University of West Hungary
Faculty of Forestry
Pál Kitaibel Doctoral School of Environmental Sciences

Modelling the future distribution of beech at low-elevation xeric limits - comparison of empirical and stochastic models

DOCTORAL (PHD) DISSERTATION

Ervin Rasztovits

Supervisor: Prof. Dr. Csaba Mátyás

Sopron
2011

Modelling the future distribution of beech at low-elevation xeric limits
- comparison of empirical and stochastic models

Értekezés doktori (PhD) fokozat elnyerése érdekében készült a Nyugat-magyarországi Egyetem Kitaibel Pál Környezettudományi Doktori Iskolájának Biokörnyezet-tudomány programja keretében

Írta:
Rasztovits Ervin

Témavezető: Prof. Dr. Mátyás Csaba
Elfogadásra javaslom (igen / nem) ……………………………..
aláírás

A jelölt a doktori szigorlaton ....%- ot ért el.
Sopron, ………………………………. ……………………………

....
a Szigorlati Bizottság elnöke

Az értekezést bírálóként elfogadásra javaslom (igen / nem)

Első bíráló (Dr. ………………………………) igen / nem ……………………………
(aláírás)

Második bíráló (Dr. ………………………………) igen / nem …………………………
(aláírás)

A jelölt az értekezés nyilvános vitáján ………..%-ot ért el.

Sopron, ...
a Bírálóbizottság elnöke

A doktori (PhD) oklevél minısítése:………………………………

....
Az EDT elnöke

Contents

Abstract

Modelling the future distribution of beech at low-elevation xeric limits - comparison of empirical and stochastic models

Potential future distribution of beech (*Fagus sylvatica* L.) was modelled for three terms (2025, 2050 and 2100) in the XXI. century in Hungary using stochastic species distribution models (SDMs) and a novel extreme drought event based empirical approach (EM). Although new SDM algorithms generally outperformed established ones, except the artificial neural networks all models performed poorly under future climate. Even advanced models failed in regions, where beech is situated close to its distributional range limit. Sanitary logging information as a proxy of vitality status was coupled with the modified Ellenberg's climate quotient in a selected study area to obtain the vitality response of beech in the EM. Prediction for 2025 obtained from the EM was in agreement with those of the SDM, but for the end of the century the EM predicted a more serious decline in all regions of Hungary. The result of the comparison suggests that the increasing frequency and severity of extremes could play an important role in limiting the distribution of beech in the future.

Kivonat

A bükk jövőbeni elterjedésének modellezése az alsó szárazsági határ közelében - empirikus és korrelatív elterjedés modellek összehasonlítása

A bükk (*Fagus sylvatica* L.) potenciális jövőbeni elterjedésének modellezését végeztem el három jövőbeni időpontra (2025, 2050 és 2100) korrelatív elterjedés-modellek és egy új extrém szárazsági eseményen alapuló empirikus megközelítés segítségével. A korrelatív modellek általában jól teljesítettek a jelenlegi előfordulás leírásánál, de az alkalmazott nyolc módszerből csupán egy, a neurális hálózatok elvén működő modell adott konzisztens becslést a jövőre. Még a legfejlettebb algoritmusok is jelentős túlbecslést mutattak azokban az erdészeti tájakban, ahol a bükk az alsó szárazsági elterjedési határa közelében található, amely egyértelműen jelezte ezen statikus modellek alkalmazhatóságának korlátait. Az empirikus modellben a bükk szárazságra adott vitalitás-válaszreakciójának meghatározásához egészségügyi kitermelési adatok kerültek összevetésre a módosított Ellenberg indexszel a 2000 – 2003-as bükkpusztulással érintett délnyugat-magyarországi mintaterületen. Az empirikus és korrelatív modellek közeljövőre adott becslése hasonló volt, de a század végére az extrém szárazsági eseményen alapuló empirikus modell sokkal nagyobb mértékű vitalitás-gyengülést jelzett előre. Az eredmények alapján valószínűsíthető, hogy a klímaváltozással gyakoribbá és súlyosabbá váló száraz időszakok fontos szerepet játszanak a bükk jövőbeni előfordulásának alakításában.

1 Introduction

Although *Fagus sylvatica* L. is one of the dominant tree species' in central European temperate forests with high physiological tolerance and competitiveness (*Ellenberg et al., 1992*), drought sensitivity is assumed to be a key factor limiting growth and distribution of beech near to its lower distributional limit (xeric limit) (*Mátyás et al., 2009*) in southern and south-eastern Europe (*Backes and Leuschner, 2000*).

Several studies suggest a decline in beech regeneration (*Rennenberg et al., 2004; Penuelas et al., 2007*) or extensive beech dieback (*Berki et al., 2009; Czúcz et al., 2011; Kramer et al., 2010; Lindner et al., 2010*) with worsening climatic conditions (*Gálos et al., 2007*). Consequently modelling the vitality response of beech to predicted changes of climate is a critical issue (*Franke and Köstner, 2007; Mátyás, 2009*).

Drought is a common phenomenon of continental climate, supported also by historical datasets in Hungary (*Pálfai et al., 1999*). A significant drought event emerged between 2000 and 2003 in Southwest of Hungary which was unprecedented in duration and strength since the beginning of the 50's. After this drought event large volume of declining or already dead beech was logged by forest managers supervised by forest inspectors. First, solitary trees showed the typical symptoms of reduced water availability (leaf yellowing, top drying) in 2002. The symptoms of xylo- and phloeophagous insect attack (*Agrilus viridis, Taphrorychus bicolor*) and fungal infection (*Biscogniauxia nummularia, Nectria coccinea*) appeared in 2003 and expanded rapidly after 2004 (*Lakatos and Molnár, 2009*).

For management and conservation issues (*Hannah et al., 2002*) species distribution models (*SDMs*) have been extensively used. SDMs connect the species' environmental requirements of the localities where it is currently known to occur. They can be evaluated for their ability to predict current distributions but it is not tested whether models that are successful in predicting current distributions are equally powerful in predicting distributions under different climates. Studies comparing modelling algorithms are now common (*Segurado and Araujo, 2004; Elith et al., 2006; Tsoar et al., 2007*), but *Thuiller et al. (2004)* have pointed out the problem of strong variation between SDM predictions of future distributions. SDMs are "statistical" models without specific ecological knowledge, they do not describe "cause and effect" between model parameters and response (*Guisan and Zimmermann, 2000; Pearson and Dawson, 2003; Kearney and Porter, 2004*).

Empirical models (*EM*) are considered superior for understanding the relationship between climate and the distribution of species (*Woodward and Rochefort, 1991; Malanson et al., 1992; Prentice et al., 1992; Guisan and Zimmermann, 2000*) and have been used to study the effects of climate change on distribution and production of trees and crops (*Rosenzweig and Parry, 1994; Hijmans, 2003*). In an EM, the distribution of a species is defined by functions based on ecological response of that species. A drawback of EMs is that ecological data limiting the distribution are not available for most species.

