GER training and EUR prediction: blue: GER training and prediction)

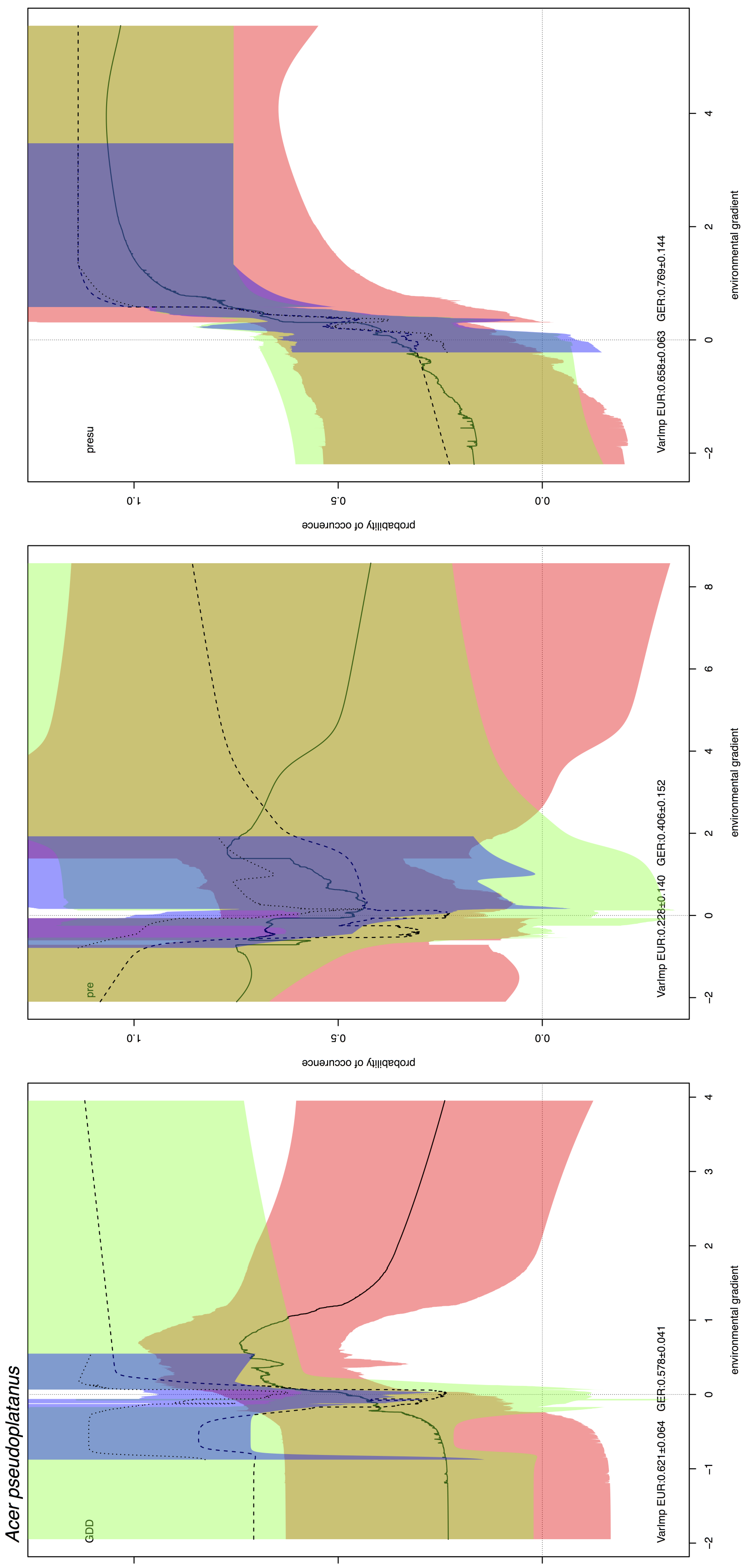


Figure A.4: Figure showing the averaged response curves for *Abies alba* and their corresponding standard deviations as well the weighting of variables according to the training data used (red: EUR training and prediction; green: GER training and prediction; blue: GER training and EUR prediction: blue: GER training and prediction)

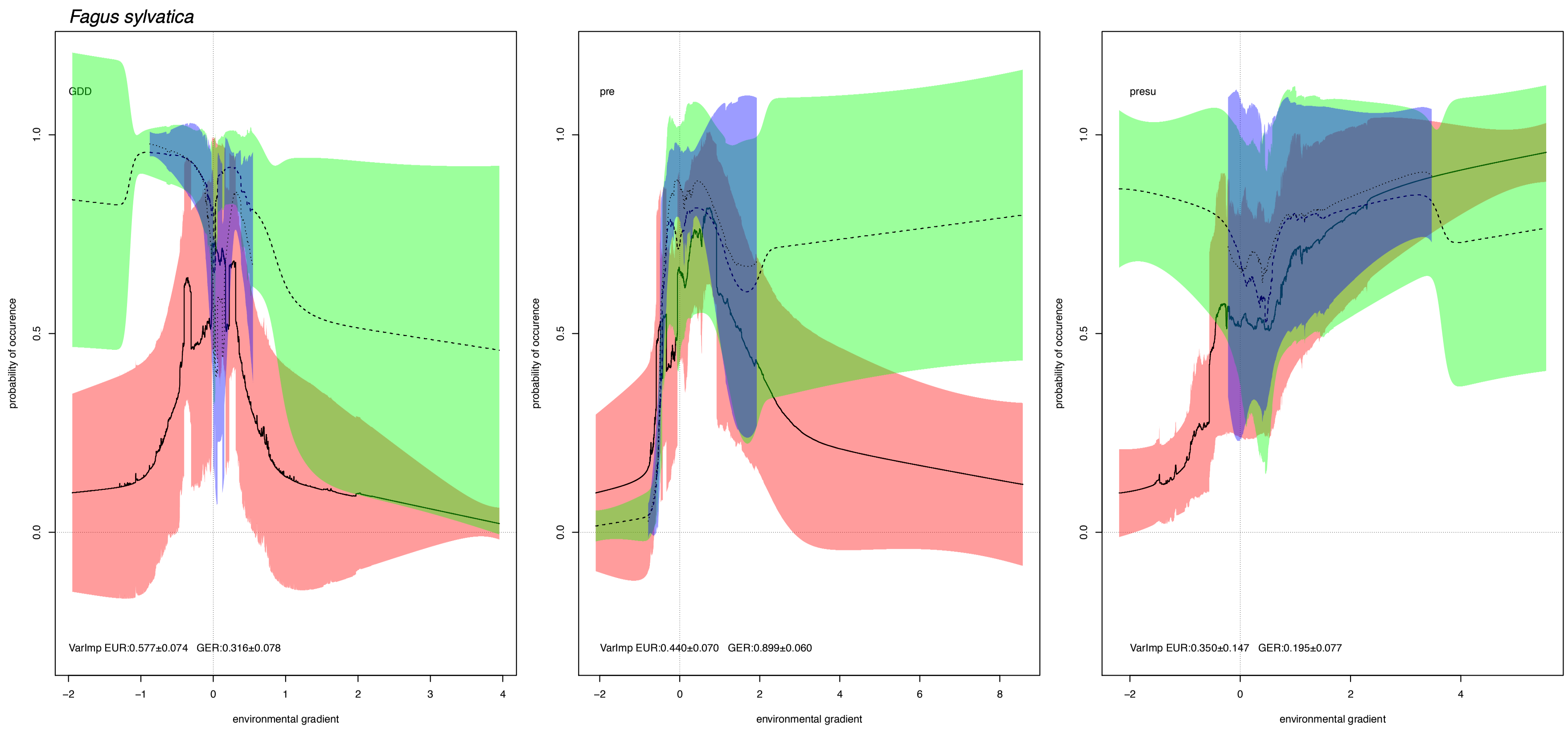


Figure A.5: Figure showing the averaged response curves for *Fagus sylvatica* and their corresponding standard deviations as well the weighting of variables according to the training data used (red: EUR training and prediction; green: GER training and EUR prediction: blue: GER training and prediction)

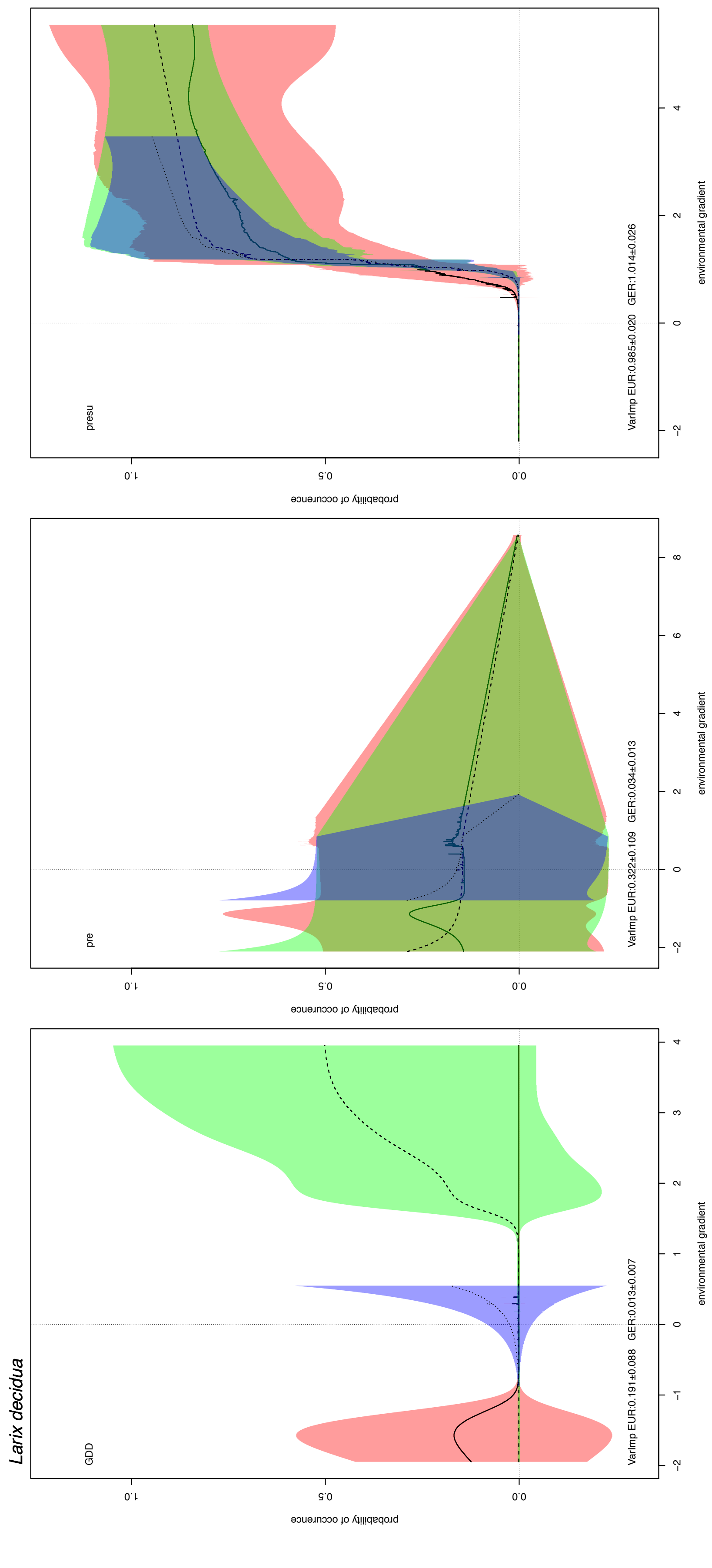


Figure A.6: Figure showing the averaged response curves for *Larix decidua* and their corresponding standard deviations as well the weighting of variables according to the training data used (red: EUR training and prediction; green: GER training and EUR prediction; blue: GER training and prediction)

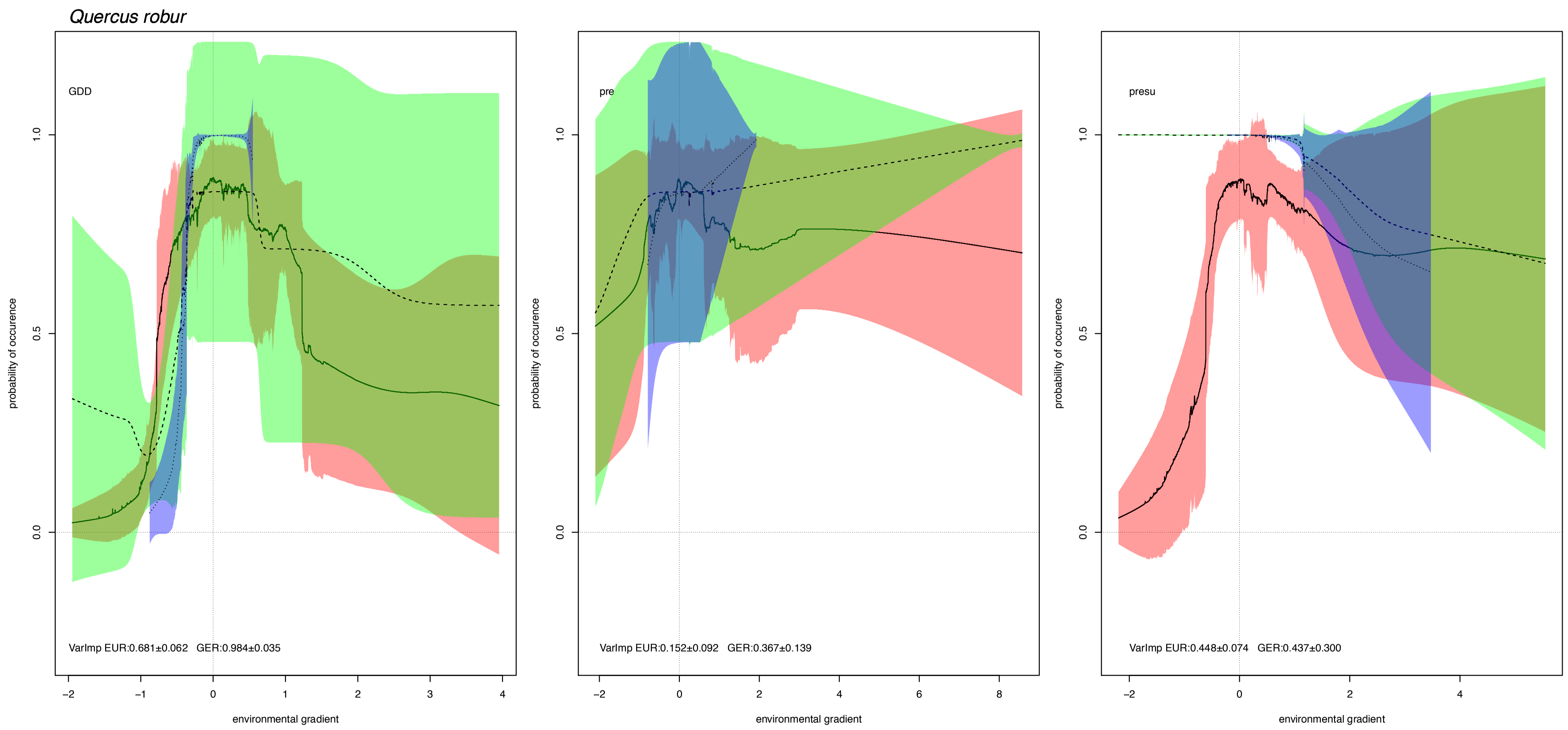


Figure A.7: Figure showing the averaged response curves for *Quercus robur* and their corresponding standard deviations as well the weighting of variables according to the training data used (red: EUR training and prediction; green: GER training and EUR prediction: blue: GER training and prediction)

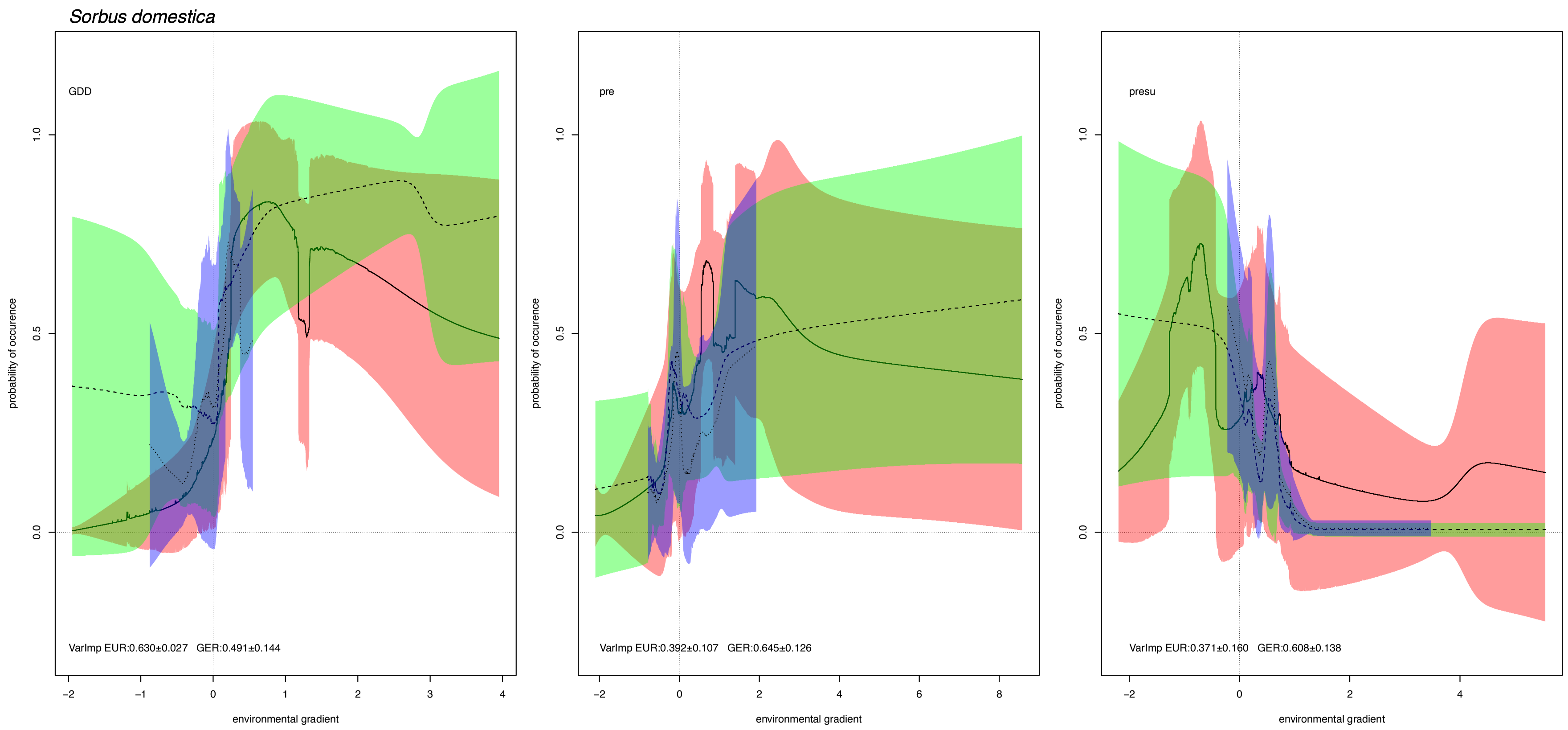


Figure A.8: Figure showing the averaged response curves for *Sorbus domestica* and their corresponding standard deviations as well the weighting of variables according to the training data used (red: EUR training and prediction; green: GER training and EUR prediction: blue: GER training and prediction)

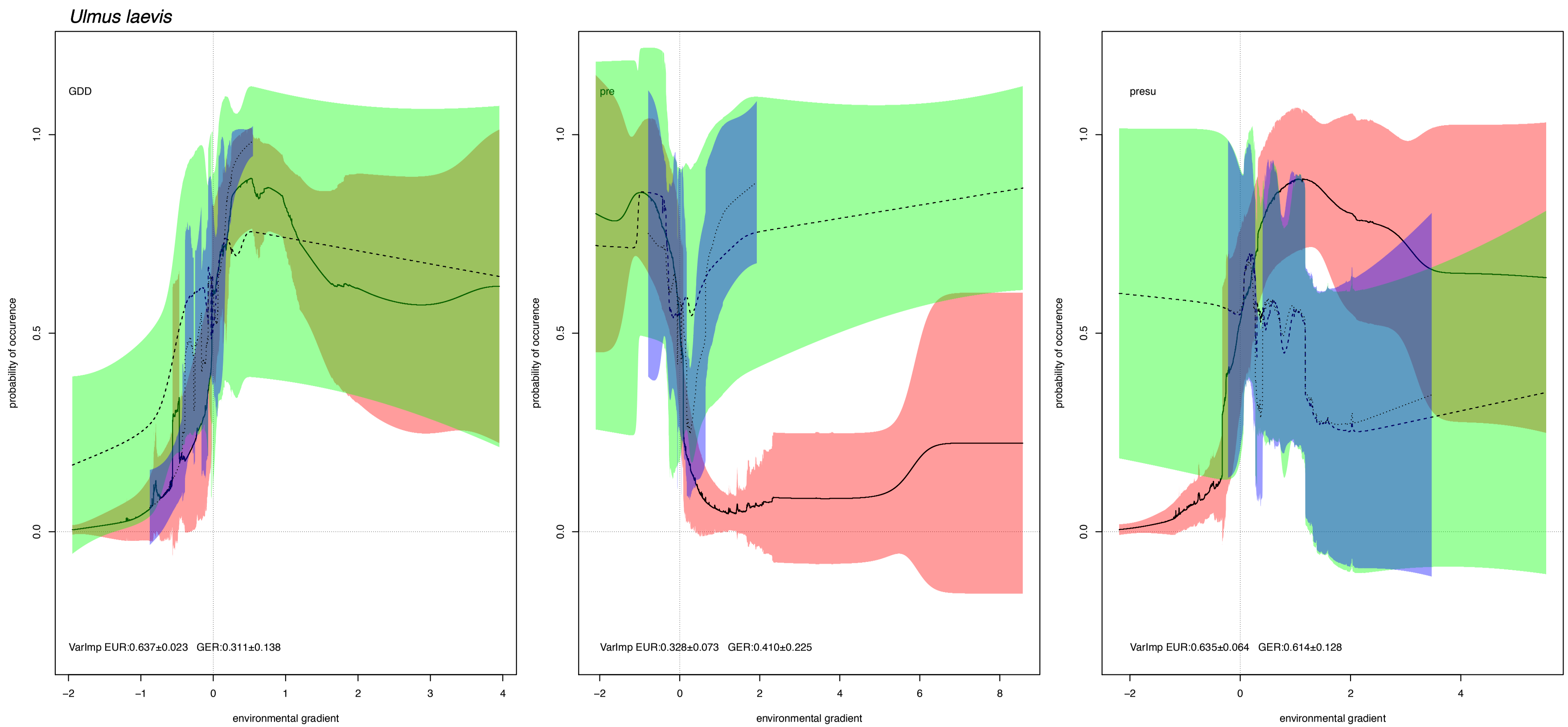


Figure A.9: Figure showing the averaged response curves for *Ulmus laevis* and their corresponding standard deviations as well the weighting of variables according to the training data used (red: EUR training and prediction; green: GER training and EUR prediction: blue: GER training and prediction)

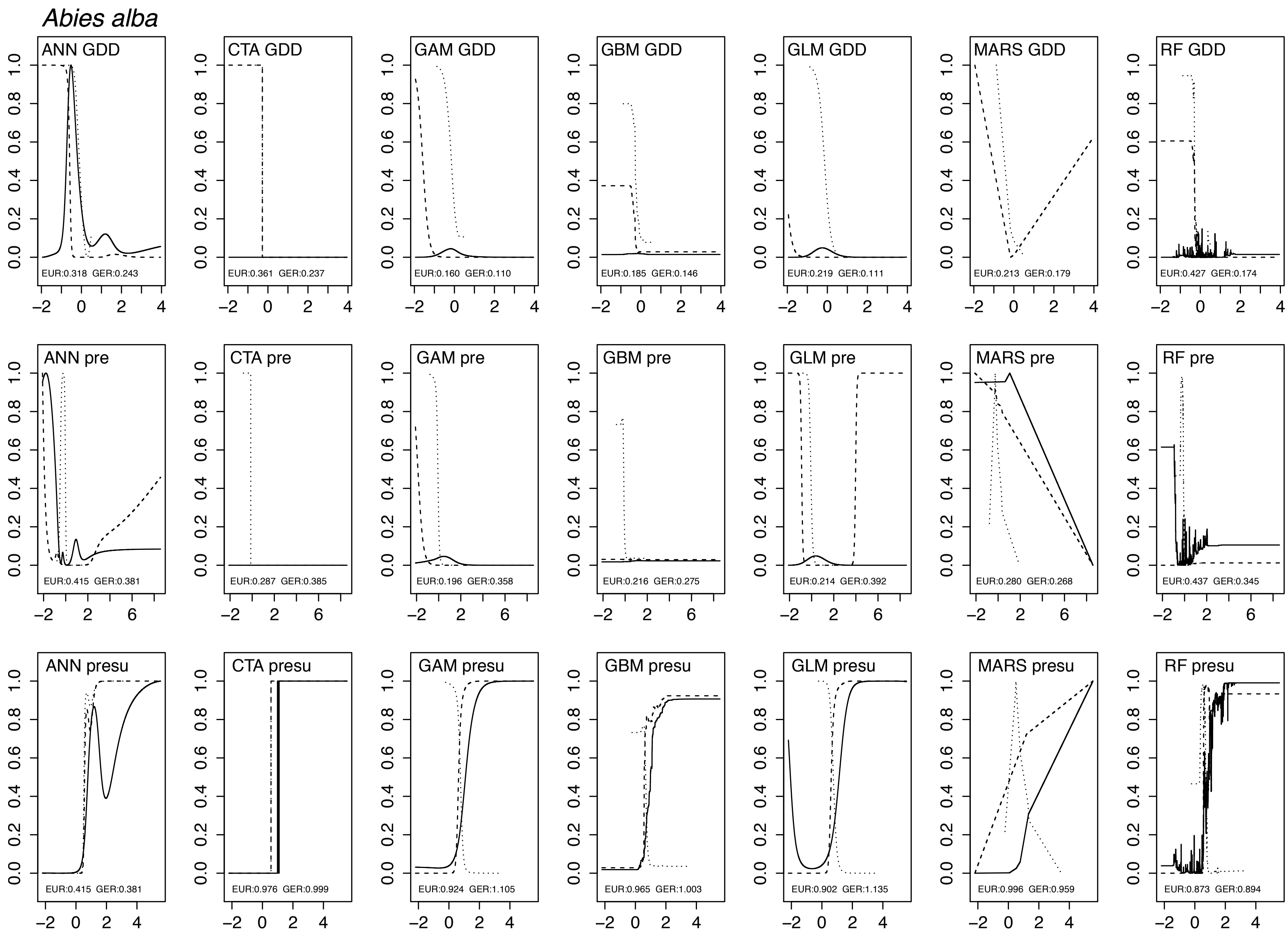


Figure A.10: Figure showing the individual response curves for *Abies alba* for all variables and model types. Dotted denotes GER training and projection data; dashed denotes GER training and EUR projection data, continuous line denotes EUR training and projection data.

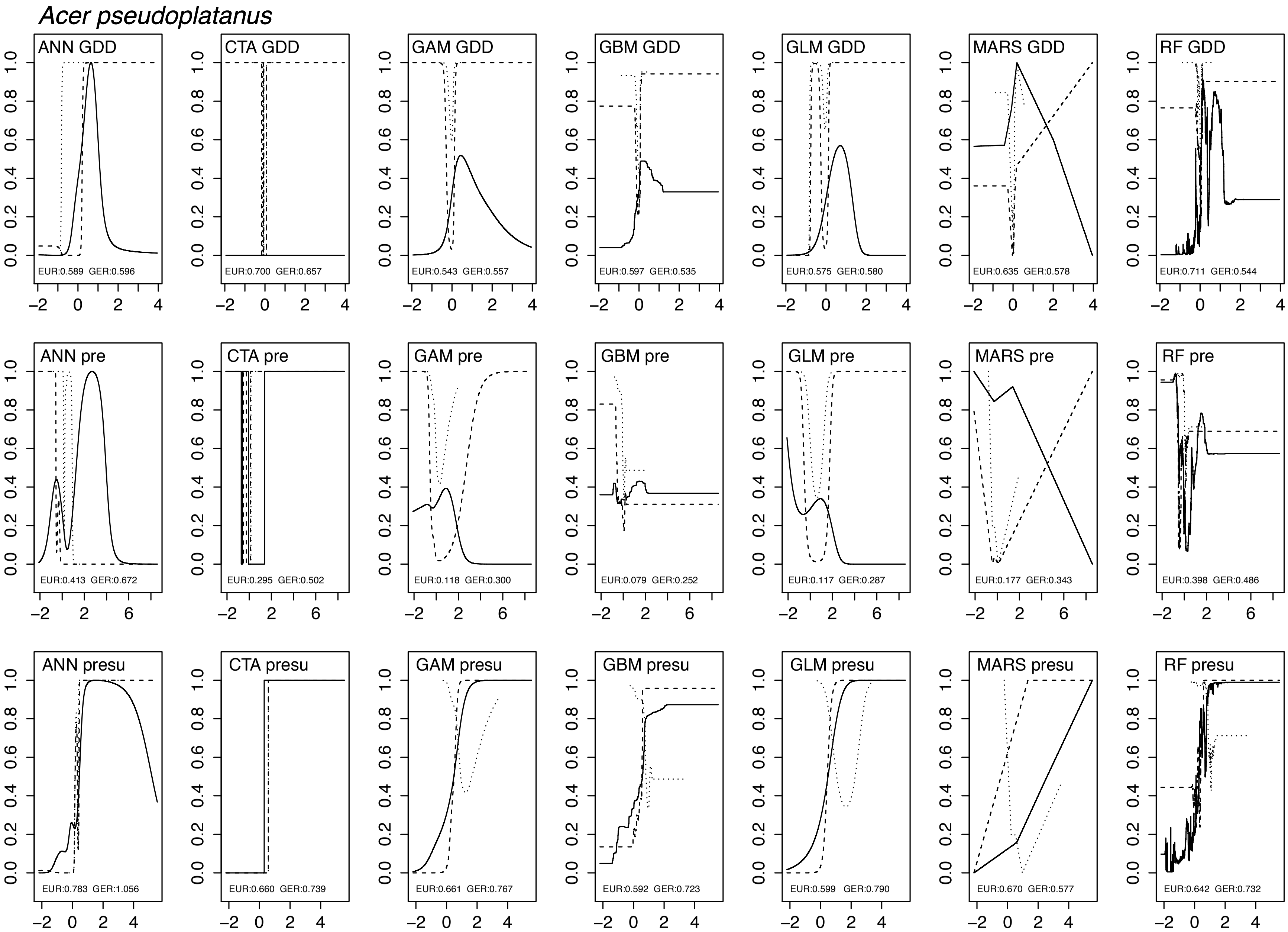


Figure A.11: Figure showing the individual response curves for *Acer pseudoplatanus* for all variables and model types. Dotted denotes GER training and projection data; dashed denotes GER training and EUR projection data, continuous line denotes EUR training and projection data.

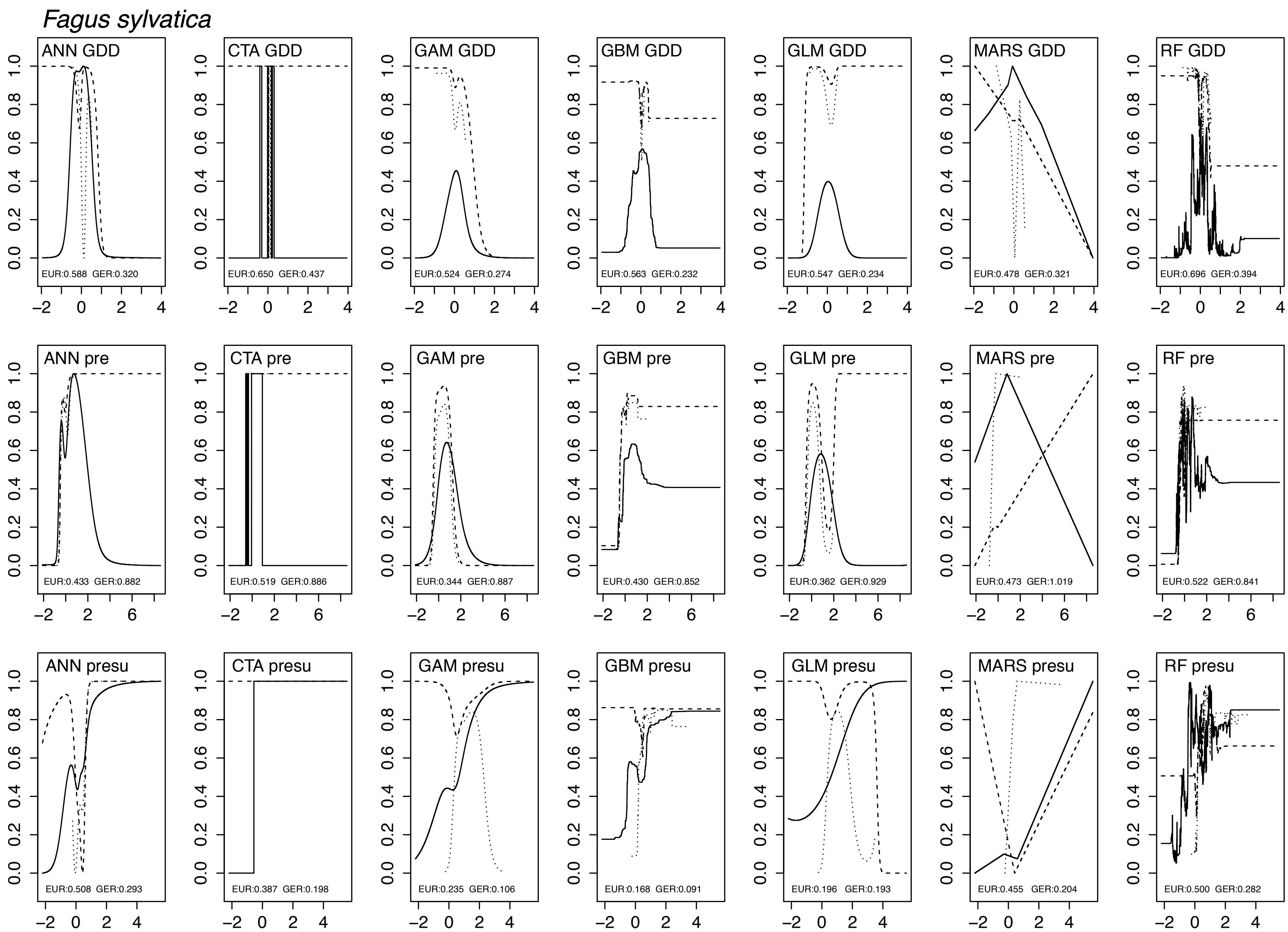


Figure A.12: Figure showing the individual response curves for *Fagus sylvatica* for all variables and model types. Dotted denotes GER training and projection data; dashed denotes GER training and EUR projection data, continuous line denotes EUR training and projection data.

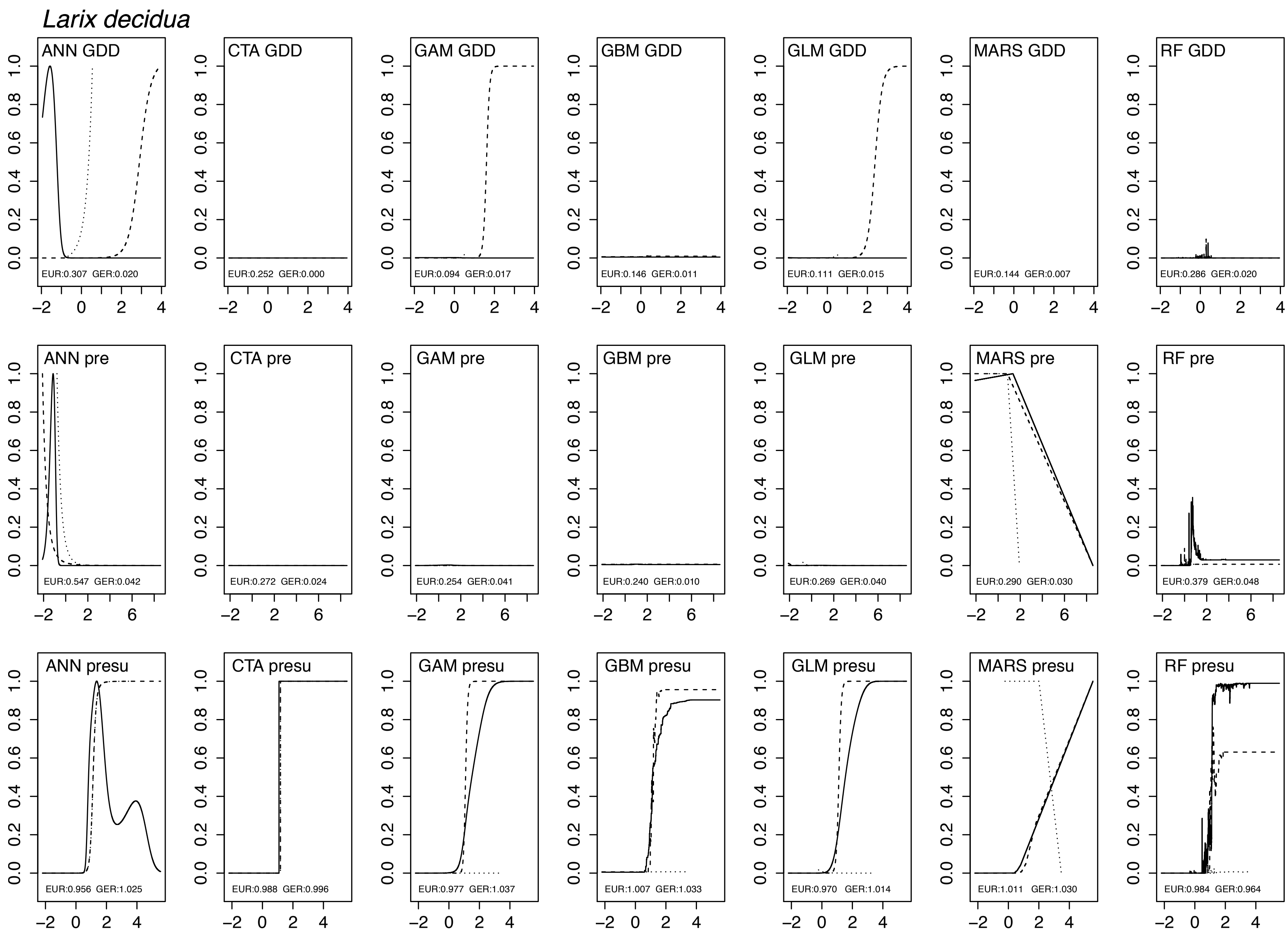


Figure A.13: Figure showing the individual response curves for *Larix decidua* for all variables and model types. Dotted denotes GER training and projection data; dashed denotes GER training and EUR projection data, continuous line denotes EUR training and projection data.

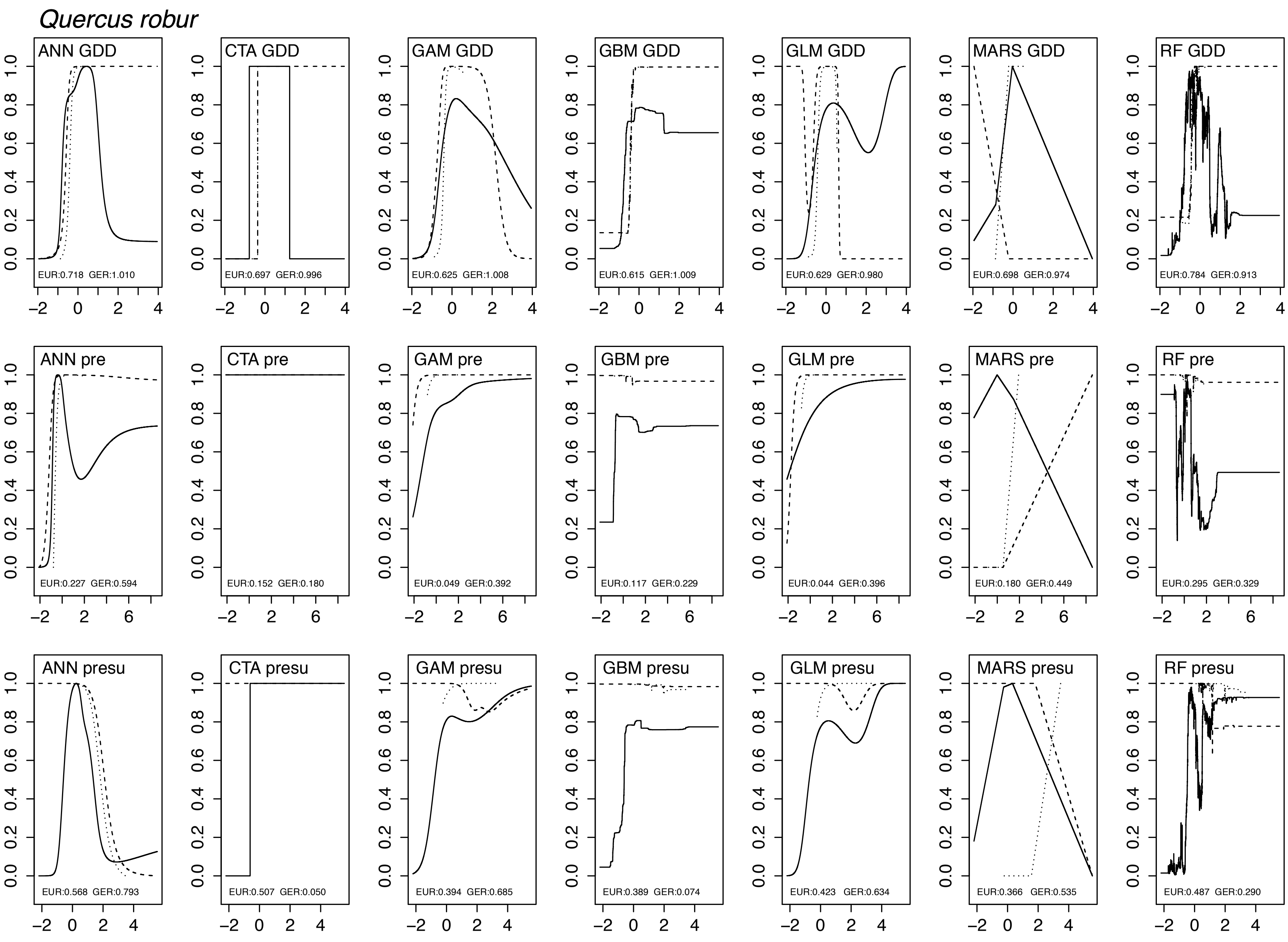


Figure A.14: Figure showing the individual response curves for *Quercus robur* for all variables and model types. Dotted denotes GER training and projection data; dashed denotes GER training and EUR projection data, continuous line denotes EUR training and projection data.