The multidimensional climatic envelope created by niche based models is often described by long-term averages, but long-term climatic means do not express the importance of extreme drought events, which act as triggering effect on growth decline and pests or diseases attacking populations of weakened vitality causing mortality (*Bréda et al., 2006; Lakatos and Molnár, 2009*).

Aim and scope

The aim of this study was to develop a consistent method to model potential future distribution of beech (*Fagus sylvatica* L.) near to the xeric limit with respect to the specific (ecological and climatic) problems of the region. Most of the species distribution models do not differentiate between the “leading” and “trailing” edge, although the processes are fundamentally different (*Mátyás and Nagy, 2005; Aitken et al., 2008*). Xeric limits of distribution are determined by climatic aridity, modified by local soil water regime conditions. These limits are more difficult to trace than thermal “upper” limits. This ecologically and climatically specific area has been chosen for the modelling which is largely neglected by European studies (*Jump et al., 2009; Lindner et al., 2010; Mátyás, 2010*).

Beech is considered a climate sensitive species, which is uniquely vulnerable in the region, therefore well suited for modelling. Another advantage is, that compared to other tree species in Hungary it is in a relatively natural condition as it was seldom regenerated artificially and its reproductive material was not subject to commercial relocations (*Mátyás, 2010*).

In this work it was hypothetised that:

- the fitness of beech with worsening climatic conditions declines gradually and ends up in mass mortality when reaching the genetically set tolerance limit,
- this decline is strongly connected to certain extreme drought events and the relationship could be described using an EM,
- the EM could provide a better tool for predicting potential future distribution of beech near the xeric limit than SDMs.

The following scientific questions were addressed:

1. Which SDM can best describe the present distribution of beech in Hungary?
2. What is the relationship between weather conditions and vitality status of beech?
3. What are the projections for the potential future distribution of beech using SDMs and vitality condition using an EM?

To answer the research questions first (*1*) the current and potential future distribution of beech was modelled in Hungary using different SDMs, (*2*) sanitary logging information of beech as a proxy of vitality condition was coupled with meteorological data to obtain the vitality response of beech, (*3*) the future vitality status of beech was modelled and compared to different terms of this century by applying the same regional climate model projection as used for the SDMs.

2 Literature review

2.1 Climate change

2.1.1 Global changes

Since 1900 the global surface temperature of the Earth has risen by about 0.8°C. The closing decades of the twentieth century and the early years of present century were unusually warm. Globally, the last 30 years have been the warmest since accurate records began over 100 years ago (*Figure 1*).

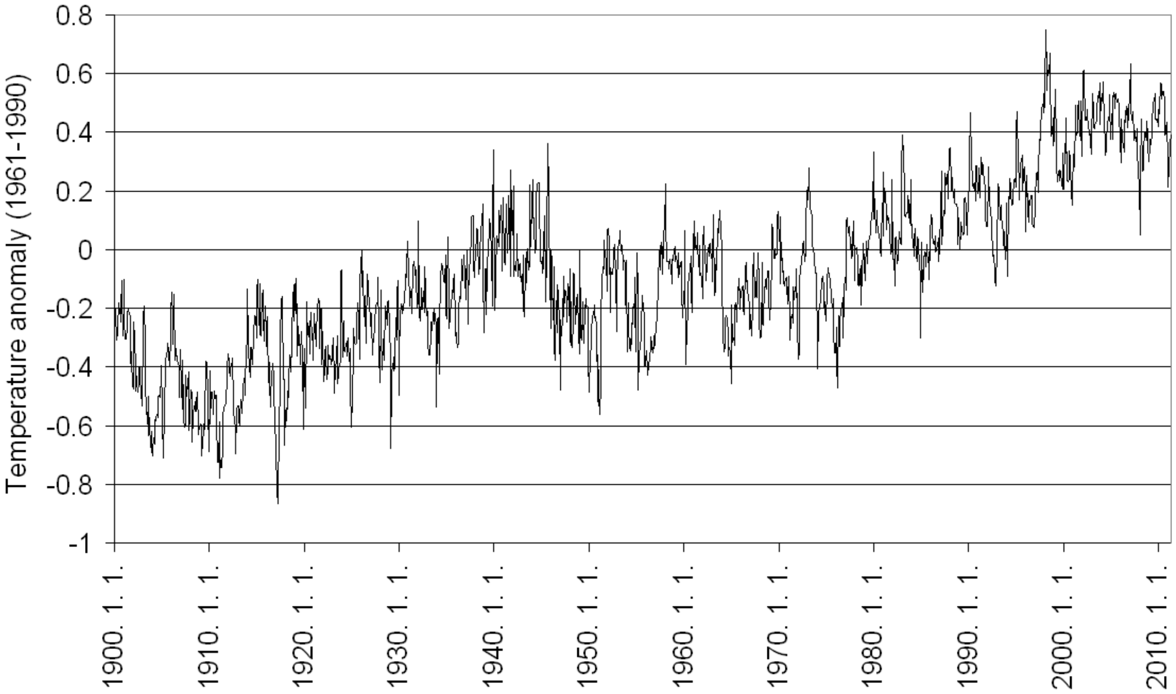


Figure 1: Global surface temperature (land and sea) HADCRUT3 (Climatic Research Unit, *http://www.cru.uea.ac.uk*).

This temperature increase occurred during a significant atmospheric concentration increase of some greenhouse gases, especially CO_2 and CH_4, which is known to be mainly due to human emissions. The fourth report of the *IPCC (2007*) stated clearly the anthropogenic climate change: “Most of the observed increase in global average temperatures since the mid-20th century is very likely due to the observed increase in anthropogenic greenhouse gases concentrations.”

Even under conservative scenarios, future climate changes are likely to include further increases in mean temperature (about 2–4 ^{o}C globally) with significant drying in some regions (*Christensen et al., 2007*), as well as increases in frequency and severity of extreme droughts, hot extremes, and heat waves (*IPCC, 2007*; *Sterl et al., 2008*). The source of the uncertainty in the temperature range originates from the different emission scenarios and uncertainty in the feedback processes (e.g. clouds).

2.1.2 Climate change in Europe

In case of Europe, it is likely that the increase of annual mean temperature will exceed the global warming rate in the 21st century. The largest increase is expected in winter in northern Europe and in summer in the Mediterranean area (*Figure 2*).

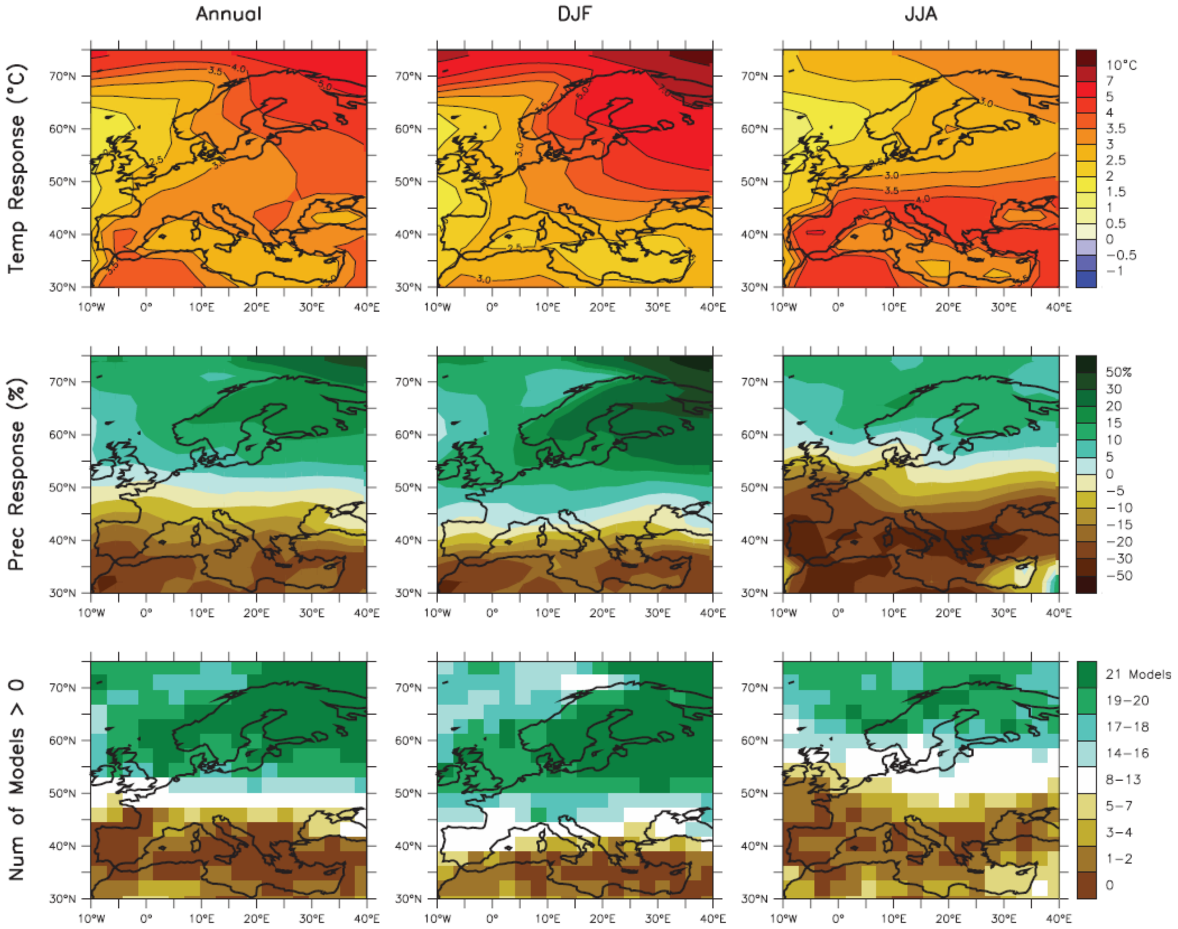


Figure 2: Temperature and precipitation changes over Europe from the MMD-A1B simulations. Top row: Annual mean, winter (DJF) and summer (JJA) temperature change between 1980 to 1999 and 2080 to 2099, averaged over 21 models. Middle row: same as top, but for fractional change in precipitation. Bottom row: number of models out of 21 that project increases in precipitation (*IPCC, 2007*).

For precipitation, the annual sum is very likely to increase in northern Europe and decrease in the Mediterranean area (*IPCC, 2007*). The largest decrease is expected in the Mediterranean during the summer months.

2.1.3 Climate change in Hungary

For the 20th century several climate extreme indices have been studied for Hungary (*Bartholy and Pongrácz, 2007*). Strong increasing trends have been observed in Central Europe for the annual numbers of hot days, summer days, warm days and warm nights in the second half of the 20th century. Additionally, intensity and frequency of extreme precipitation events have increased, while the total precipitation amount has decreased (*Bartholy and Pongrácz, 2007*).

In Hungary, which is located at the transitional zone of these regions, precipitation is likely to increase in winter, while decrease in summer. In case of the summer drought events, the risk is likely to increase in Central-Europe and in the Mediterranean area due to decreasing summer precipitation and increasing spring evaporation (*Figure 3*).

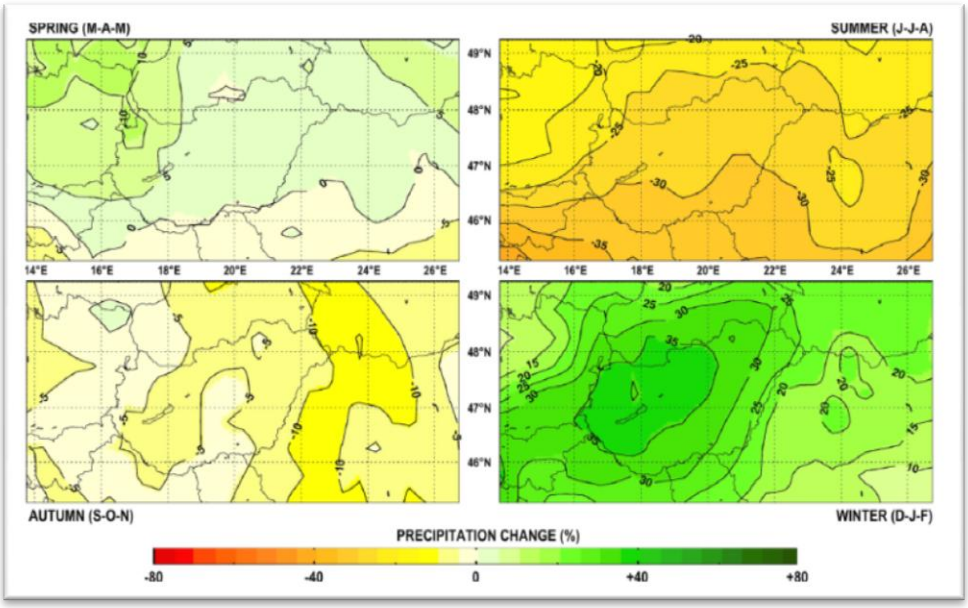


Figure 3: Projected precipitation increase over Hungary for 2071-2100 using the A2 scenario (*Bartholy et al., 2007*).

In summer, the projected precipitation decrease is 24-33% (A2) and 10 – 20% (B2). In winter, the expected precipitation increase is 23 – 37% (A2) and 20 –27% (B2) (*Bartholy et al., 2007*).