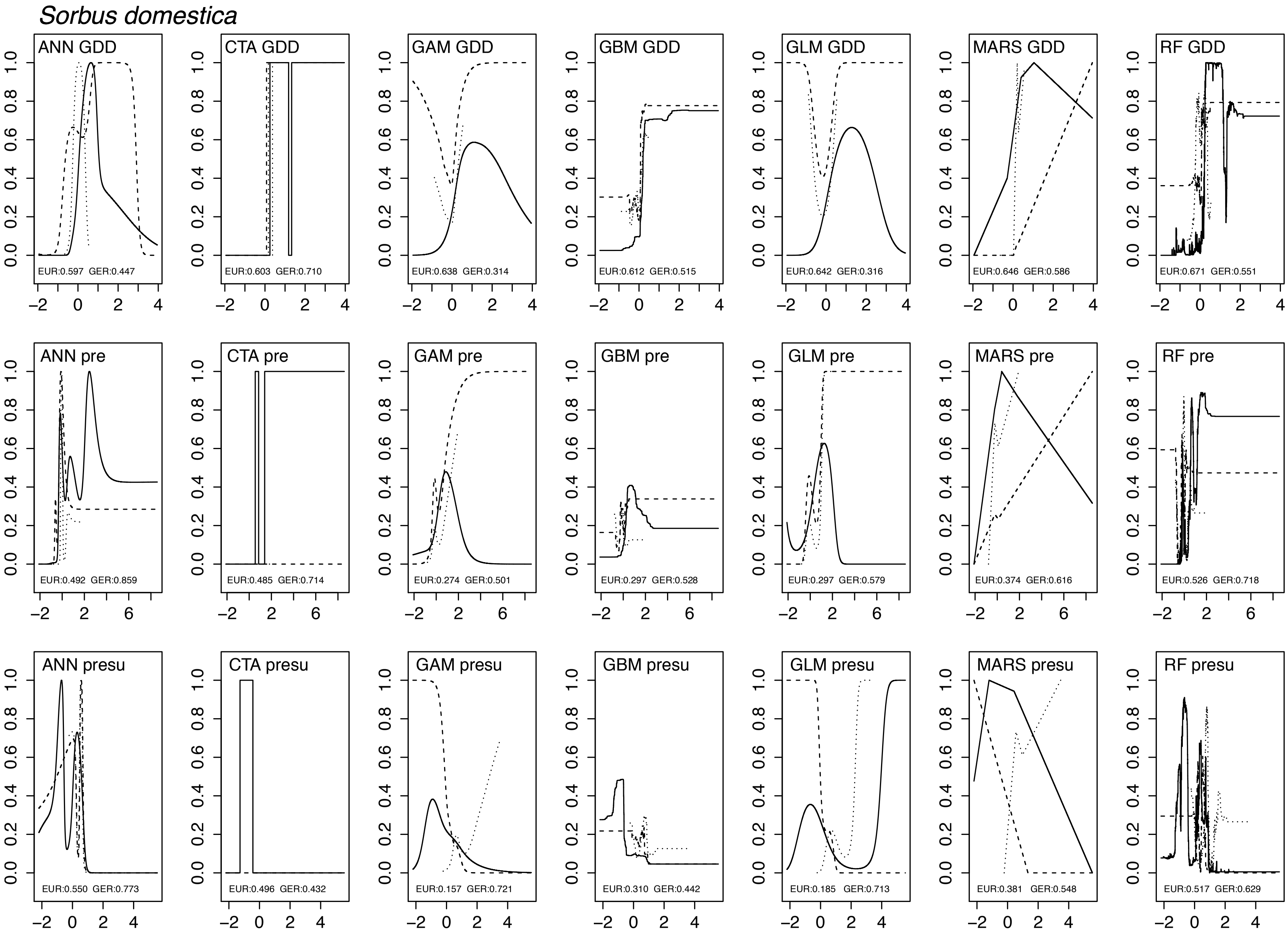


Figure A.15: Figure showing the individual response curves for *Sorbus domestica* for all variables and model types. Dotted denotes GER training and projection data; dashed denotes GER training and EUR projection data, continuous line denotes EUR training and projection data.

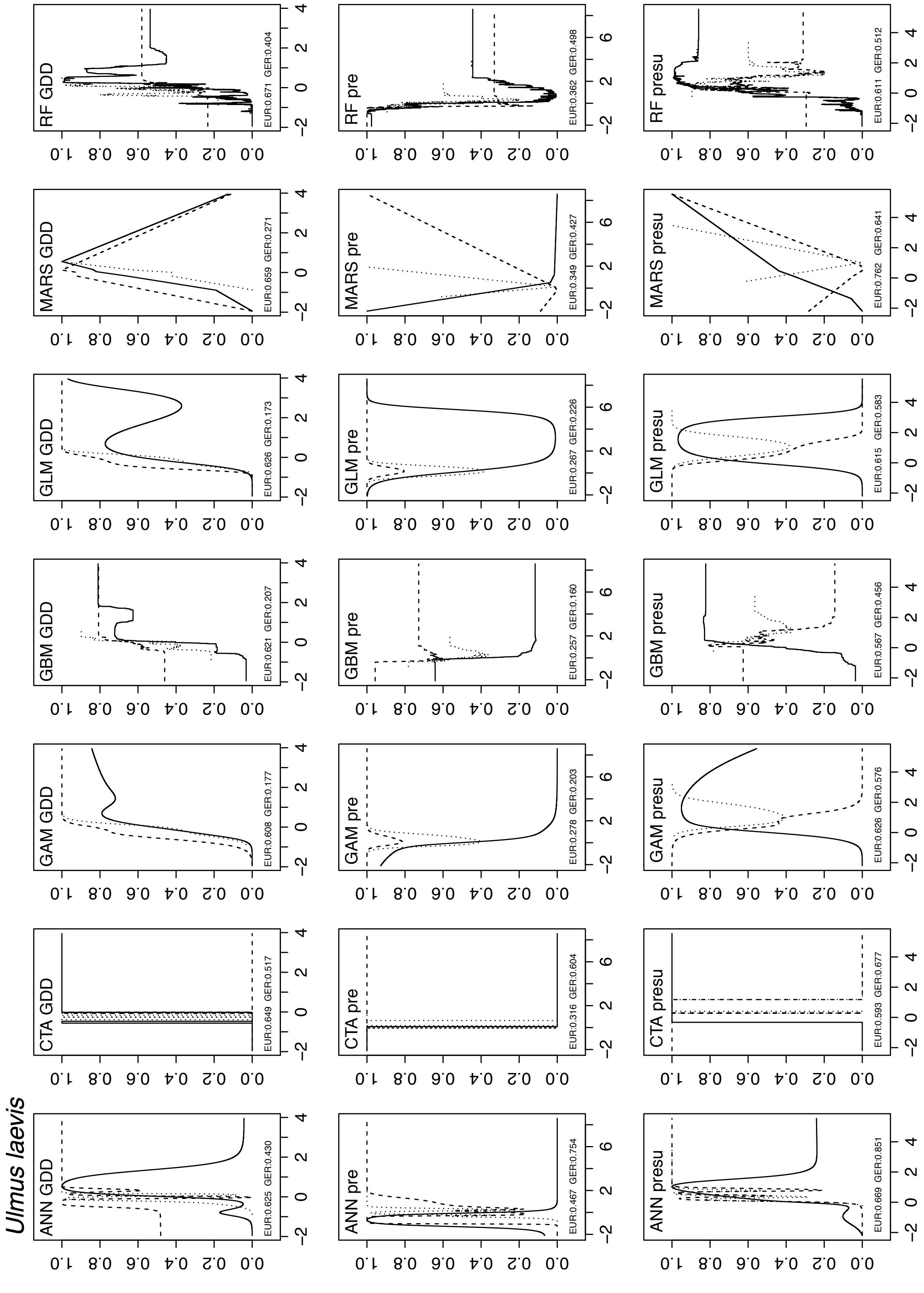


Figure A.16: Figure showing the individual response curves for *Ulmus laevis* for all variables and model types. Dotted denotes GER training and projection data; dashed denotes GER training and EUR projection data, continuous line denotes EUR training and projection data.

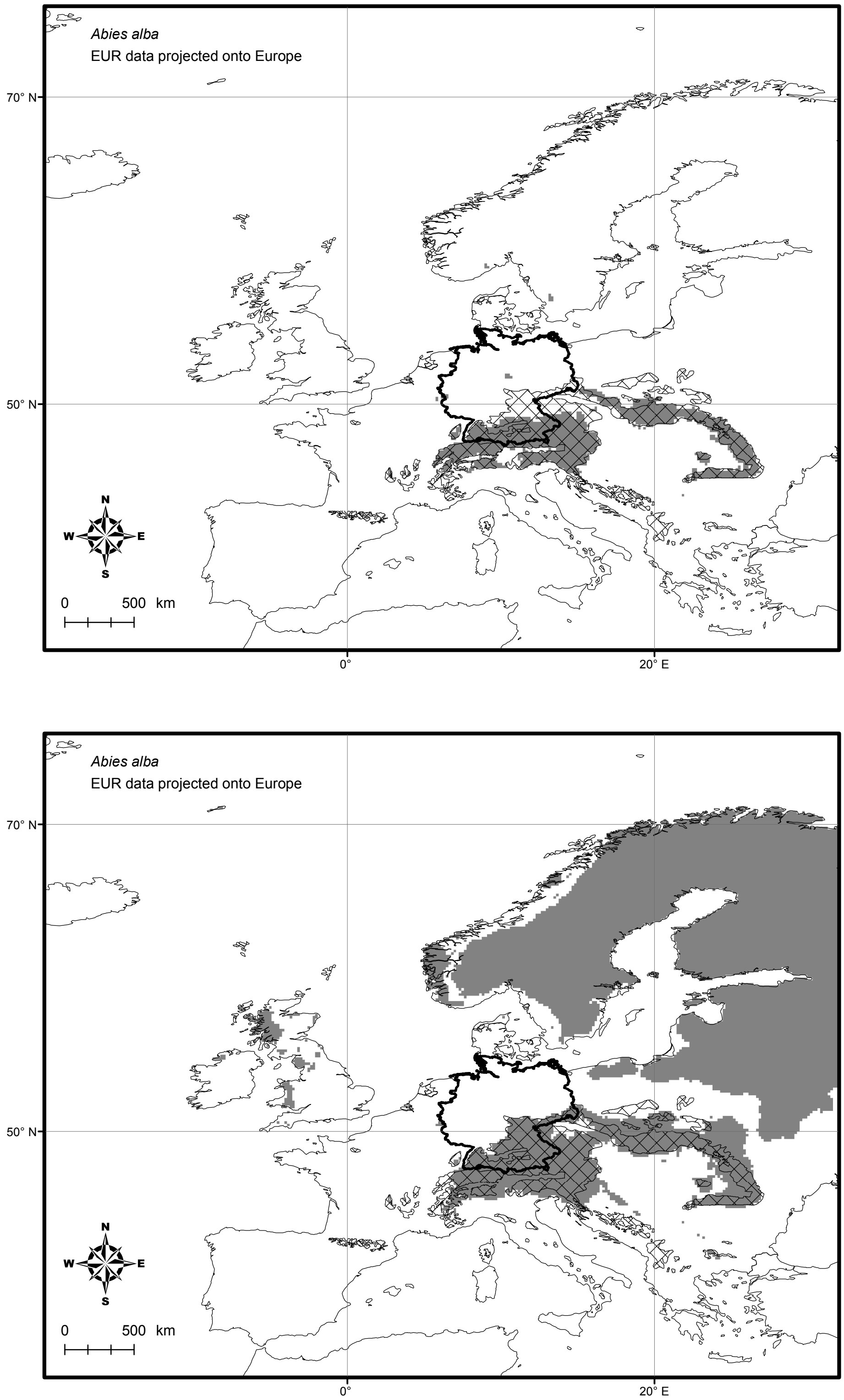
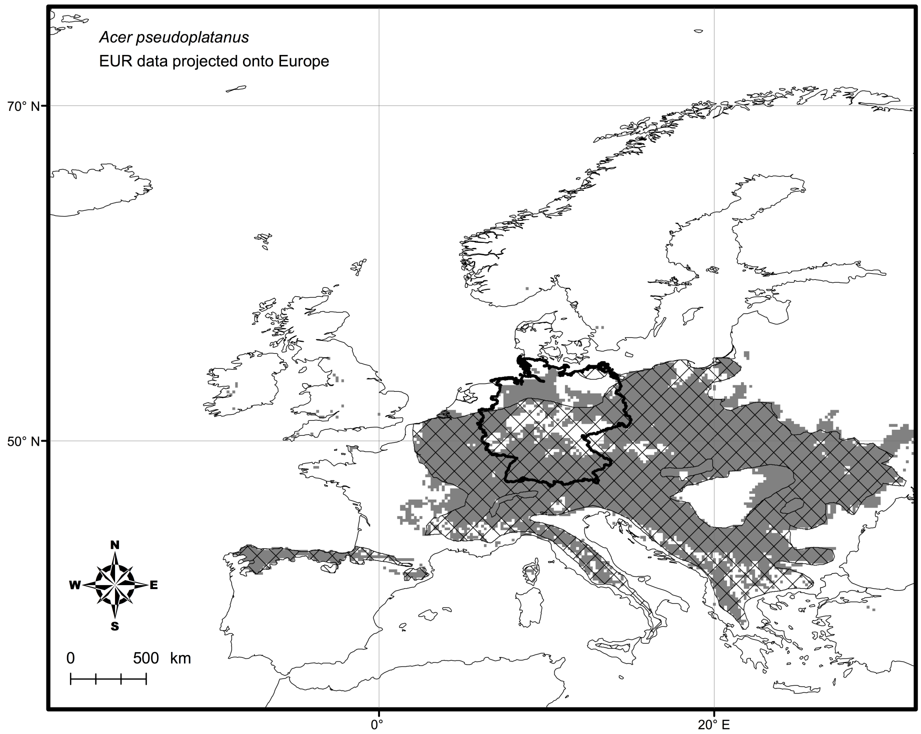


Figure A.17: Occurrence maps showing the current distribution of *Abies alba* (crosshatched) overlayed with the modelled distribution (grey) according EUR training data (top) and according GER training data (bottom).



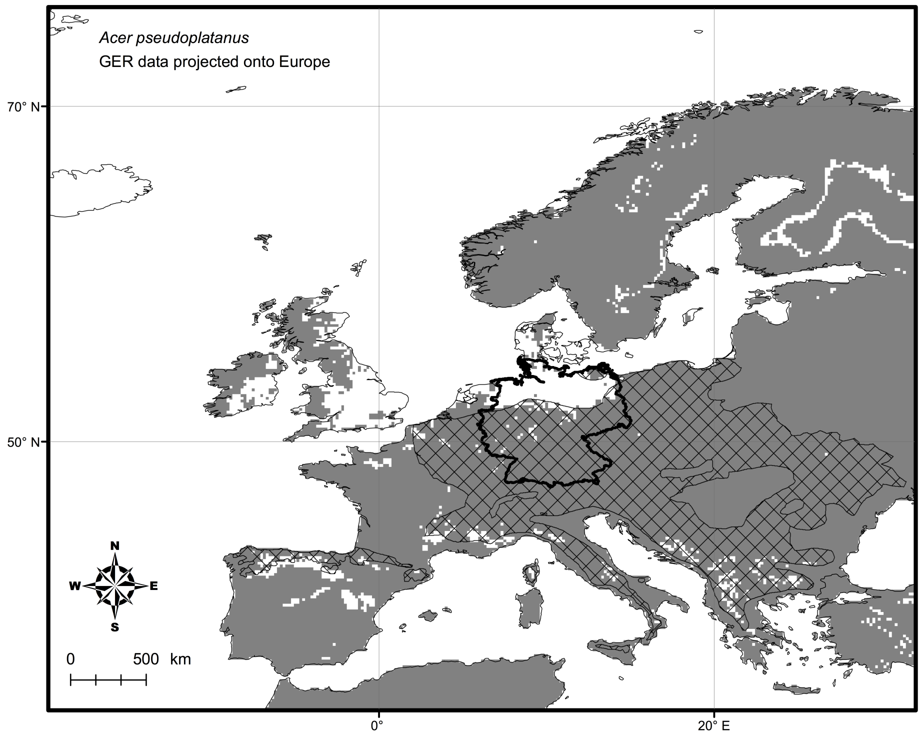


Figure A.18: Occurrence maps showing the current distribution of *Acer pseudoplatanus* (crosshatched) overlayed with the modelled distribution (grey) according EUR training data (top) and according GER training data (bottom).

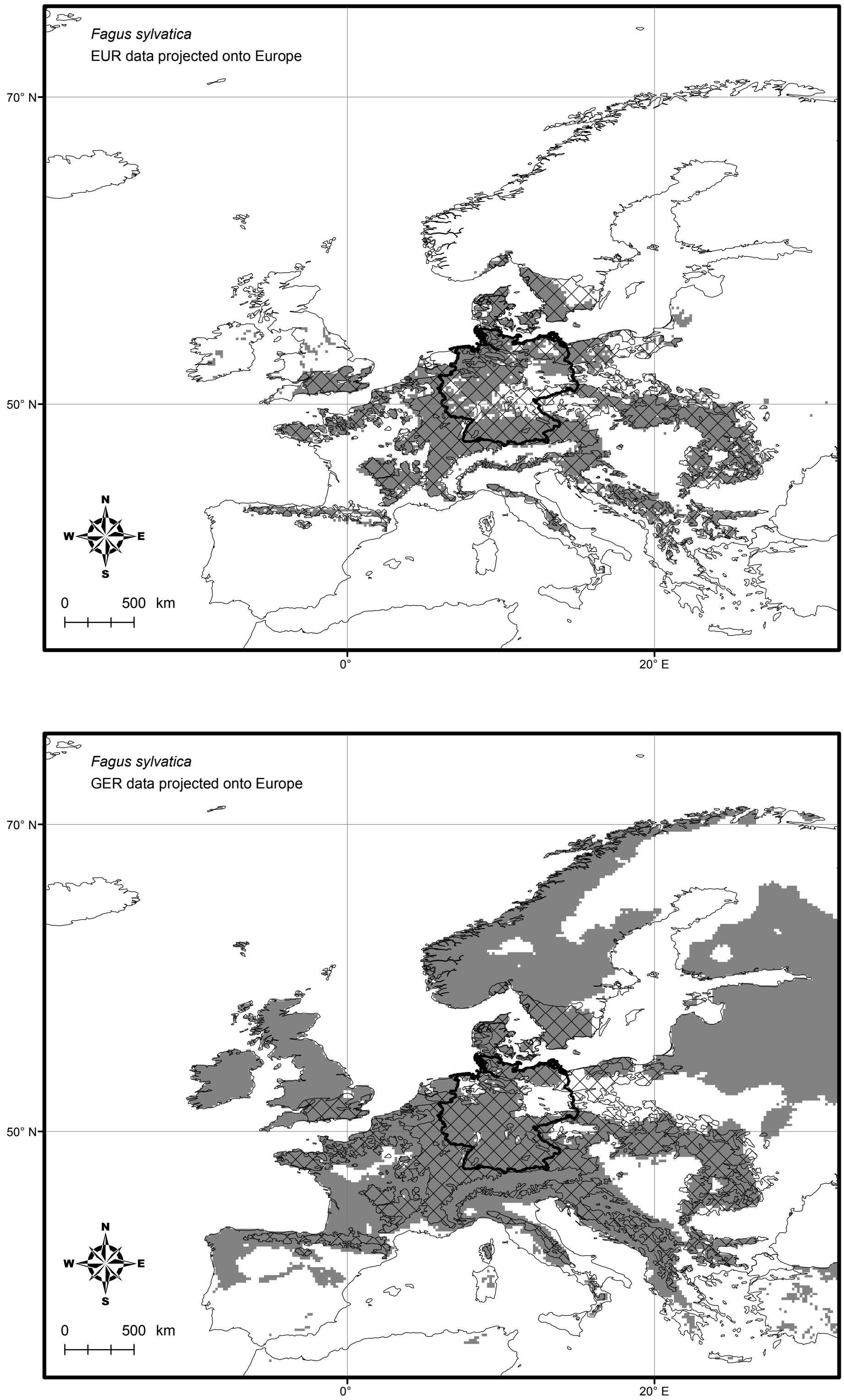


Figure A.19: Occurrence maps showing the current distribution of *Fagus sylvatica* (crosshatched) overlayed with the modelled distribution (grey) according EUR training data (top) and according GER training data (bottom).

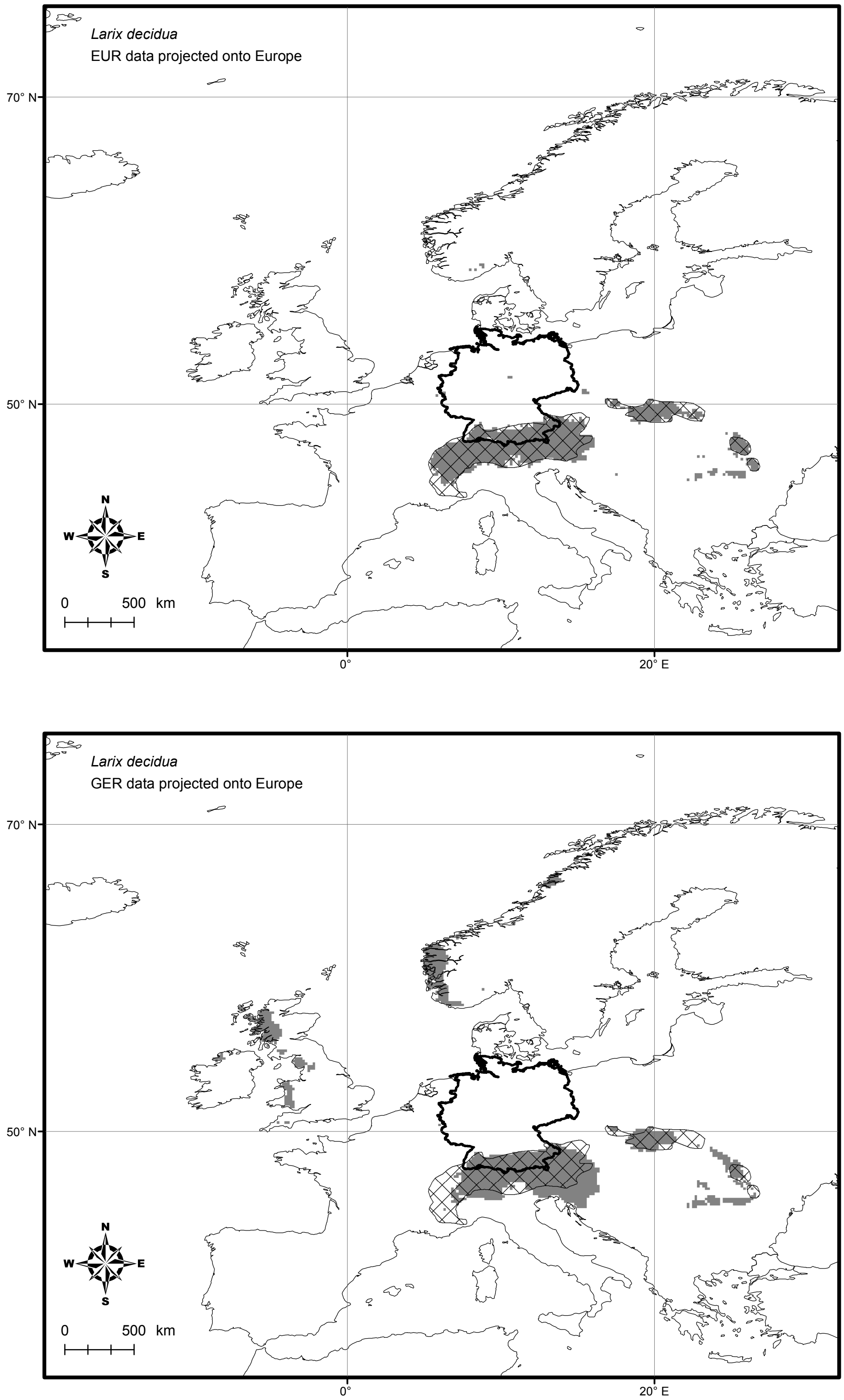
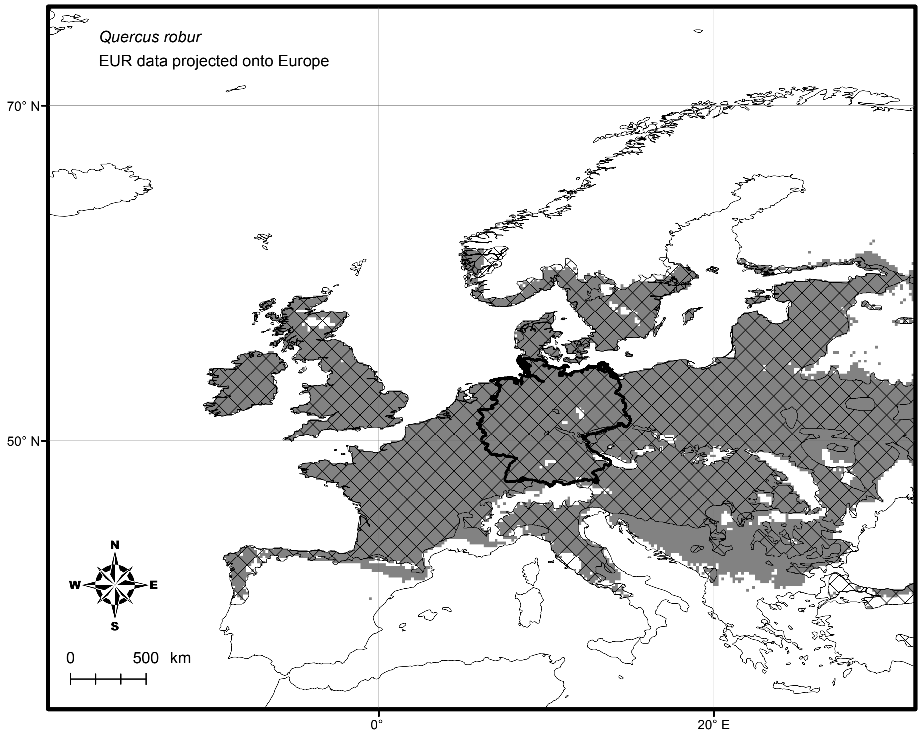


Figure A.20: Occurrence maps showing the current distribution of *Larix decidua* (crosshatched) overlayed with the modelled distribution (grey) according EUR training data (top) and according GER training data (bottom).



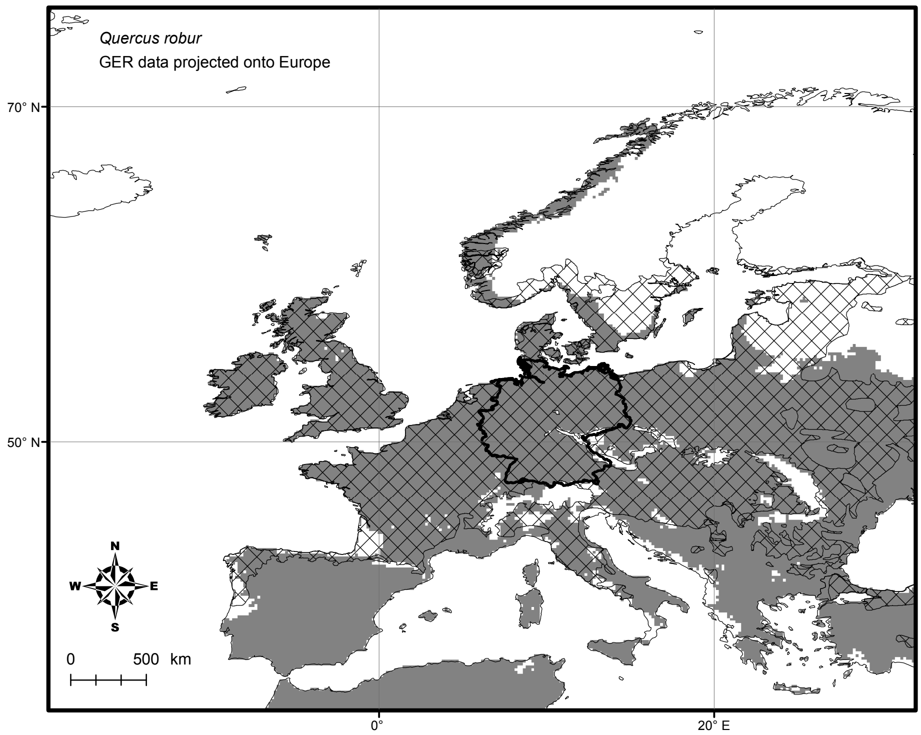


Figure A.21: Occurrence maps showing the current distribution of *Quercus robur* (crosshatched) overlayed with the modelled distribution (grey) according EUR training data (top) and according GER training data (bottom).

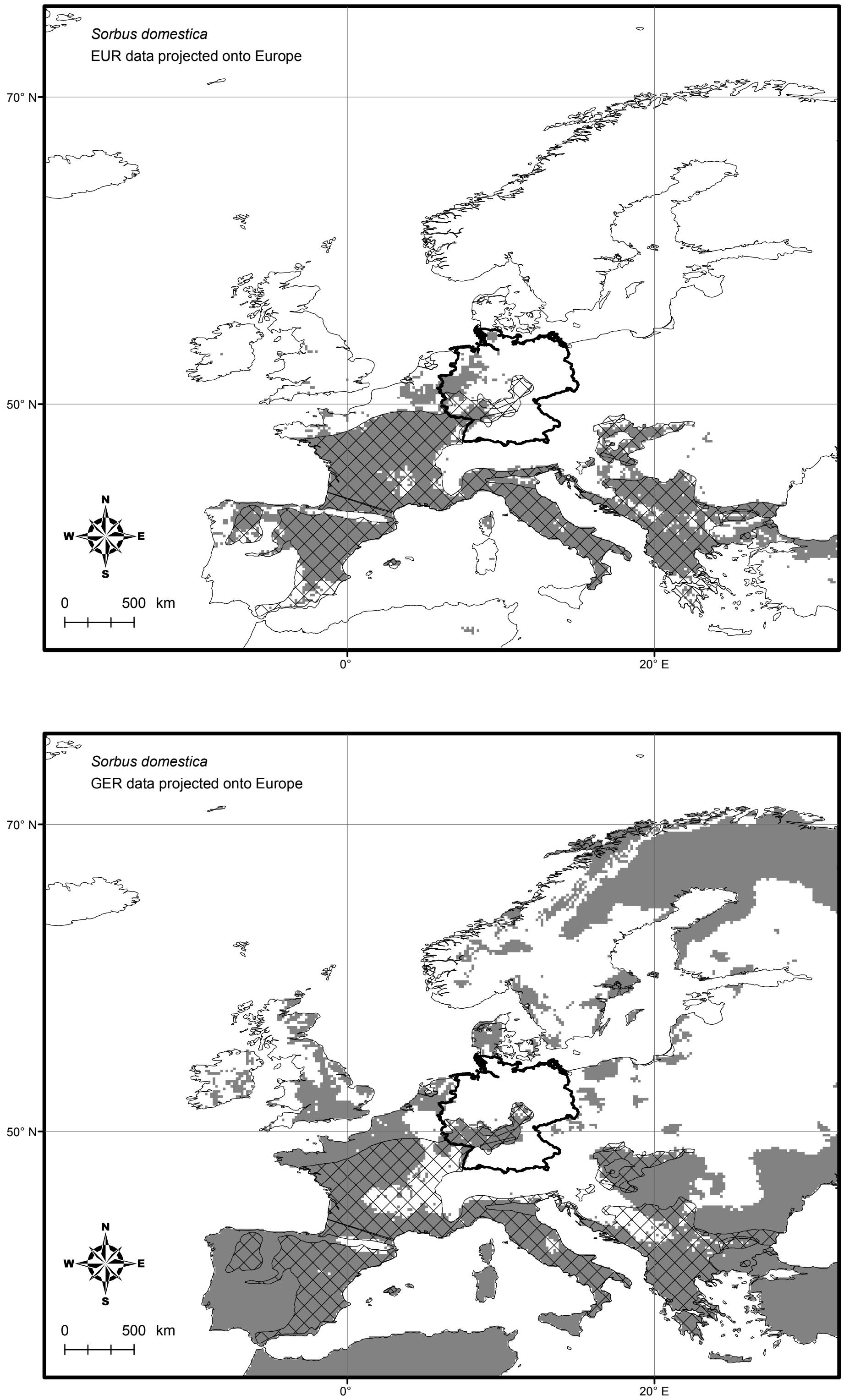


Figure A.22: Occurrence maps showing the current distribution of *Sorbus domestica* (crosshatched) overlayed with the modelled distribution (grey) according EUR training data (top) and according GER training data (bottom).

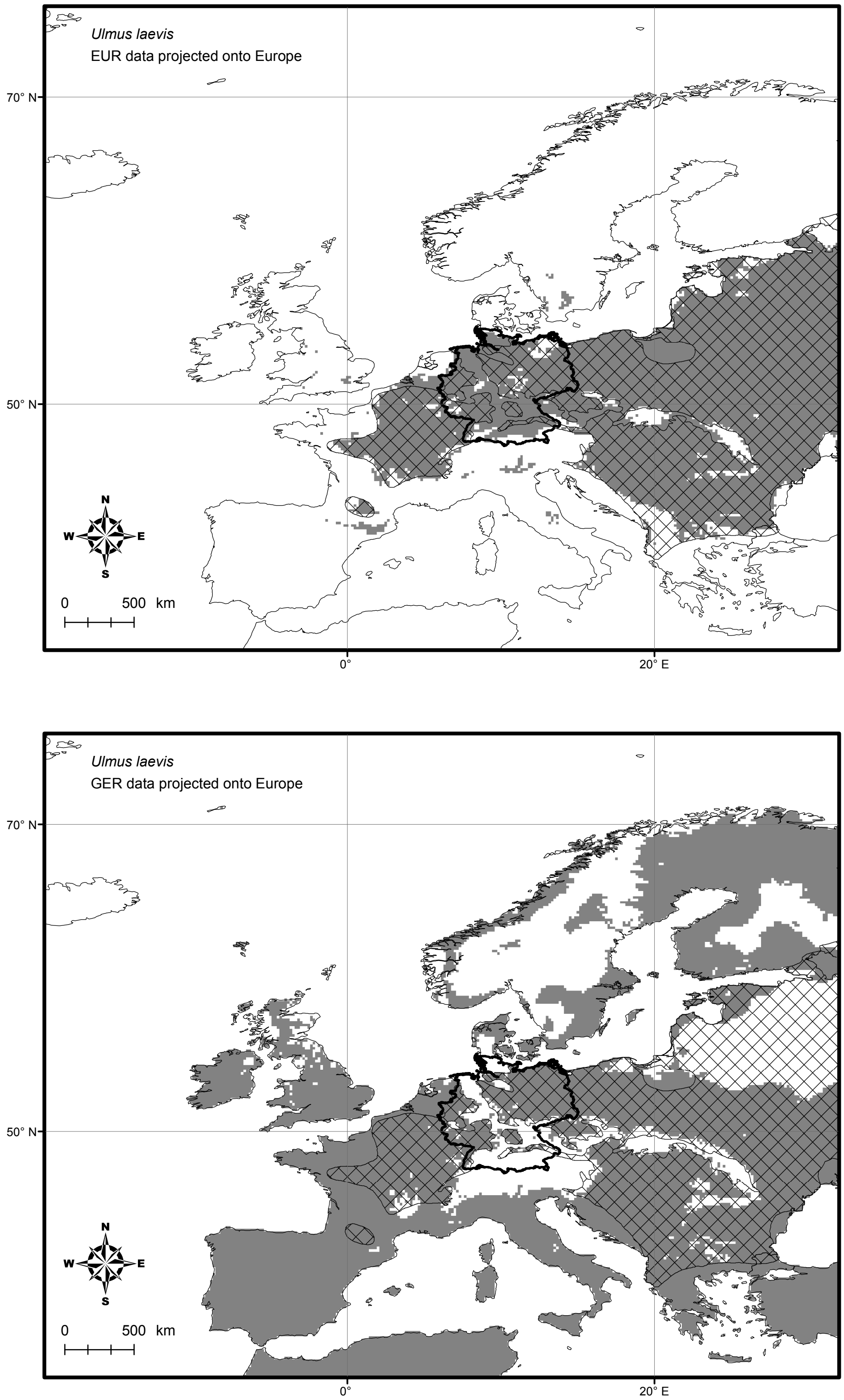


Figure A.23: Occurrence maps showing the current distribution of *Ulmus laevis* (crosshatched) overlayed with the modelled distribution (grey) according EUR training data (top) and according GER training data (bottom).

B
Supplementary materials - Chapter 5

The supplementary materials show the model output information for all genera. The maps are split into the nine timeslices (**A** to **I**) and represent both the probability distribution and the persistence as maximised by AUC as presence/absence. The timeslice is indicated by 1,000 years ago (kya). The sub figure **K** represents the aggregated probability or persistence respectively across all nine model outputs.

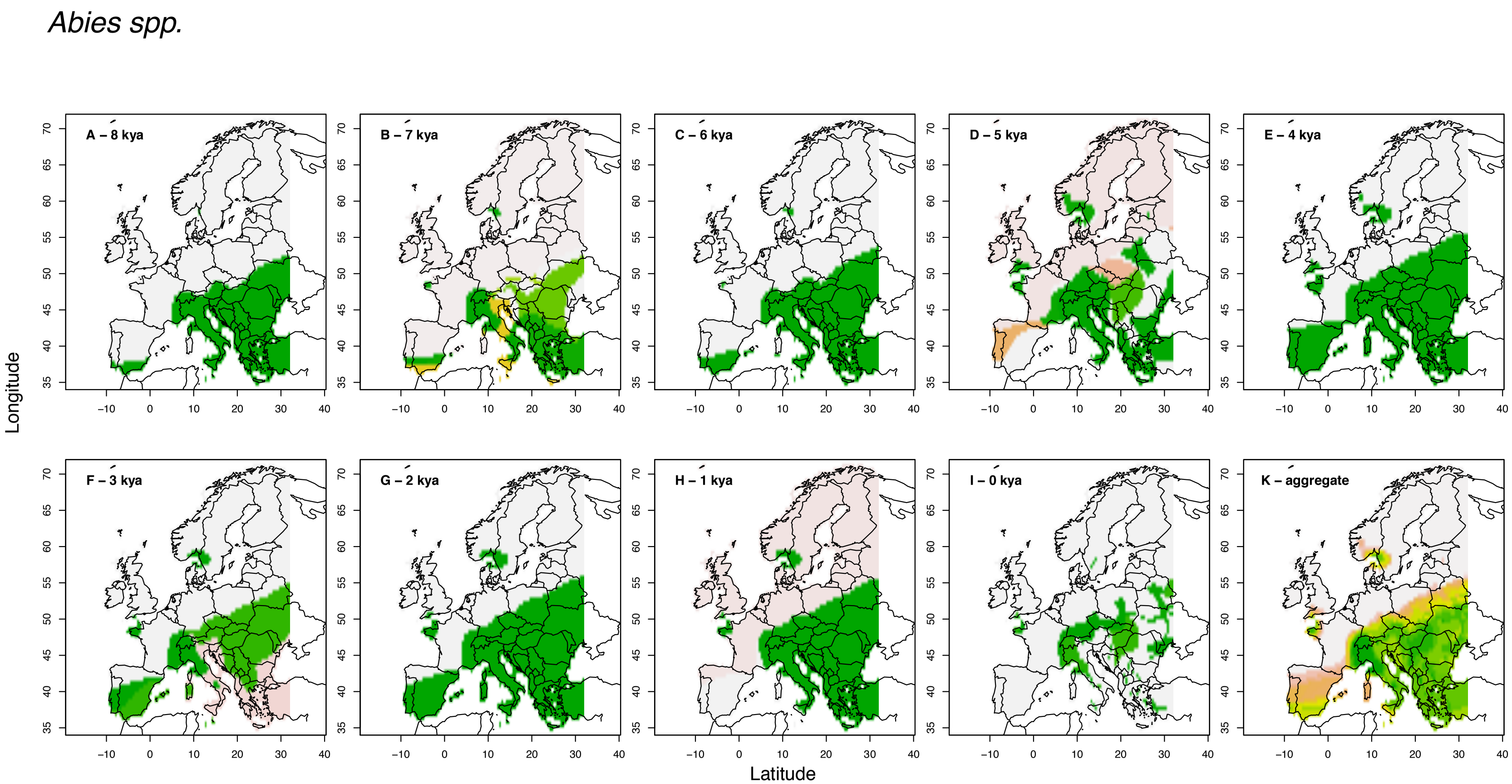


Figure B.1: Probability distribution map for *Abies*. Map of *Abies* showing the predicted presence according to the modelling results per time period. White indicates no probability, beige a low probability, scaled through to green indicating high probability.