Concerning air temperature, the largest increase is expected in summer, while the smallest increase in spring. The expected summer warming ranges are 4.5 – 5.1°C and 3.7 – 4.2°C for the A2 and B2 scenario, respectively. In case of spring, the expected temperature increase inside Hungary is 2.9 – 3.2°C (for A2 scenario) and 2.4 – 2.7°C (for B2 scenario).

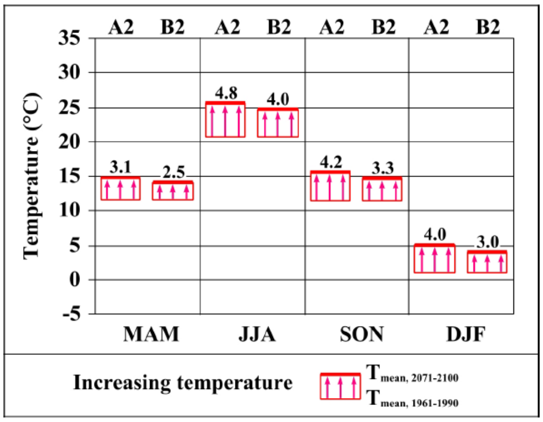


Figure 4: Projected temperature increase over Hungary for 2071-2100 using the A2 scenario (*Bartholy et al., 2007*).

Droughts are common characteristic of the climate in Hungary supported also by historical data (*Szinell et al., 1998*). Similar to global and continental trends, annual mean temperatures became higher during the second half of the 20th century and the most affected region was Northwest Hungary (*Szalai et al., 2005*).

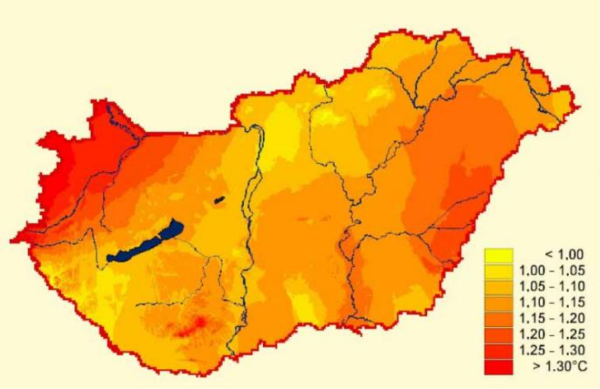


Figure 5: Change of the annual mean temperature during 1975-2004 in Hungary using linear trend analysis (*Szalai et al., 2005*).

Precipitation has decreased during the last century; the strongest negative trend appeared in West-Hungary (*Szalai et al., 2005)*.

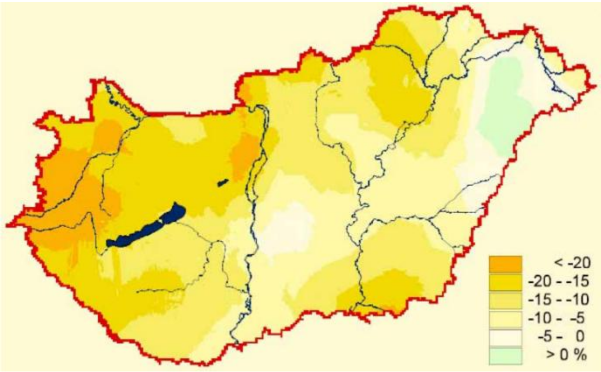


Figure 6: Change of the annual precipitation sum during 1951-2004 in Hungary using linear trend analysis (*Szalai et al., 2005*).

Gálos et al., (2007) have analyzed the dry events in Hungary using the regional climate model REMO for the 21st century. Drought periods were defined by considering the deviations of the modelled precipitation (>5% at annual and >15% at summer level) from the climate period 1961–90.

Based on the results of three IPCC scenario simulations (B1, A1B, A2), the probability of drought events will be higher in the second half of the 21st century (*Figure 7*).

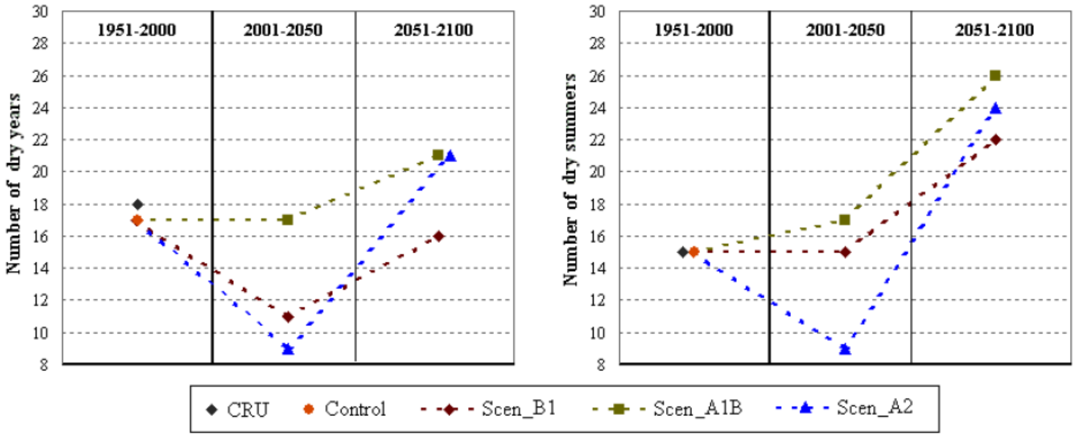


Figure 7: Total number of dry years (left) and dry summers (right) (*Gálos et al., 2007*).

According to the scenarios A1B and A2 a drought summer may happen every second year, compared to the reference term (1961-1990) and the dry periods will last longer. The intensity of dry events increases also significantly in all scenarios compared to the control period.

For the 21th century climate simulation results agree on increasing frequencies of warm extremes (i.e. heat waves, hot periods) and on decreasing probability of cold extremes (i.e. frost days, cold days) compared to 1961-1990. In summer, the strong warming and drying may increase the probability of severe droughts (*Mika 1988, 2007; Bartholy et al., 2007*).

2.1.4 Uncertainty of climate models

The numerical climate models, both global (GCMs) and regional (RCMs) have undergone considerable improvements recently and many experiments have been realized. All models simulate the present-day temperature and (to some degree) precipitation adequately on large scales (*Randall et al., 2007*), and simulated trend patterns are consistent with observations (*Hegerl et al., 2007*) if models are forced with all radiative forcings. Projected future warming patterns are robust (*Meehl et al., 2007*), but global temperature change is uncertain by approximately 50% (*Knutti et al., 2008*) owing to carbon cycle uncertainties (*Friedlingstein et al., 2006*) and models differing in their feedbacks (*Bony et al., 2006*). Models project changes in precipitation, extreme events (*Tebaldi et al., 2006*) and many other aspects of the climate system that are consistent with our understanding, but agreement between models declines from continental (regional) to local scales. The simulations of present and past climate help to improve our understanding of processes in the climate system, but it is not possible for any model to exactly simulate the full complexity of the climate system (*Räisänen, 2007*). That is why the results of climate models can only be taken as climate projections with numerous uncertainties.