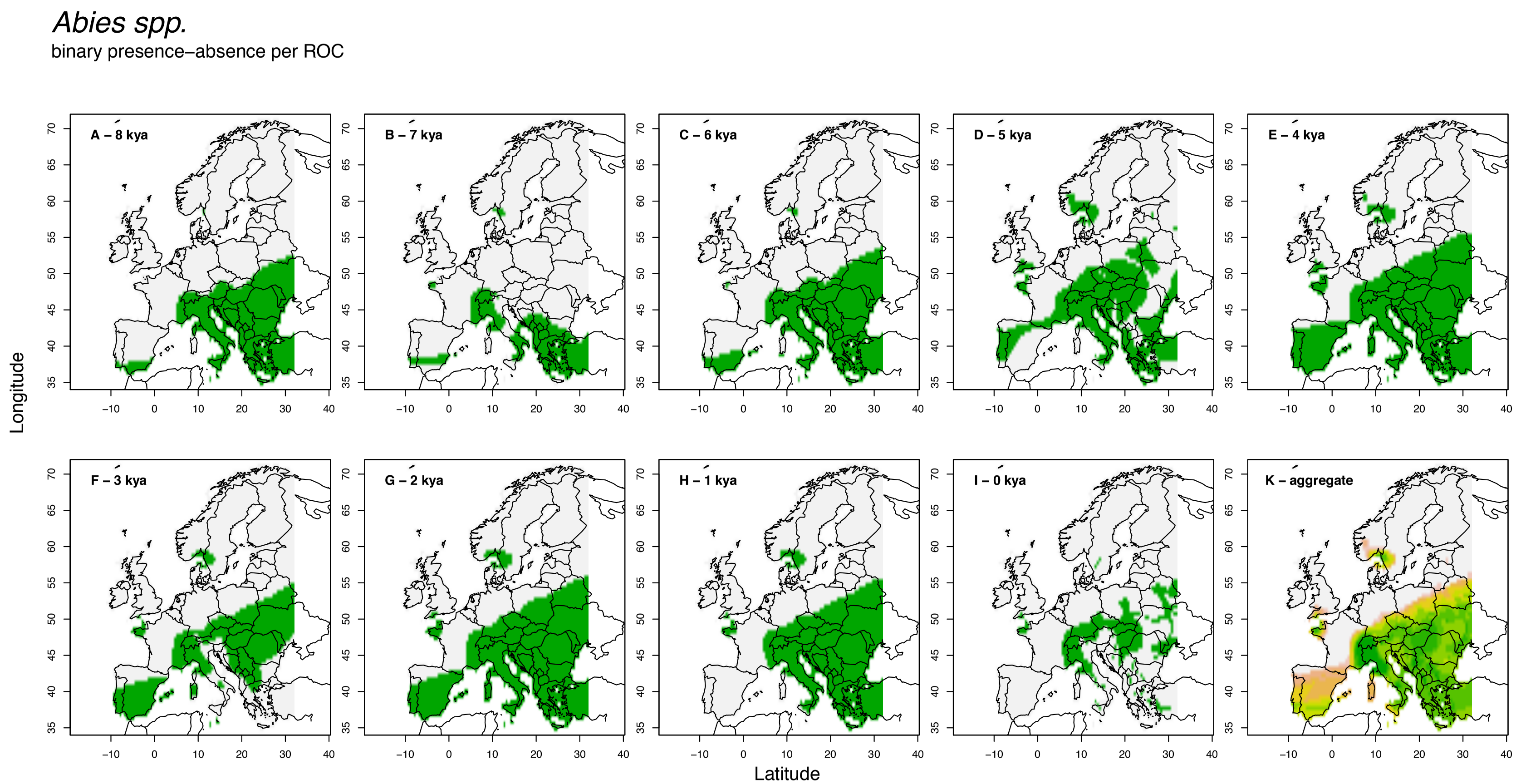


Figure B.2: Persistence distribution map for *Abies*. Map of *Abies* showing the modelled presence/absence per AUC for the genus for each time period.

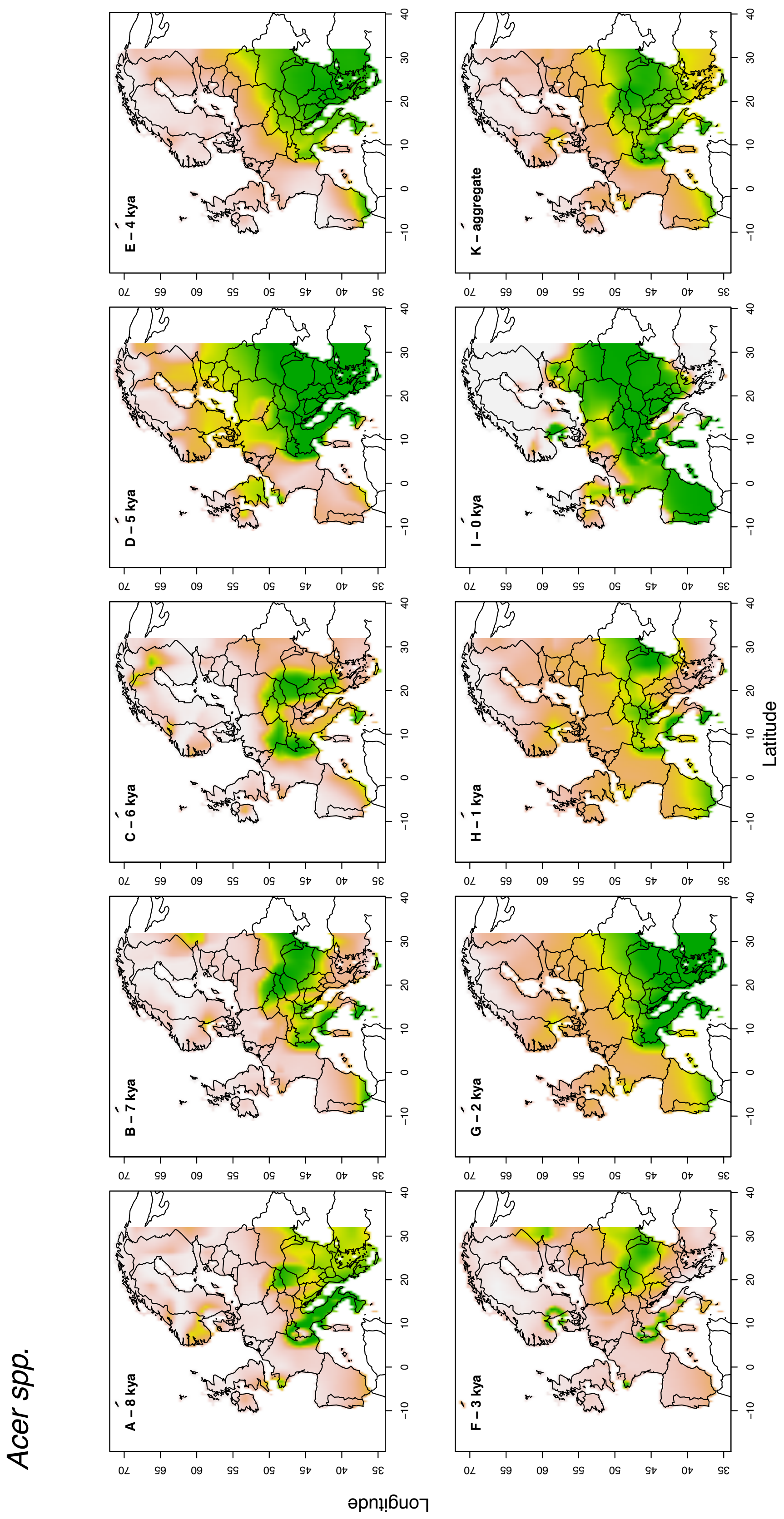


Figure B.3: Probability distribution map for *Acer*. Map of *Acer* showing the predicted presence according to the modelling results per time period.White indicates no probability, beige a low probability, scaled through to green indicating high probability.

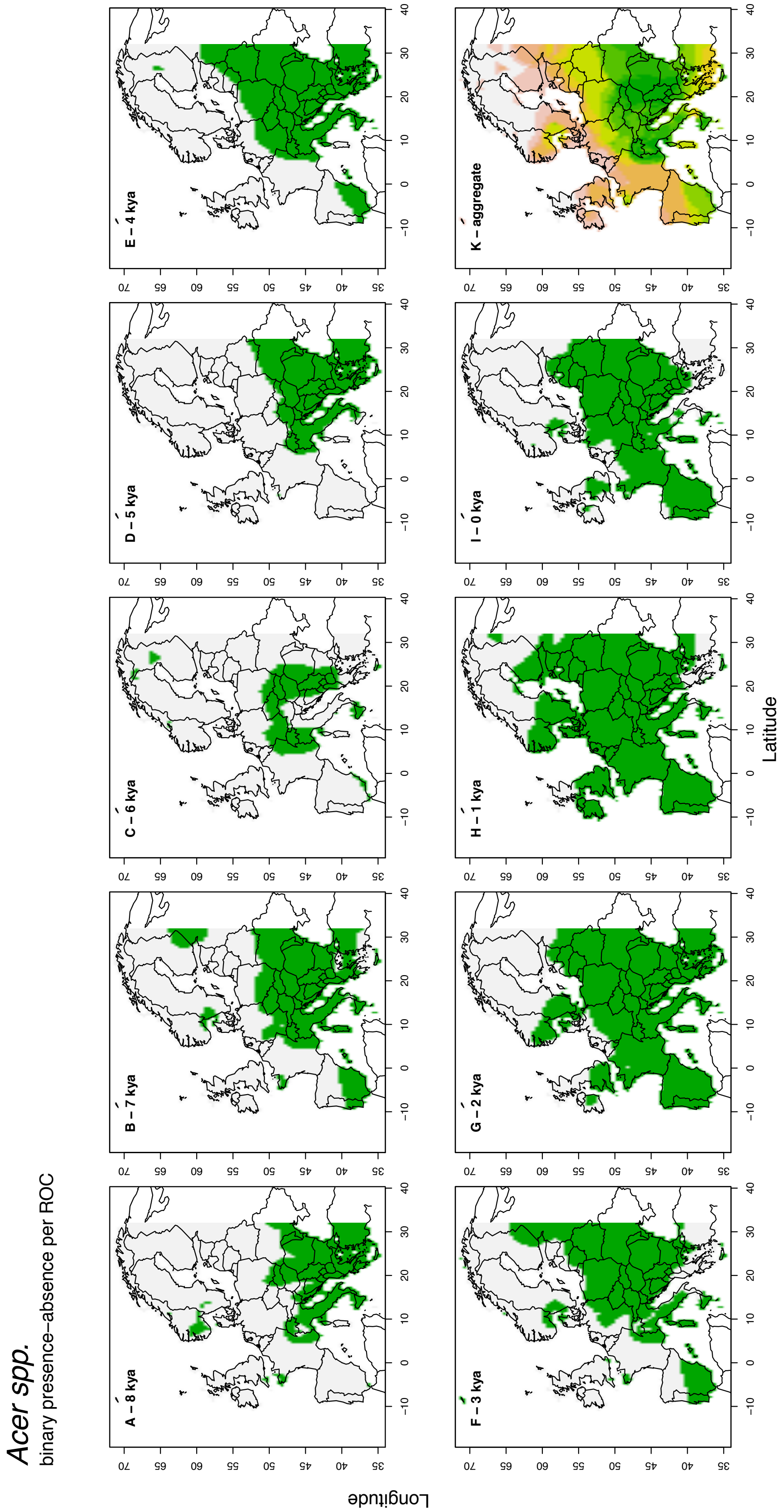


Figure B.4: Persistence distribution map for *Acer*. Map of *Acer* showing the modelled presence/absence per AUC for the genus for each time period.

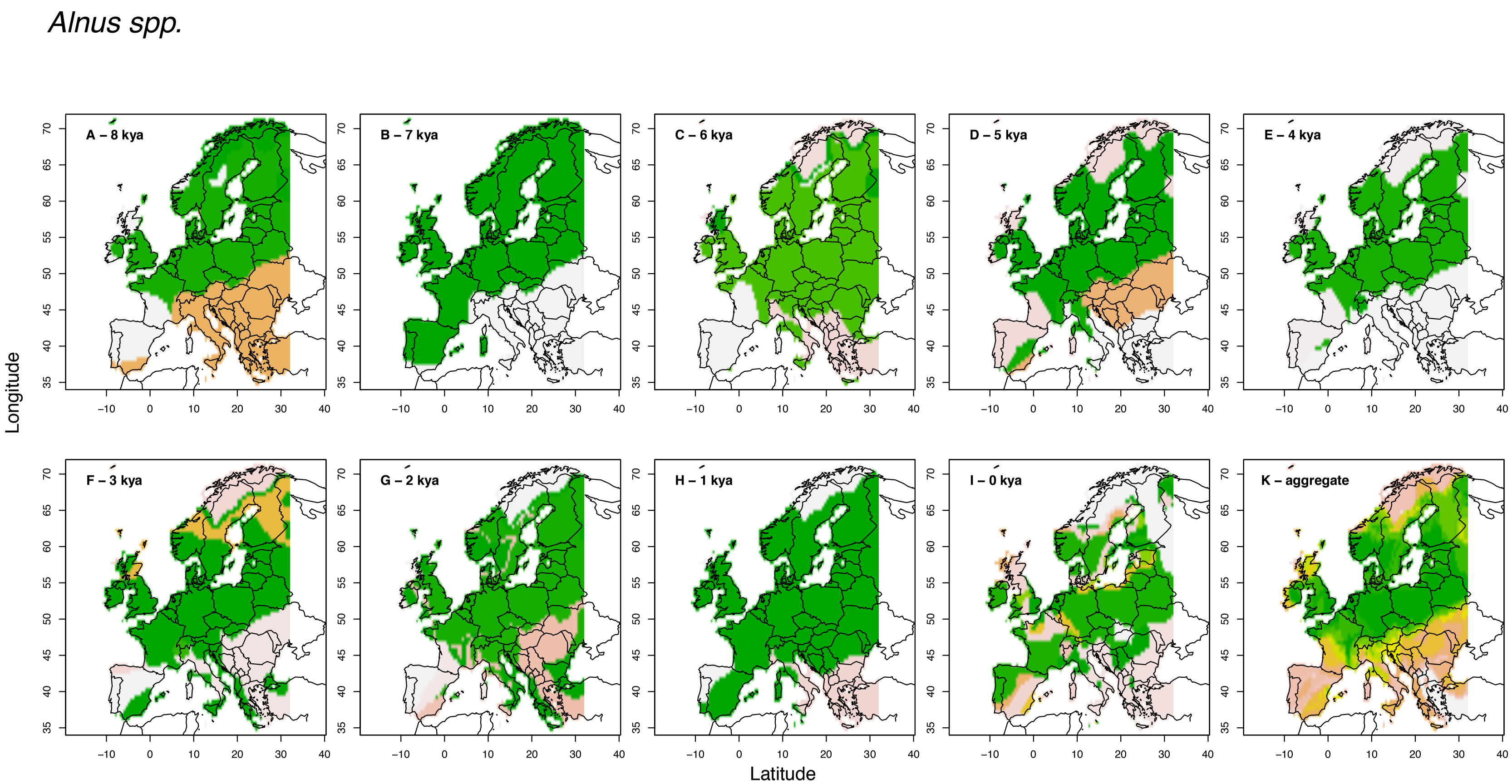


Figure B.5: Probability distribution map for *Alnus*. Map of *Alnus* showing the predicted presence according to the modelling results per time period.White indicates no probability, beige a low probability, scaled through to green indicating high probability.

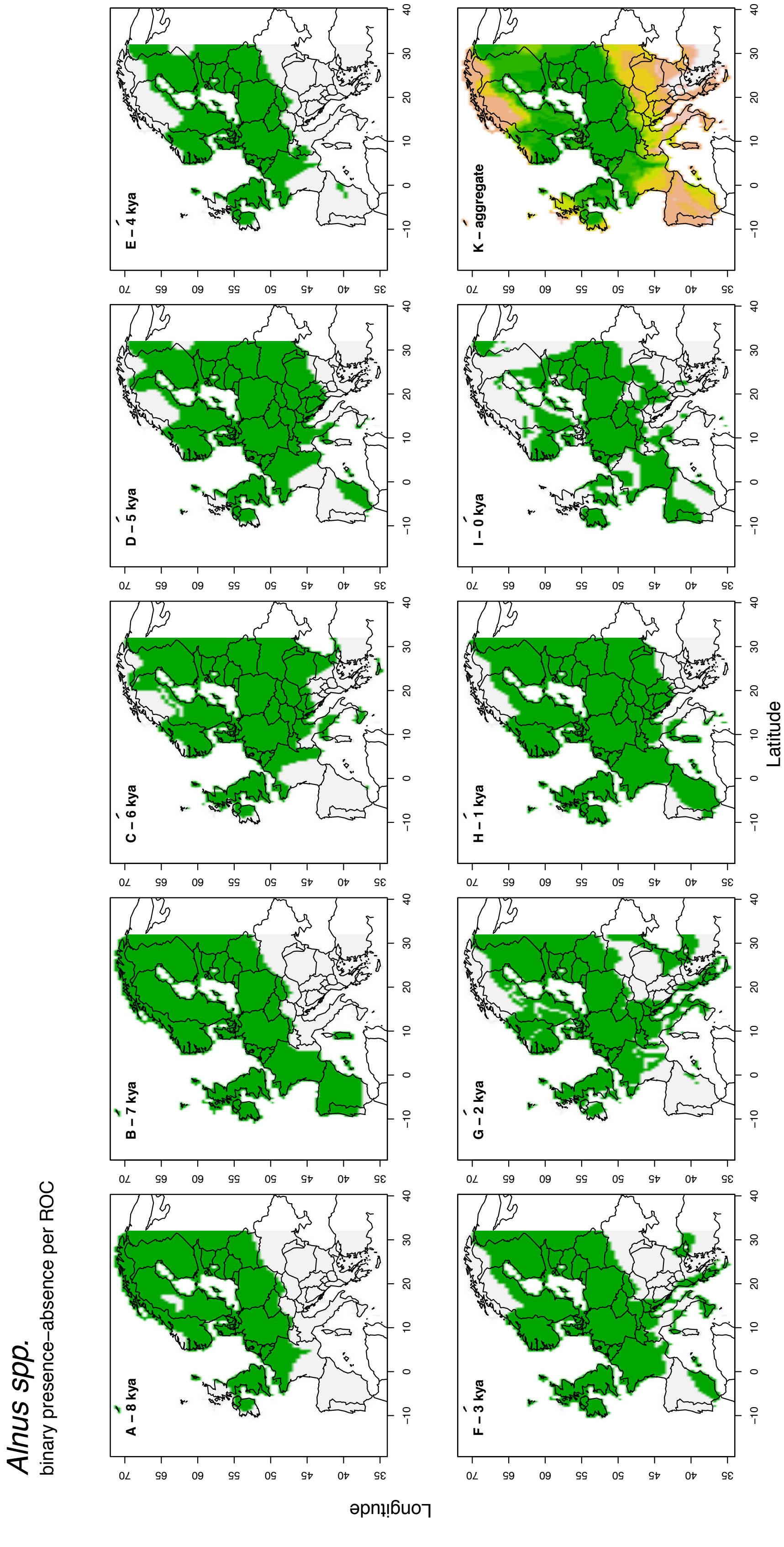


Figure B.6: Persistence distribution map for *Alnus*. Map of *Alnus* showing the modelled presence/absence per AUC for the genus for each time period.

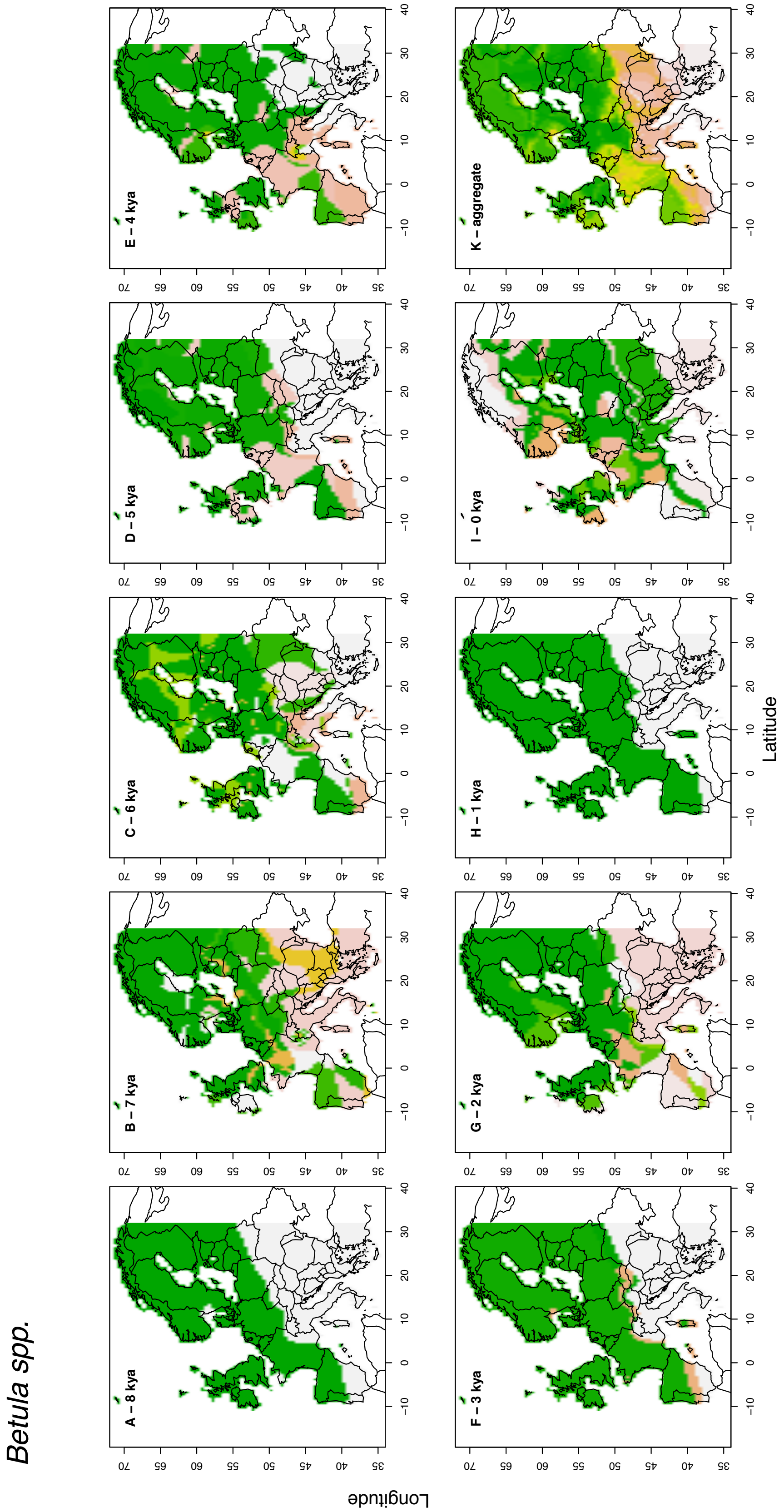


Figure B.7: Probability distribution map for *Betula*. Map of *Betula* showing the predicted presence according to the modelling results per time period. White indicates no probability, beige a low probability, scaled through to green indicating high probability.

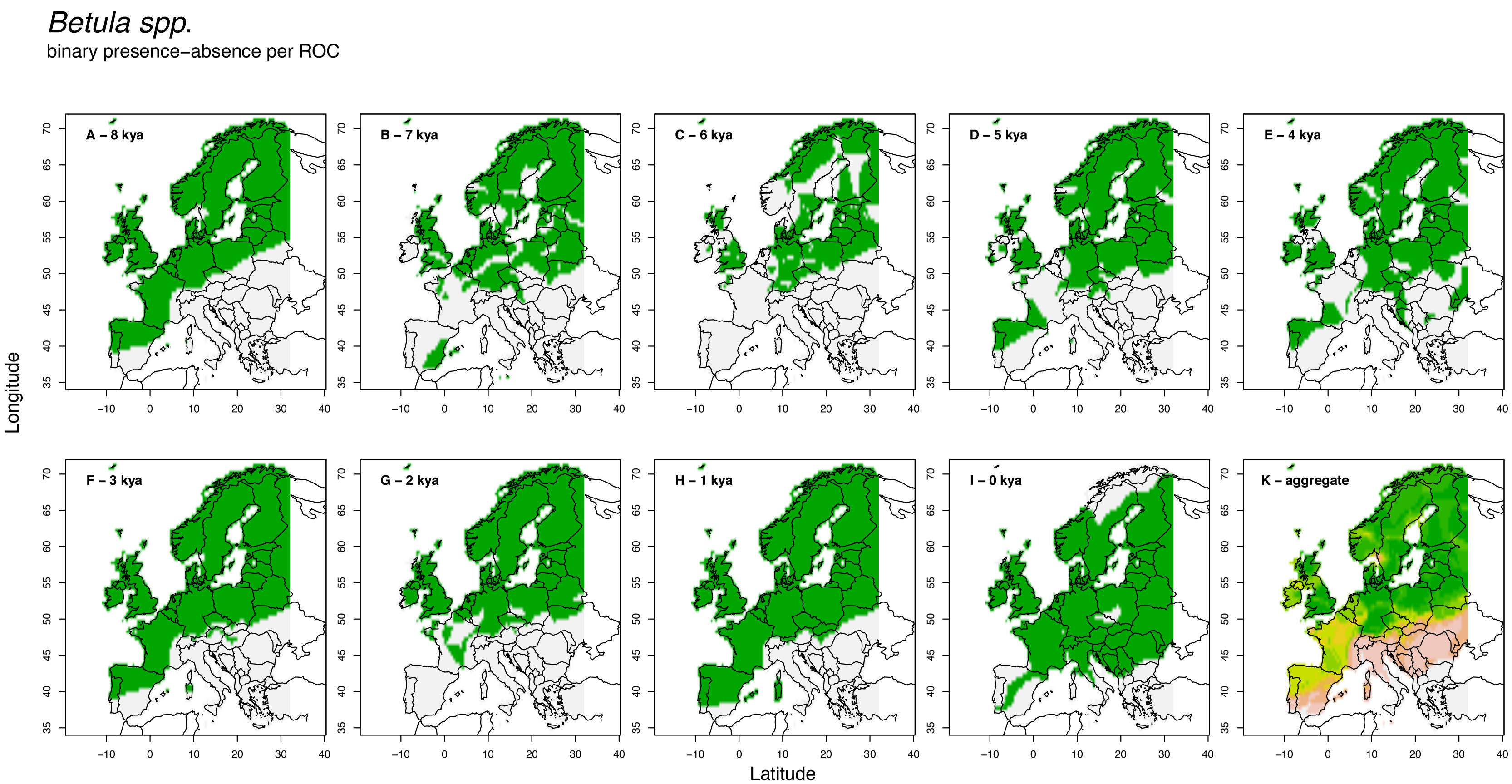


Figure B.8: Persistence distribution map for *Betula*. Map of *Betula* showing the modelled presence/absence per AUC for the genus for each time period.

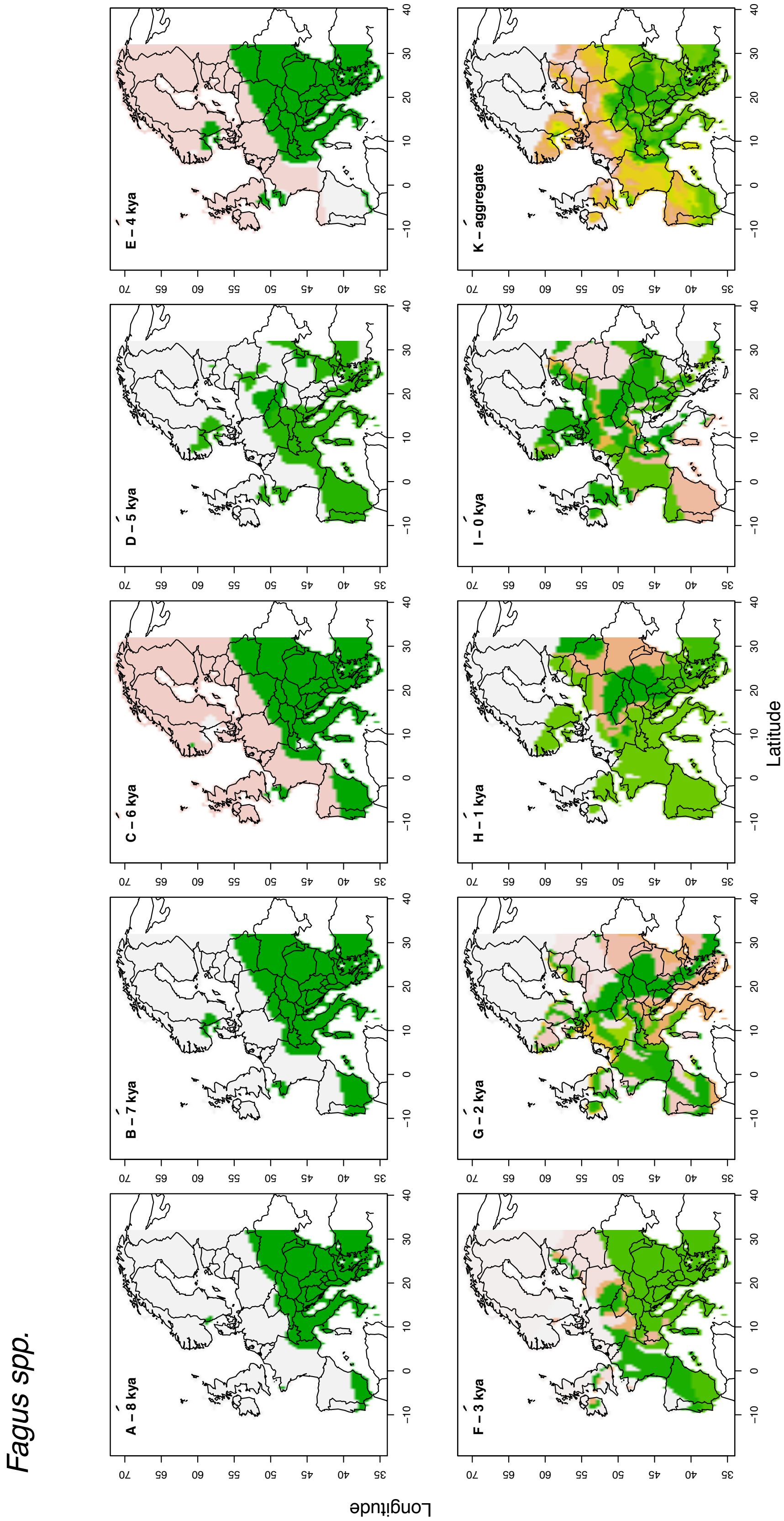


Figure B.9: Probability distribution map for *Fagus*. Map of *Fagus* showing the predicted presence according to the modelling results per time period. White indicates no probability, beige a low probability, scaled through to green indicating high probability.

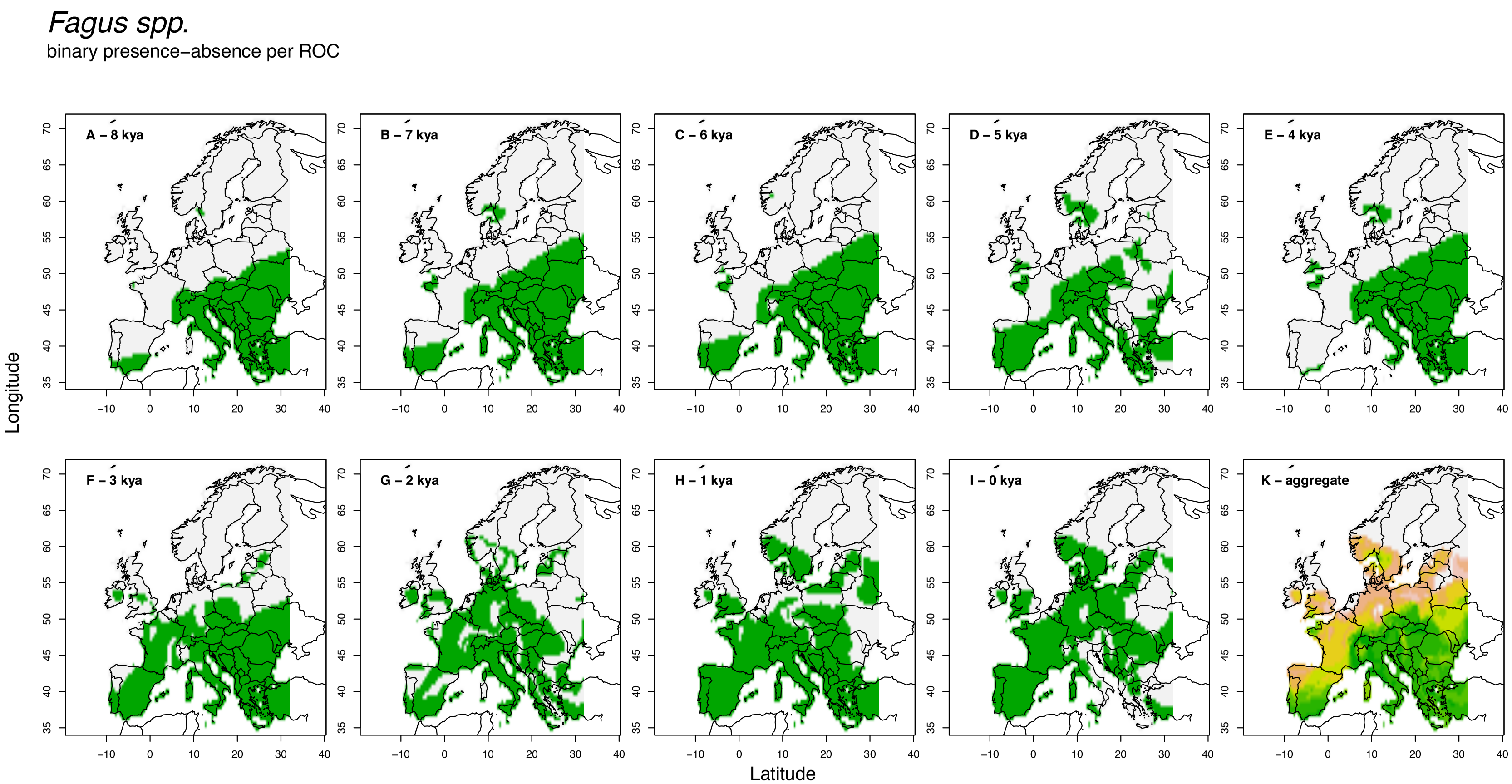


Figure B.10: Persistence distribution map for *Fagus*. Map of *Fagus* showing the modelled presence/absence per AUC for the genus for each time period.

Fraxinus spp.

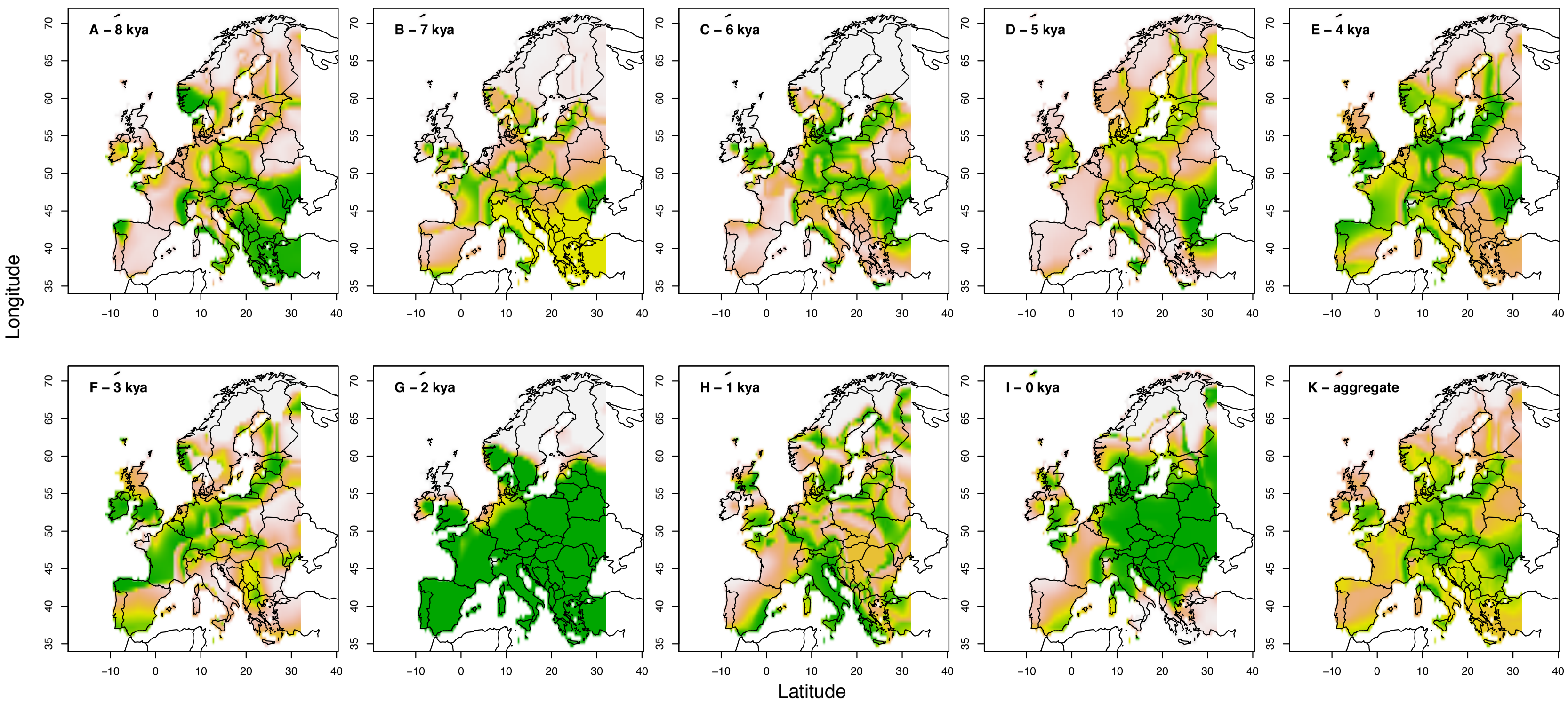


Figure B.11: Probability distribution map for *Fraxinus*. Map of *Fraxinus* showing the predicted presence according to the modelling results per time period. White indicates no probability, beige a low probability, scaled through to green indicating high probability.