The uncertainties in climate models output can be attributed to variations of the initial conditions or boundary conditions provided by the GCMs, as well as parameterizations and the fact that models are imperfect (*Stainforth et al., 2007*; *Tebaldi and Knutti, 2007*).

The initial conditions uncertainty comes from the deterministic chaotic nature of weather and the resulting sensitivity to the initial state. The initial condition problem is eliminated by running multiple ensemble members (simulations with the same model, parameters, boundary conditions and scenario, but slightly different initial conditions) or by averaging over longer time periods.

The boundary conditions-related uncertainty emerges from the fact that the regional climate models need determined values of variables on the border of the selected domain. Applying of different regional climate models with the same GCM may produce significantly different results. As it is not possible to simulate processes acting on spatial scales smaller than the model resolution (current RCMs have horizontal resolution of 10-50 km), the impact of these processes on large scale variables needs to be parameterized. This is the source of parameter uncertainty. The behaviour of a climate model in response to a forcing scenario on multi-decadal time scales is determined much more by the details of its parameterizations rather than the initial state (*Annan and Hargreaves, 2007*).

Another important source of uncertainty in case of model simulations of future climate is that we do not know the effect of all natural and anthropogenic forcings on the climate system. The natural forcings include in particular changes in solar and volcanic activity. The anthropogenic forcings include greenhouse gas emissions, aerosol emissions and changes in land-use.

Land-use change influence the climate by physical, chemical and biological processes, which affect the hydrological cycle and composition of the atmosphere. In general, tropical forests cool the climate by evapotranspiration on the other hand boreal forests have warming effect due to the low albedo (*Bonan, 2008*). In the Carpathian Basin the land use change contributed to the warming of the summer half-year by approximately 0.1°C, albeit forest cover has significantly increased (*Drüszler et al., 2009*). The uncertainty in greenhouse gas emissions has led the Intergovernmental Panel on Climate Change (IPCC) to the creation of a set of future emission scenarios (SRES scenarios) (*Nakicenovic and Swart, 2000*). Climate modellers will conduct new climate model experiments using the time series of emissions and concentrations associated with four Representative Concentration Pathways (RCPs), as part of the preparatory phase for the development of new scenarios for the IPCC's Fifth Assessment Report (expected to be completed in 2014).

Finally, all current climate models are known to be empirically inadequate in the sense that no set of parameters can always fit the observations within their uncertainty (*Sanderson et al., 2008*).

The summer drying problem is a disadvantageous feature of climate models in Central-Europe. A strong bias towards an extensive drying of the soil was detected during summer months in large areas of the Danube river basin, where the largest differences occurred in the Hungarian Lowlands. The validation has shown that summer months temperatures are overestimated (*Figure 8*).

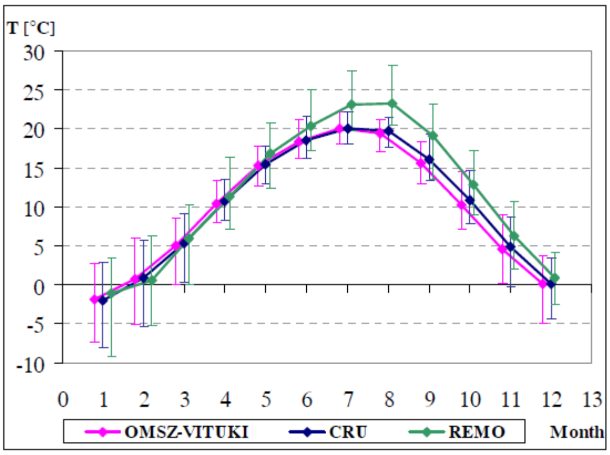


Figure 8: Validation for the monthly temperature (*T*) means (Hungarian mean, 1961-1990). Bars represent the spread of values within the 30-year period (*Gálos, 2010*).

The reasons for the disagreement between simulated and observed precipitation and temperature in the Danube river basin are not clear yet. The solution is complex and requires a more detailed investigation.

2.2 The effect of global climate change on forests

The effects of climate change on forests include some positive (e.g. increases in growth from CO_2 fertilization, longer growing season and colonisation in the leading edge) but mainly negative effects (e.g. reduced growth and increases in stress and local extinction due to mass mortality in the trailing edge).

2.2.1 Drought-induced tree mortality and forest die-off[1]

Increases in the frequency, duration, and severity of drought and heat stress connected with global climate change could fundamentally change the composition, structure, and distribution of forests. Increased tree mortality and die-offs triggered by drought are well documented for Europe and for temperate and boreal forests of North America (*van Mantgem et al., 2009*).

Forest mortality in Europe

Examples of forest mortality due to dry and warm conditions in the 1990’s and 2000’s in Europe (*Table 1*) includes increased death among many tree species in Spain (*Penuelas et al., 2001*), increased mortality of oak, fir, spruce, and pine species in France after the extreme heat wave and drought during the summer of 2003 (*Bréda et al., 2006; Landmann et al., 2006*), and increases in mortality of *Pinus sylvestris* near the species’ range limits in Switzerland and Italy (*Dobbertin and Rigling, 2006; Bigler et al., 2006*).

Summer drought has been tied with biotic stressors and led to mortality of *Quercus robur* in Poland (*Siwecki and Ufnalksi, 1998*), *Picea abies* in Norway (*Solberg, 2004*), and *Picea obovata* in northwest of European Russia (*Kauhanen et al., 2008*).

---

[1] die-off: a sudden sharp decline of a population of animals or plants that is not caused directly by human activity

Regionally extensive increase in the mortality of *Fagus sylvatica* was only reported from France (Ardennes, Vosges), Germany (Baden-Württemberg) (*Petercord, 2008*) and Hungary (*Lakatos and Molnár, 2009*).

Table 1: Documented drought and/or heat-induced mortality events in Europe, 1990–2010 (*Allen et al., 2010*).