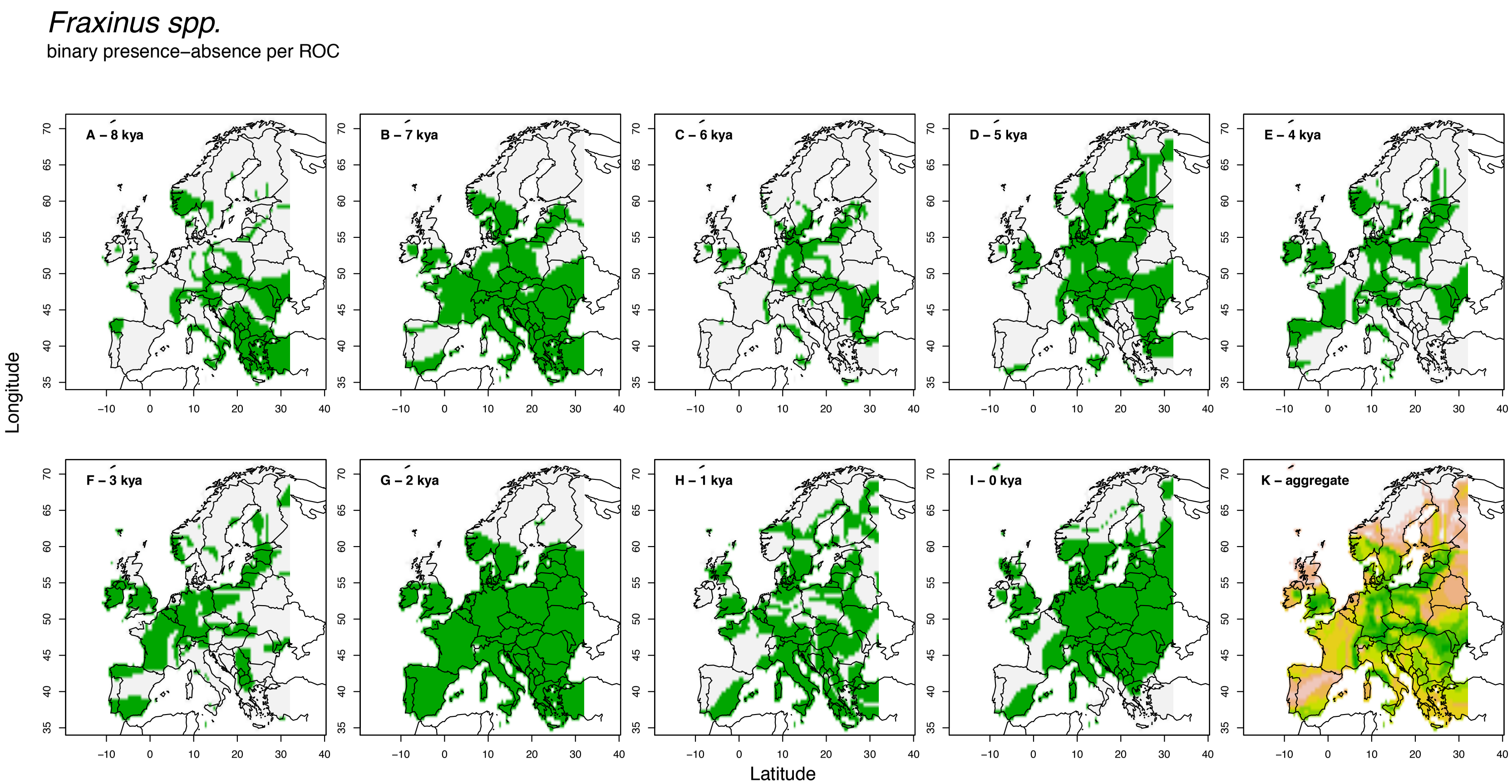


Figure B.12: Persistence distribution map for *Fraxinus*. Map of *Fraxinus* showing the modelled presence/absence per AUC for the genus for each time period.

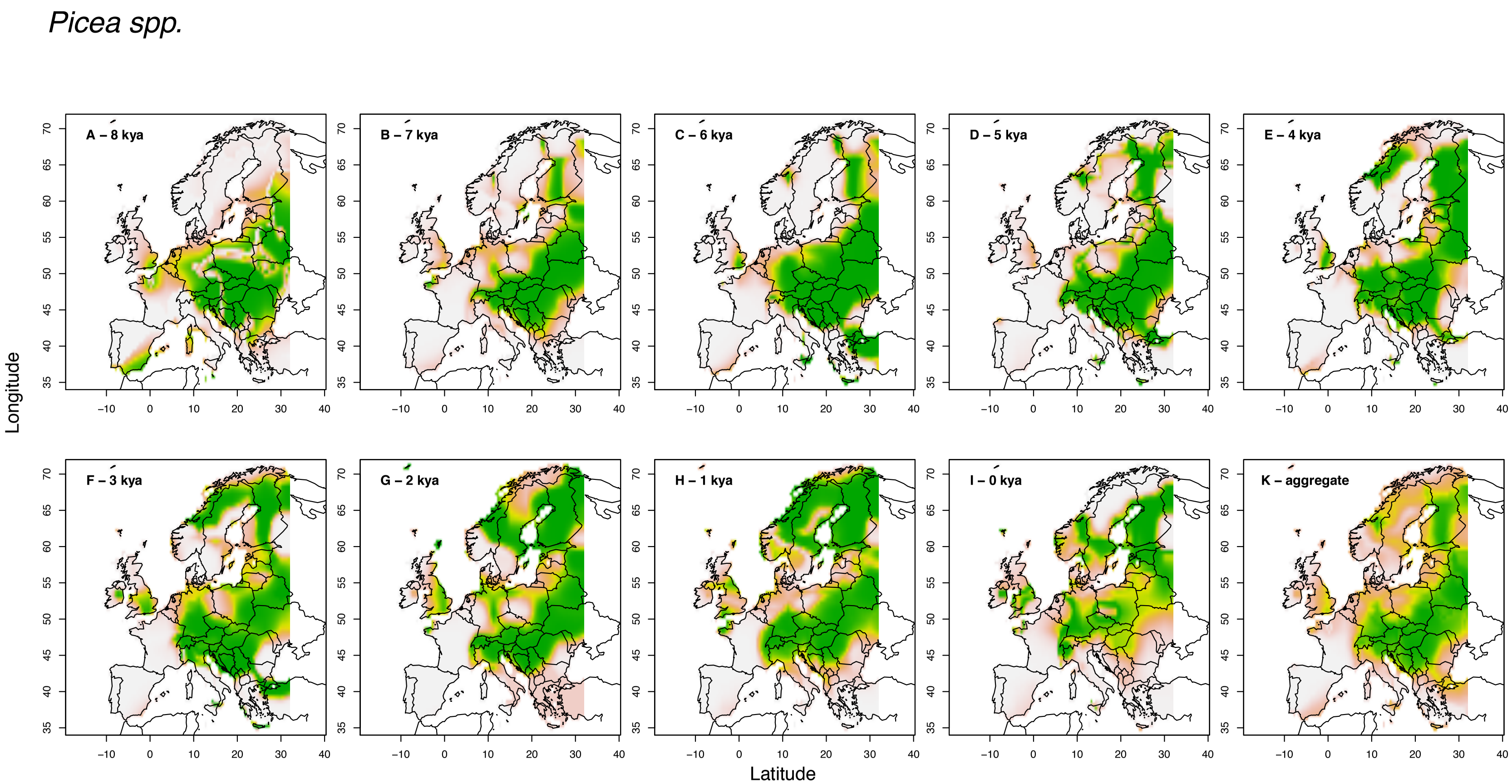


Figure B.13: Probability distribution map for *Picea*. Map of *Picea* showing the predicted presence according to the modelling results per time period. White indicates no probability, beige a low probability, scaled through to green indicating high probability.

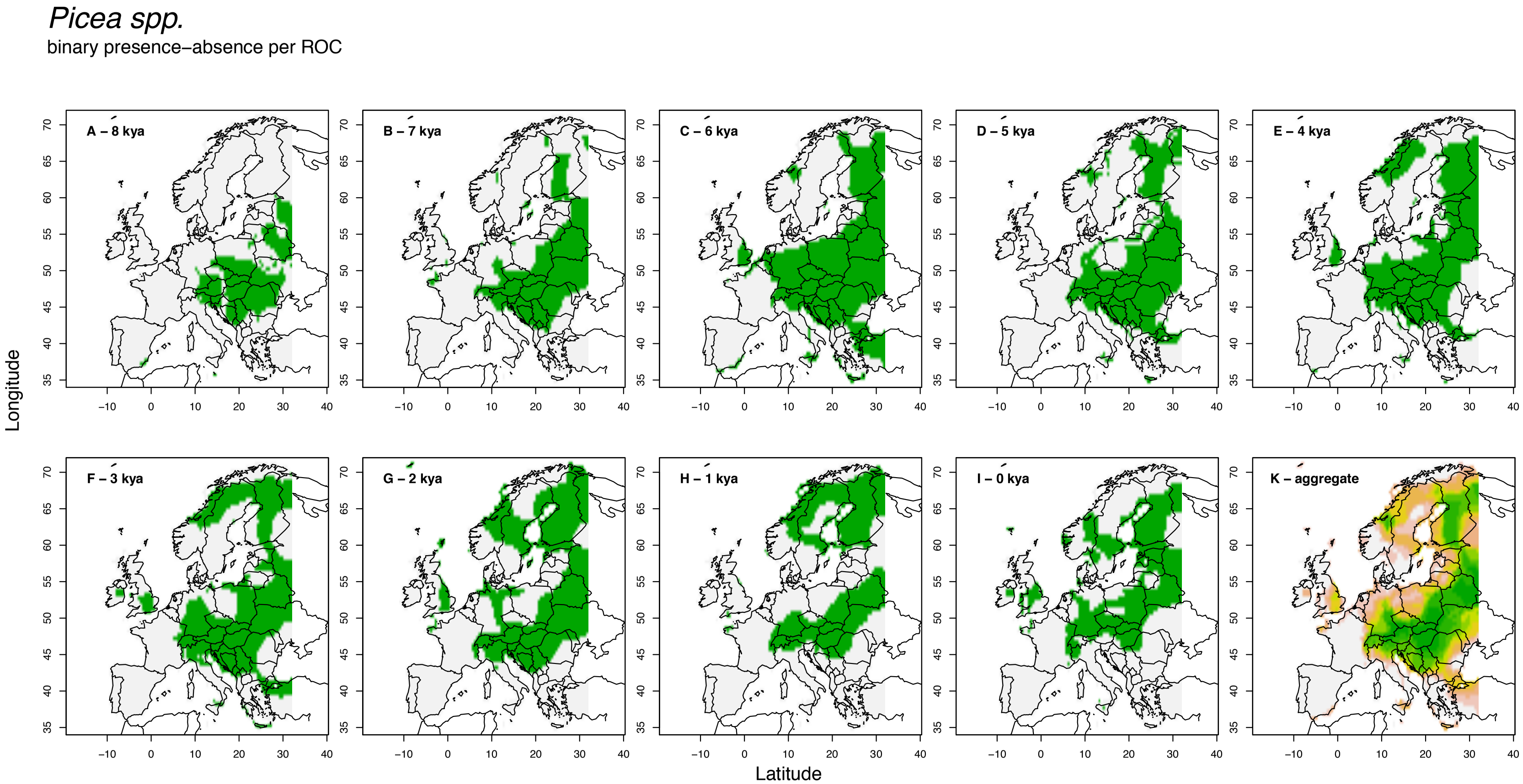


Figure B.14: Persistence distribution map for *Picea*. Map of *Picea* showing the modelled presence/absence per AUC for the genus for each time period.

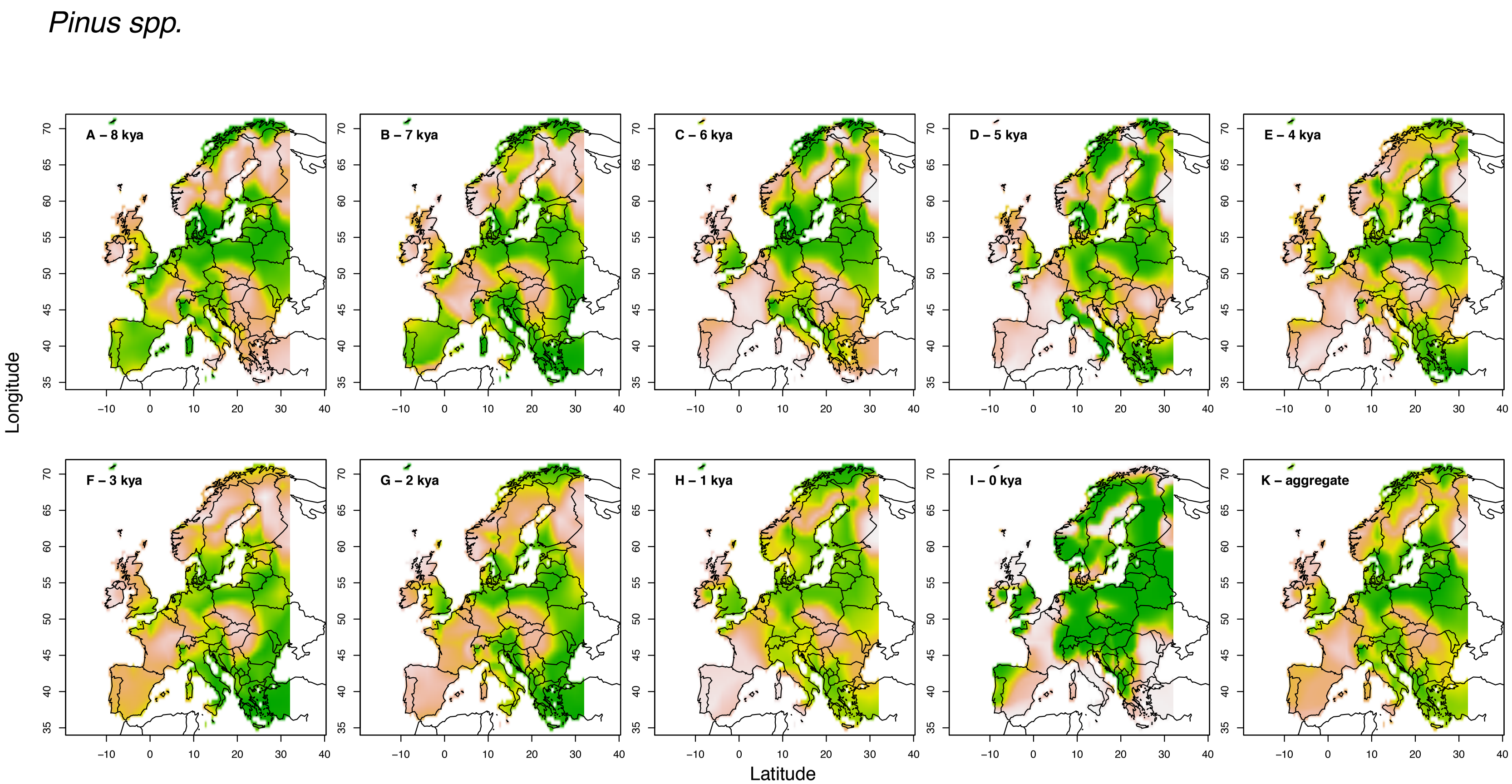


Figure B.15: Probability distribution map for *Pinus*. Map of *Pinus* showing the predicted presence according to the modelling results per time period. White indicates no probability, beige a low probability, scaled through to green indicating high probability.

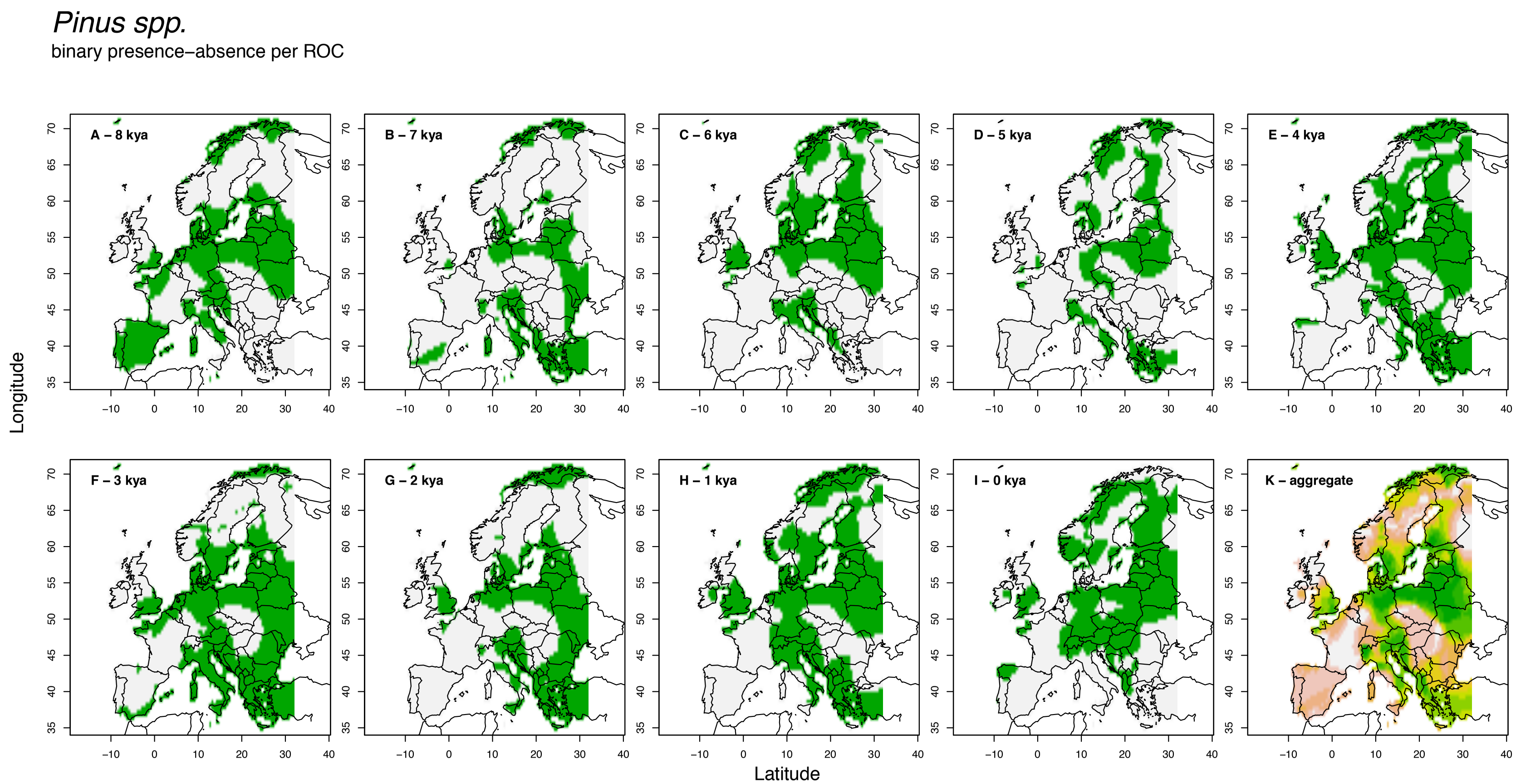


Figure B.16: Persistence distribution map for *Pinus*. Map of *Pinus* showing the modelled presence/absence per AUC for the genus for each time period.

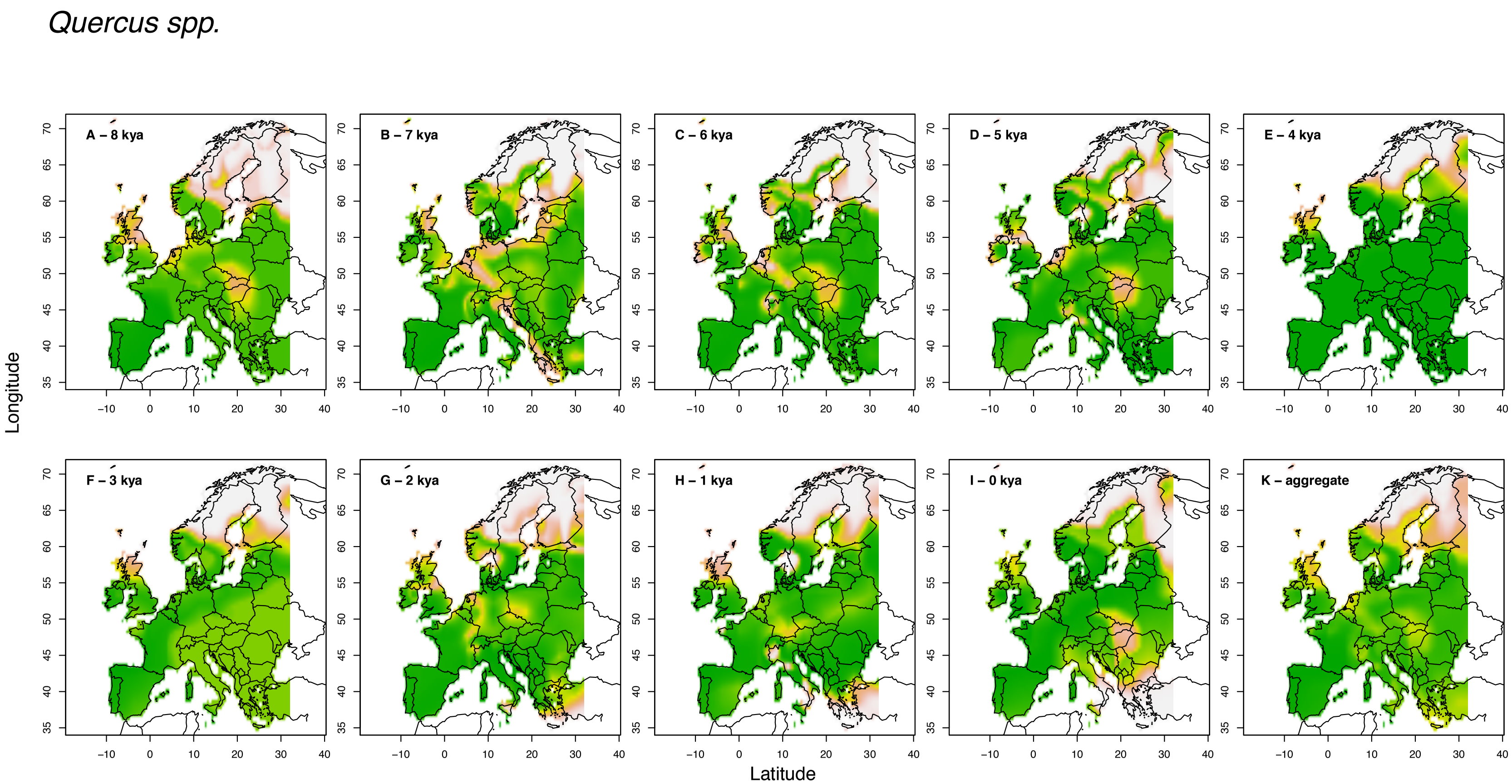


Figure B.17: Probability distribution map for *Quercus*. Map of *Quercus* showing the predicted presence according to the modelling results per time period. White indicates no probability, beige a low probability, scaled through to green indicating high probability.