Location	**Year(s) of mortality**	**Dominant tree/ taxa**	**Spatial concentration of mortality within geographic or elevational range**	**Stand/ population level mortality (%)**	**Scale of impact/ area affected**	**Biotic agents associated with mortality**	**Reference**
Italy (South Tyrol)	1992	*Pinus sylvestris*	Lower/southern edges of ranges	-	Landscape–subregional	insects	*Minerbi* (*1993*)
Austria (Lower Austria)	1990-1996	*Pinus sylvestris, Pinus nigra*	Lower edge of elevational range	27.6-49.2	Stand–landscape	Various insects	*Cech and Tomiczek (1996)*
Austria (Tyrol)	1991-1997	*Pinus sylvestris*	Lower edge of elevational range	10.0-70.0	landscape	Various insects	*Cech and Perny (2000)*
Italy (Aosta)	1985-1998	*Pinus sylvestris*	Lower/southern edges of ranges	-	Landscape–subregional	Fungi (*Armillaria spp.*); wood borers	*Vertui and Tagliaferro (1998)*
Spain (Northeast, Central, South)	1994, 1998	*Quercus spp., Pinus spp., Juniperus spp.*	Patchy within elevational range; southern edge of geographic range	0.0-19.4	Landscape–subregional	Not reported	*Penuelas et al., (2001); Lloret et al., (2004); Martinez-Vilalta and Pinol (2002*)
France (Ardennes, Vosges)	1998	*Fagus sylvatica*	Middle of ranges	5-30	Subregional; patchy across ~200.000 ha	non	French Forest Health Department (1998–1999)
Norway	1992-2000	*Picea abies*	Patchy across ranges	2-6.6	Landscape–subregional	Bark beetles (*Polygraphus poligraphus*)	*Solberg (2004)*
Greece (Samos)	2000	*Pinus brutia*	Lower edge of elevational range	-	Not reported	Not reported	*Körner et al., (2005); Sarris et al., (2007)*
Austria (Tyrol)	2001	*Pinus sylvestris*	Lower edge of elevational range	-	Landscape–subregional	Not reported	*Oberhuber (2001)*
Greece (South, Central)	2000-2002	*Abies cephalonica*	Not reported	5-10/yr in drought 0.17-0.50/ yr in non-drought	Landscape	Primary role, bark beetles (*Phaenopsknoteki, Pityokteines spinidens*)	*Tsopelas et al., (2004); Raftoyannis et al., (2008)*
Switzerland	2003	*Picea abies*	Not reported	~2.0Mm^3 timber lost	Landscape–subregional	Bark beetles (*Ips typographus*)	*Forster et al., (2008)*
Switzerland (Valais)	1973-1976, 1987-1993, 1996-2000, 2000-2004	*Pinus sylvestris*	Lower/southern edges of ranges	7–59	Landscape–subregional	Primary role, bark beetles (*Phaenops cyanea, Ips acuminatus*); nematodes; mistletoe	*Wermelinger et al., (2008); Dobbertin et al., (2007); Bigler et al., (2006); Dobbertin and Rigling (2006); Rigling et al., (2006); Dobbertin et al., (2005); Rigling and Cherubini (1999)*

Location	**Year(s) of mortality**	**Dominant tree/ taxa**	**Spatial concentration of mortality within geographic or elevational range**	**Stand/ population level mortality (%)**	**Scale of impact/ area affected**	**Biotic agents associated with mortality**	**Reference**
Germany (B.-Württemberg)	2003-2006	*Fagus sylvatica*	Not reported	~98.000m^3 timber lost	Landscape–subregional	Bark, ambrosia beetles (*Taphrorychus bicolor*, *Trypodendron domesticum*); wood borer	*Petercord (2008)*
Russia (Northwest)	2004-2006	*Picea obovata*	Patchy	208Mm3 timber lost	~1.9Mha affected	Bark beetles (*Ips typographus*), fungi	*Shtrakhov (2008);*
France (Provence, Southern Alps)	2003-2008	*Pinus sylvestris*	Lower/southern edges of ranges	20–80	Subregional; patchy across ~100.000 ha	Bark beetles	*Vennetier et al., (2007);* *Thabeet et al., (2009)*
France	2003-2008	*Quercus spp.* *Fagus sylvatica,* *Abies spp.,* *Picea abies,* *Pinus spp.*	Lower and middle of elevational range	1–3/yr	Regional	Bark beetles; fungi	*Breda et al., (2006);* *Landmann et al., (2006);* *Rouault et al., (2006);* *French Forest Health Department (2003–2008)*
France (Eastern Pyrénées)	2003-2008	*Abies alba*	Lower edge to middle of ranges	10–30	Subregional; patchy across ~150.000 ha	(*Ips, Pissodes spp.*)	*French Forest Health Department (2003–2008)*
France (Provence, Maures Mountains)	2006-2008	*Quercus suber*	Northern edge to middle of geographic range	10–70	Subregional; patchy across ~120.000 ha	Insects (*Platypus spp., Coroebus spp.*)	*Vennetier et al., (2008)*

It is important to outline that *Table 1* - contrary to the name of the table - contains mortality events where the drought and heat was only “contributing factor”. This is mainly in association with the die-off of the *Pinus* species. Furthermore the author uses the “bark beetle”phrase for species, which taxonomically does not belong to the above mentioned group (e.g.: *Pissodes spp.*).

The rate of mortality could span a wide range from modest and short-lived local increases of background mortality rates to acute, regional or landscape-scale forest die-off.

The temporal pattern of mortality is difficult to interpret because of the lag effect, but the documented data suggest, that die-off events are clearly connected with single extreme events. Mortality due to the decline has been shown to occur years or even decades after the drought stress (*Góber, 2005; Bigler et al., 2006*).

The dataset from Europe confirms, that drought-related forest mortality has been reported in most cases from the range margins (geographic or elevational) where climatic factors (particularly water) are often limiting (*Jump et al., 2009*). Greater mortality can occur also on optimum sites within the middle of the distribution range (*Horner et al., 2009; Klos et al., 2009*), where higher tree density results increased competition for water. Trees in optimum conditions often do not invest in adequate root systems and become hydraulically overextended.

Examples from North America

Drought and heat across western North America in the last decade have led to extensive insect outbreaks and large scale mortality in many forest types, affecting ~20 million ha and many tree species from Alaska to Mexico (*Raffa et al., 2008*). Examples of forest die-offs close to the xeric limit cover millions of hectares of *Populus tremuloides* (Saskatchewan and Alberta) (*Hogg et al., 2008*) and *Pinus edulis* in the Southwestern U.S. (*Shaw et al., 2005*).

It should be outlined that forests of the above mentioned *Pinus* species can be found in natural conditions with low or no human impact.

Forest mortality in Hungary

The first large scale forest mortality partly connected to climatic factors was the oak decline[2] in the late 80's. *Igmándy* (*1987*) reported that the decline of *Q. petraea* in Hungary began in 1978 in the colline northeast and extended within three years to the whole of the country. The symptoms of the oak decline were very complex. Macrosymptoms included: crown transparency, yellowing, excessive twig abscission, dieback[3] of branches and the whole crown, epicormic sprouts on branches and trunk (*Führer, 1998*). Oak mortality was originally identified as a disease caused by fungi earlier mainly saprophytic, and turning to virulent, it was later admitted that the primary reason triggering the pandemy was climatic. The total extent and damage of the dieback hitting sessile oak stands in the Northern Mountain Range and in Transdanubia may be assessed to damaging ca. 35% of all stands above the age of 40 years, amounting to a total damage of 2.5 million m^3 (*Mátyás et al., 2009*).