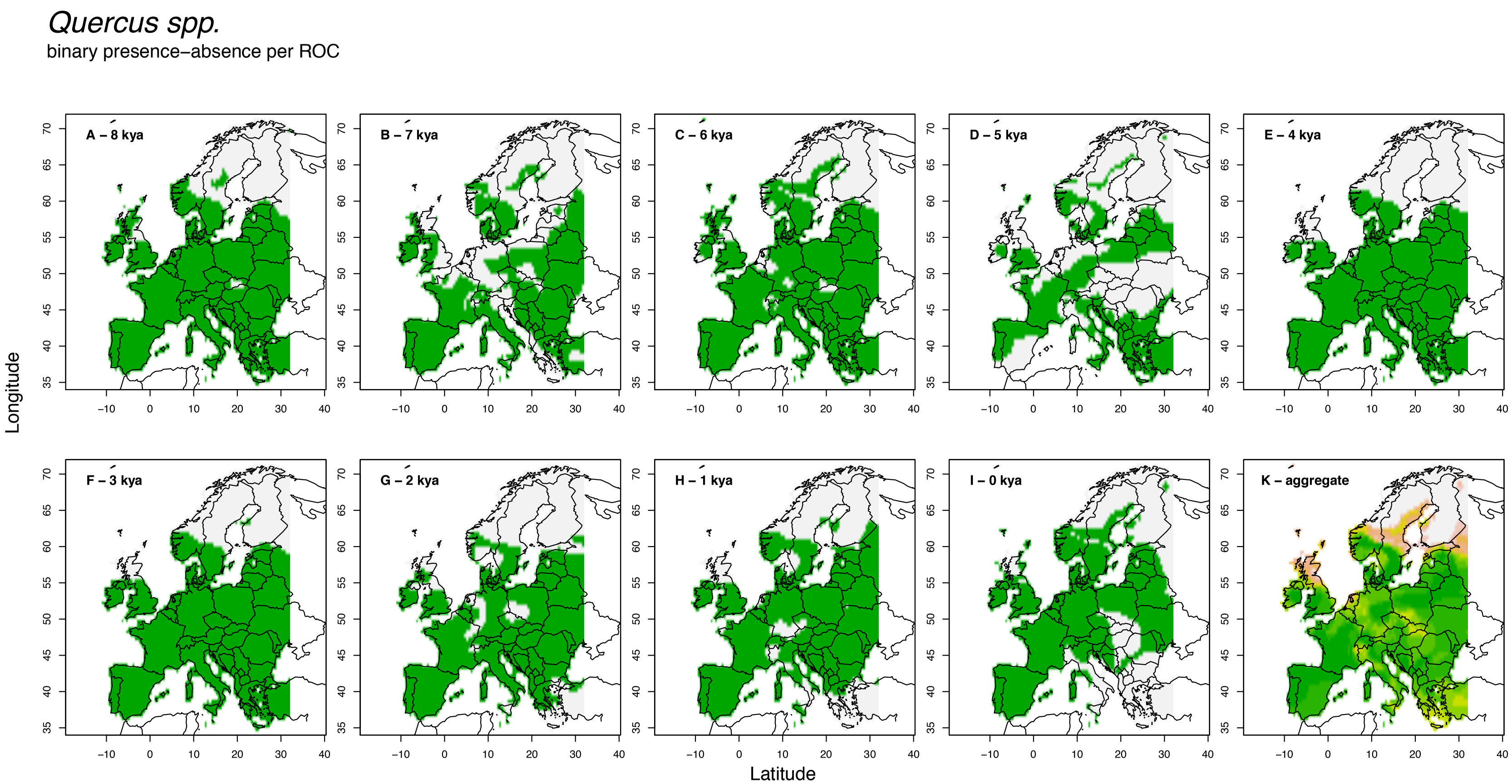


Figure B.18: Persistence distribution map for *Quercus*. Map of *Quercus* showing the modelled presence/absence per AUC for the genus for each time period.

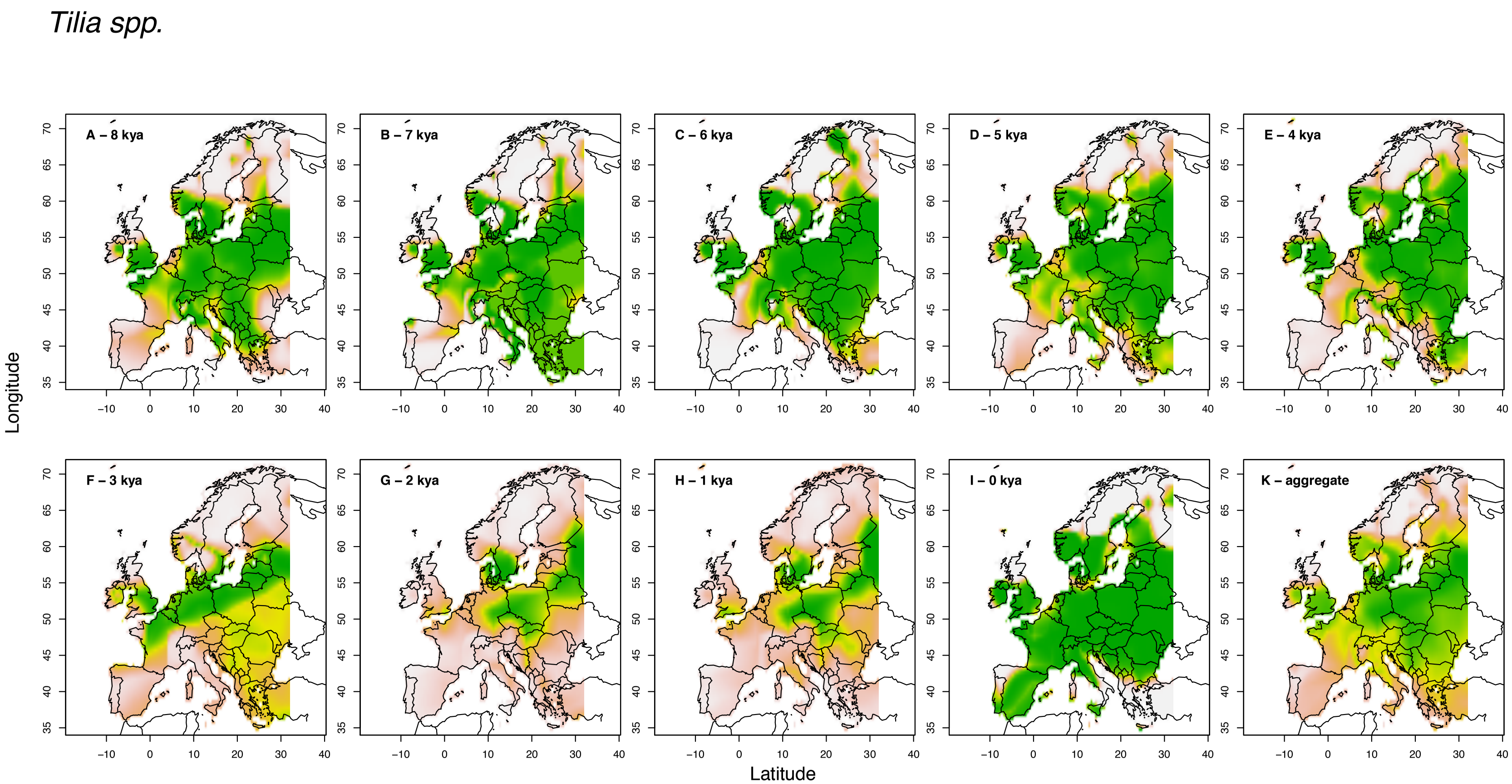


Figure B.19: Probability distribution map for *Tilia*. Map of *Tilia* showing the predicted presence according to the modelling results per time period. White indicates no probability, beige a low probability, scaled through to green indicating high probability.

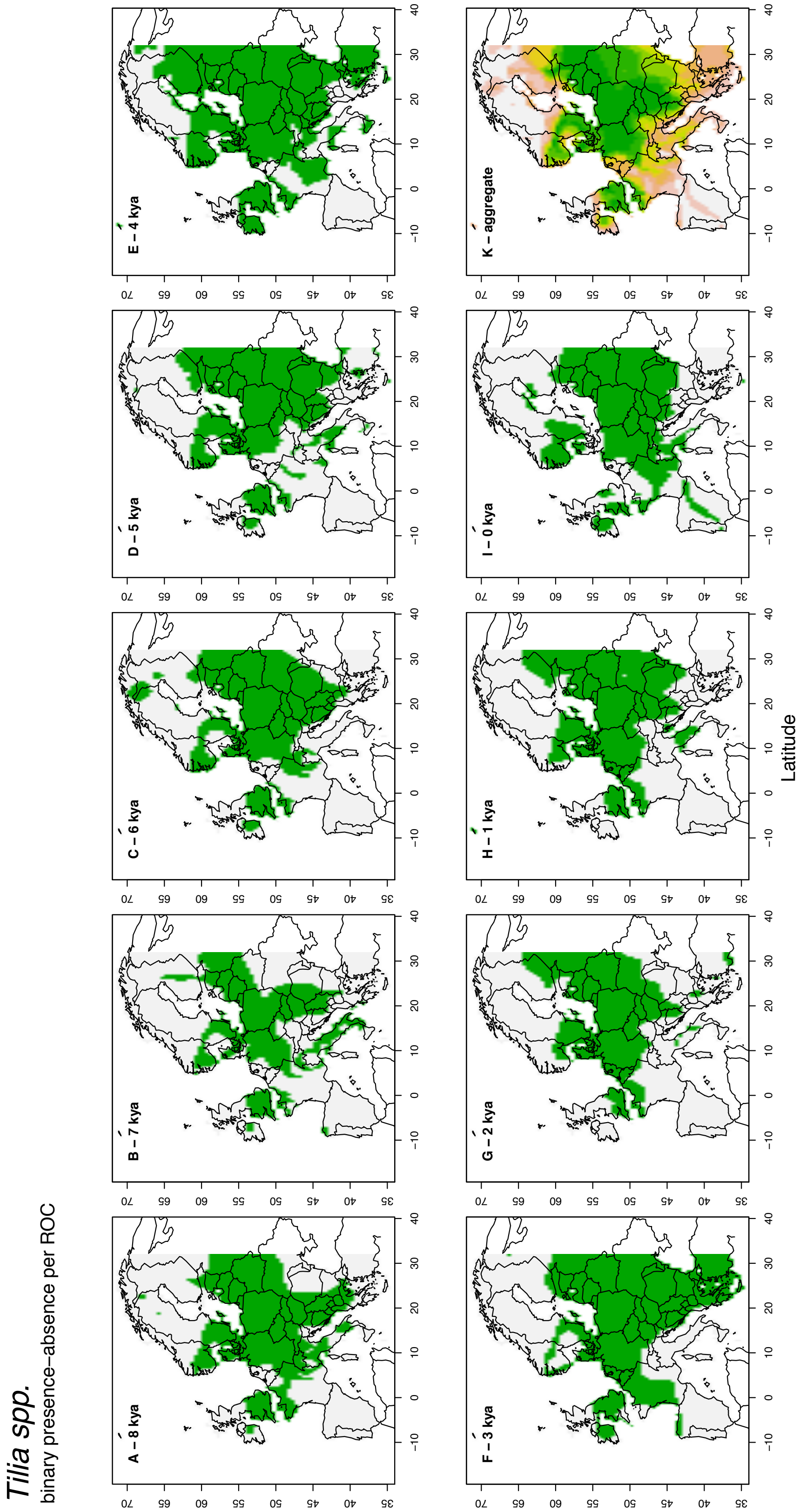


Figure B.20: Persistence distribution map for *Tilia*. Map of *Tilia* showing the modelled presence/absence per AUC for the genus for each time period.

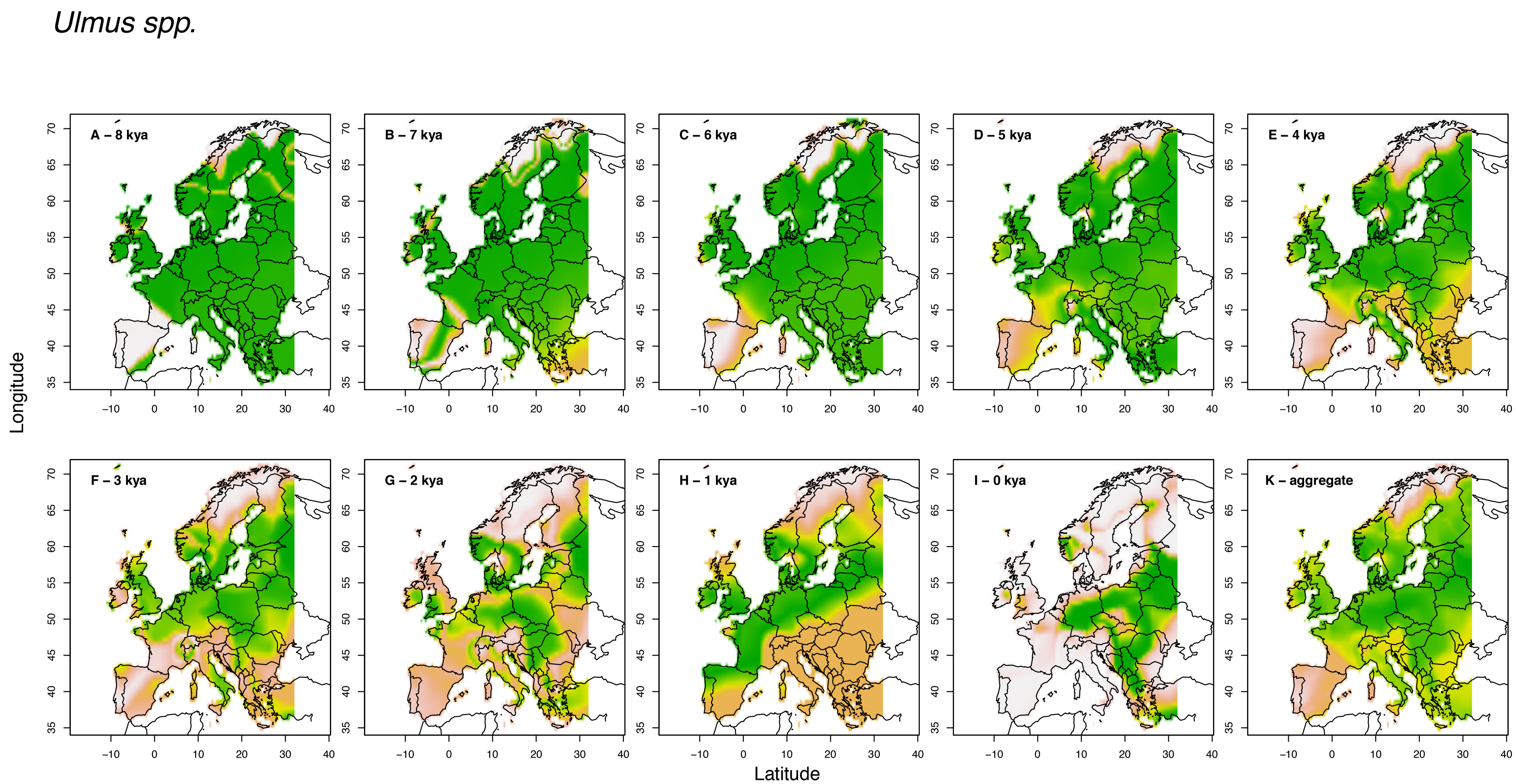


Figure B.21: Probability distribution map for *Ulmus*. Map of *Ulmus* showing the predicted presence according to the modelling results per time period. White indicates no probability, beige a low probability, scaled through to green indicating high probability.

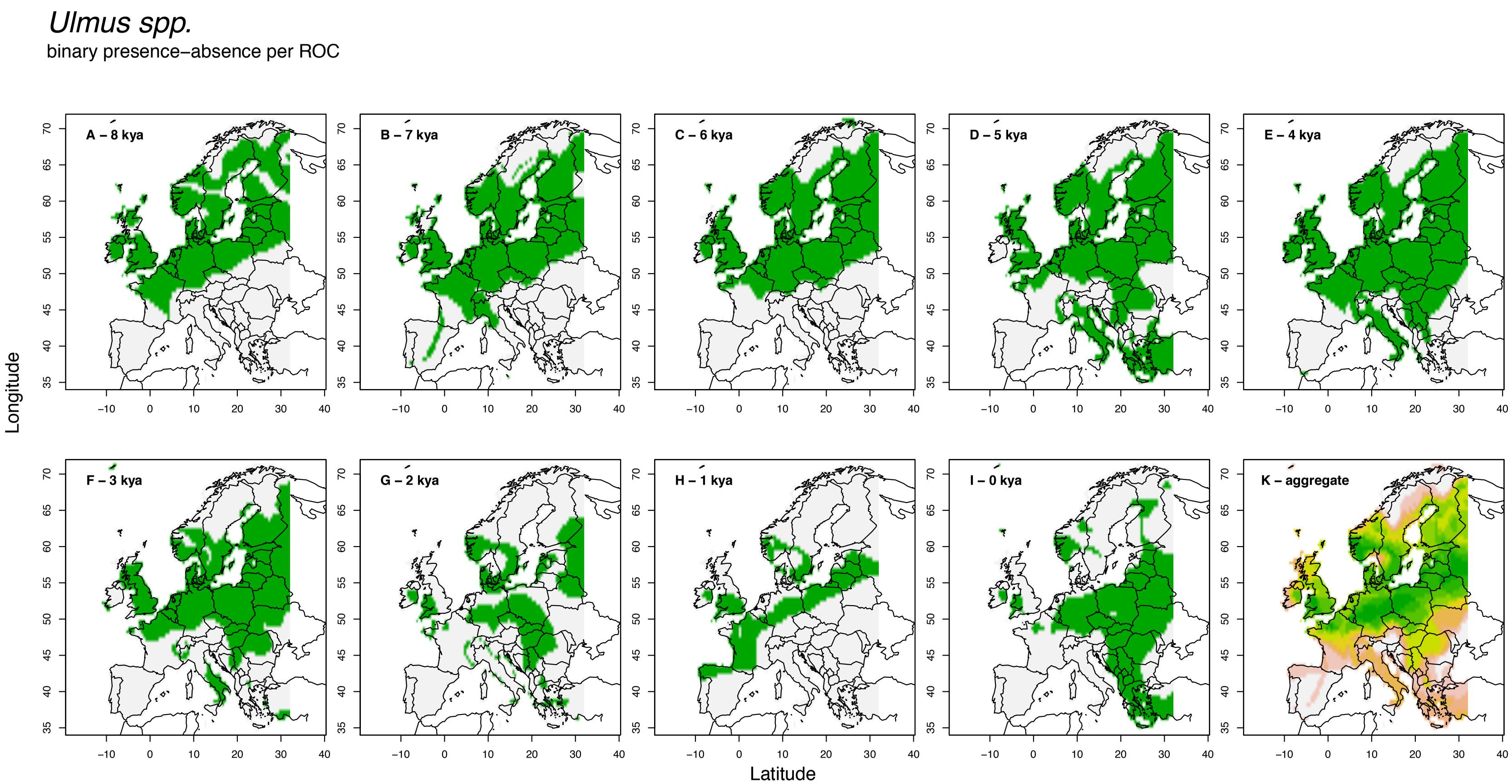


Figure B.22: Persistence distribution map for *Ulmus*. Map of *Ulmus* showing the modelled presence/absence per AUC for the genus for each time period.

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