Subregional (Sopron and Kőszeg-mounteains) mass mortality of man-made *Picea abies* stands started in the early '90s. The hot and dry summers, the decrease on winter precipitation were favourable for *Ips typographus*, which produced up to three generations per year. The outbreak of *Ips typographus* and *Pityogenes chalcographus* resulted in a strong decrease of this tree species (1990: 1.4%, 2008: 0.7%) and a high volume (~ 800.000 m^3) of sanitary cuttings (*Lakatos, 1997*; *Lakatos, 2006*).

The mass mortality of beech in Hungary is discussed later.

2.2.2 Plant physiology and biotic agents

Physiological response of trees to drought

The fundamental ecophysiological mechanisms controlling survival and mortality of trees during drought is still poorly understood (*Bréda et al., 2006; Ogaya and Penuelas, 2007*).

Raising temperature increases the vapour pressure deficit and evaporation to the atmosphere, which could results in increased water loss through transpiration. Two type of stomatal regulation mechanism exists to avoid severe consequences. The first is the drought avoidance (isohydric species), by which stomata close at a water potential threshold to minimize further transpiration. The second is drought tolerance (anisohydric species), by which stomatal closure is less severe and transpiration continues at relatively high rates (*McDowell et al., 2008*). The isohydric response protects xylem from cavitation through avoidance of low water potentials, but can cause eventual carbon starvation as stomatal

---

[2] decline: a disease that gradually weakens the body; to tend toward an inferior state or weaker condition

[3] dieback: a condition in woody plants in which peripheral parts are killed

closure shuts down photosynthesis while respiration costs continue to eat up carbon stores. The anisohydric response can allow continued carbon gain through maintaining open stomata but at greater risk of cavitation, which might kill trees directly or could increase the likelihood of future carbon deficits. It is important to outline, that trees have the ability to shift allocation of resources and change their hydraulic architecture throughout their lifetime (*McDowell et al., 2008*).

Biotic agents and tree mortality

There is evidence that biotic agents are often involved in vegetation mortality (*Molnár et al., 2010*) and plant survival may be increased via application of insecticides or semiochemicals *(Lakatos, 1997*). Not all species of insects, fungi and bacteria benefit from drought. Bark beetles, which are the major mortality agents in the northern hemisphere, are restricted to rare, highly stressed trees under optimal conditions because they lack sufficient numbers to conduct mass attacks that can overcome the defenses of vigorous trees (*Boone et al., 2011*). Population growth occurs when warm temperatures and/or the high number of breeding trees (windthrow) favour reproduction (*Csóka 1997; Gan, 2004*), and when environmental stress decreases plant defense (drought). Under these circumstances, population growth of the biotic agents can generate positive feedbacks through synchronized attacks that overwhelm the defenses of otherwise healthy trees. The final steps in biotic driven mortality can be the hydraulic failure associated with fungal occlusion of xylem or destruction of resource-acquiring tissues, such as foliage or roots (*McDowell, 2011*).

2.2.3 Climate change and future mortality rate

Plants adapted to historic climates might be exposed to novel, extreme conditions that overwhelm their acclimatory responses. For example, rising temperatures are likely to increase carbohydrate consumption owing to the temperature dependence of respiration (despite acclimation), particularly during extreme high temperature (*McDowell, 2011*). Extreme temperatures damage photosynthetic apparatus, reducing photosynthesis and increasing carbohydrate use for repair (*Mészáros et al., 2007*). Temperature rise can increase insect population growth owing to reduced over-winter mortality, decreased generation times, greater host vulnerability and access to vulnerable hosts following range expansion. Decreased water availability will compound temperature effects, by increasing cavitation and reducing xylem refilling, photosynthesis and phloem transport. Rising temperature increases evaporative demand, forcing greater stomatal closure and higher ecosystem evaporation, thus accelerating progression of mortality mechanisms (*Mészáros et al., 2007*).

2.2.4 Decline model (factors and their interactions)

Tree mortality commonly involves multiple, interacting factors. Based on the decline spiral model (*Manion, 1991*), drought can operate as an ‘‘inciting factor’’ that may ultimately lead to mortality in trees that are already under stress (by ‘‘predisposing factors’’ such as old age, poor site conditions) and result to consequent stem and root damage by biotic agents (‘‘contributing factors’’ such as insects and fungal pathogens).

McDowell et al. (*2008*) states three mutually non-exclusive mechanisms by which drought could lead to broad-scale forest mortality:

- extreme drought and heat kill trees through cavitation within the xylem;

- elongated water stress results carbon deficits and metabolic limitations that lead to carbon starvation and reduced ability to defend against attack by biotic agents such as insects or fungi and,
- extended warmth during droughts can drive increased population abundance in these biotic agents, allowing them to overwhelm their already stressed tree hosts.

Genetic background of tree mortality

Bioclimatic modelling of distribution ranges is based on the concept that distributional patterns depend on the physiological tolerance limits to climate. Tolerance can be defined as the ability of a genotype to maintain its fitness despite damage (phenotypic plasticity). This physiological tolerance is determined by genetics. Thus, adaptive response to environmental stress is ultimately a genetic issue, and bioclimatic modelling is basically dealing with the search for the genetically set tolerance limitations (*Mátyás et al., 2008*) (*Figure 9*).

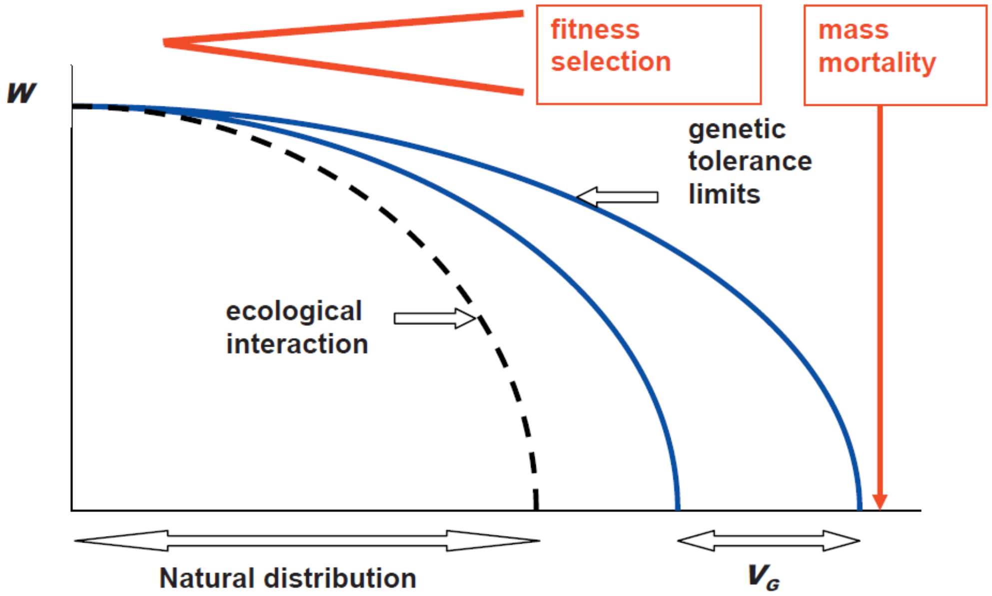


Figure 9. Ecological-genetic model of fitness decline and mortality triggered by worsening of climatic conditions. The phenotypic variance of limits of tolerance (V_G) represents the basis of natural selection. Due to interactions in the ecosystem, the natural distribution is usually stronger limited, than the genetically set critical tolerance (*Mátyás, 2006*).

Phenotypic plasticity provides the ability of instant acclimation without any change in the inherited genetic resources. Mainly for reasons of difficulty of experimental analysis, reaction norms and limits of adaptability set by phenotypic plasticity are rarely considered in connection with adaptation. It is an often underestimated issue both in forest genetics and ecology, in spite of the fact that considering the speed and magnitude of predicted changes, phenotypic plasticity is the most important and practically only natural buffering mechanism (*Mátyás and Nagy, 2005*).

Consequences (biotic and abiotic) of forest mortality

Trees grow relatively slowly but can die within a few months to a few years; therefore, mortality of trees can result in rapid changes.

Fundamental changes in species composition may occur (*Rich et al., 2008*), due to more competitive (also invasive) tree species that repopulate the overstory (*Kotroczó et al., 2007*).

Abiotic impacts include changes in solar energy fluxes with feedbacks to regional climate (*Chapin et al., 2008; Gálos et al., 2007; Drüszler et al., 2009*), and alterations in hydrology and ecosystem water budgets due to increases in evaporation and reductions in transpiration (*Huxman et al., 2005*) and changes in groundwater recharge (*Móricz, 2010*).

Forests store considerably more carbon than the atmosphere, and forest die-off could further redistribute carbon pools locally, regionally or even globally (*Jones et al., 2009*). Drought induced mass mortality have recently transformed forests of British Columbia (Canada) from a net carbon sink into a net carbon source (*Kurz et al., 2008*)!

A litter manipulation experiment in a warming and drying oak forest in the Síkfőkút Project also stated that the increasing soil temperature raised the soil respiration exponentially, which could speed up global warming by positive feed back mechanism (*Tóth et al., 2007*).

2.3 Ecology of beech

2.3.1 The current distribution range of European beech

Fagus sylvatica is a late-successional forest tree with a life span of about 300 years, and a very late reproduction age (40–50 years old). The seed production is characterized by irregular mast years (*Ellenberg, 1996*).

Beech today extends from the tree-line forests of the Cantabrian Mountains in the west to the Carpathians and Balkan Mountains in the east and latitudinally from Sicily in the south to southern Sweden and Norway in the north (*Figure 9*). Beech is widely distributed in Central and Western European forests, however, there are areas where beech is absent as a native tree, such as the Po valley and the Hungarian plain (*Pott, 2000*). Beech does not spread far into the more continental east of Europe. The most continental occurrence of beech can be found in Ukraine (Bukovina) (*Figure 10*).

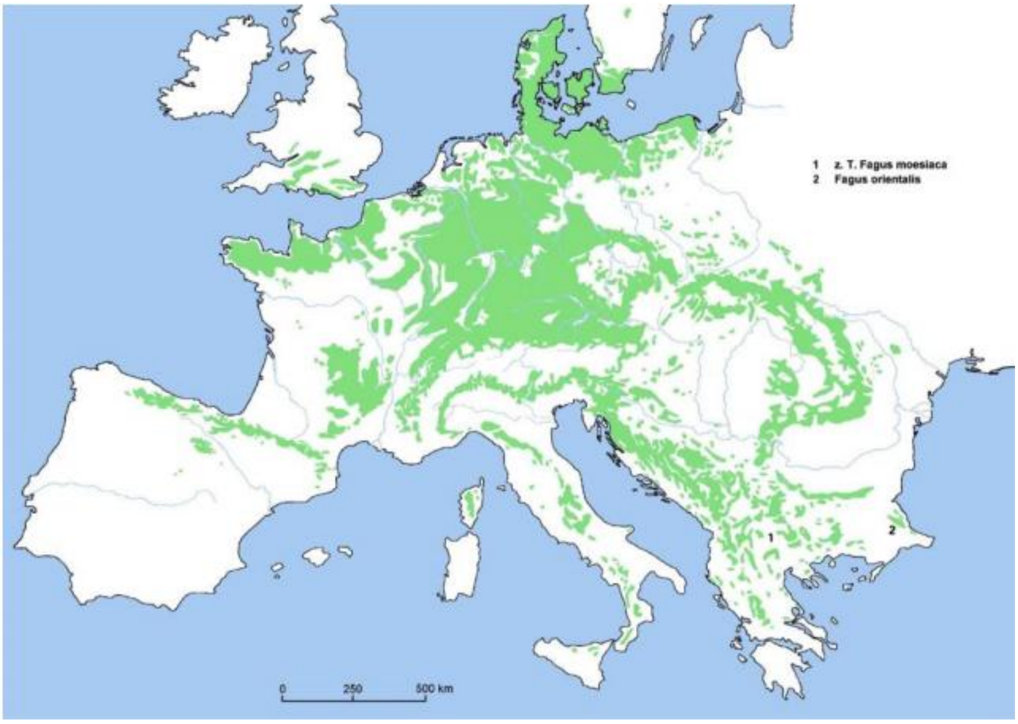


Figure 10: Present day distribution of *Fagus sylvatica* (*Bohn, 1992*).

Beech needs at least 140 days during the growing period, and for this reason it cannot survive too far north in Scandinavia (*Peters, 1997*). However beech can occupy a wide range of habitats with different soil types (*Majer, 1968; Ellenberg, 1996*), due to its intolerance against summer drought it cannot survive in southern Spain, southern Greece and in the most arid areas of southern and central Italy and the Hungarian plain. This suggests intolerance against aspects of the continental climate like low temperatures in winter as well as higher temperatures in summer (*Iversen, 1973; Huntley et al., 1989*).

After the last glacial beech spread to central and northern Europe from southern France, eastern Alps–Slovenia–Istria and possibly southern Moravia–southern Bohemia. Populations survived the last glacial period in the Mediterranean regions (Italian and Iberian peninsulas) did not spread into Central-Europe (*Magri et al., 2006; Tinner and Lotter, 2006*). Beech populated the Carpathian basin 5-6000 years ago (*Comps et al., 1998*).

In the Atlantic part of Europe (in the northwestern part of its range) beech is a typical lowland species, but in Central and Southern Europe it is connected to the middle or high mountains. In the southern part of its range it is stretching up to 2100 m above sea level (*Figure 11*). This suggests that the presence of beech is determined by specific climatic condition.

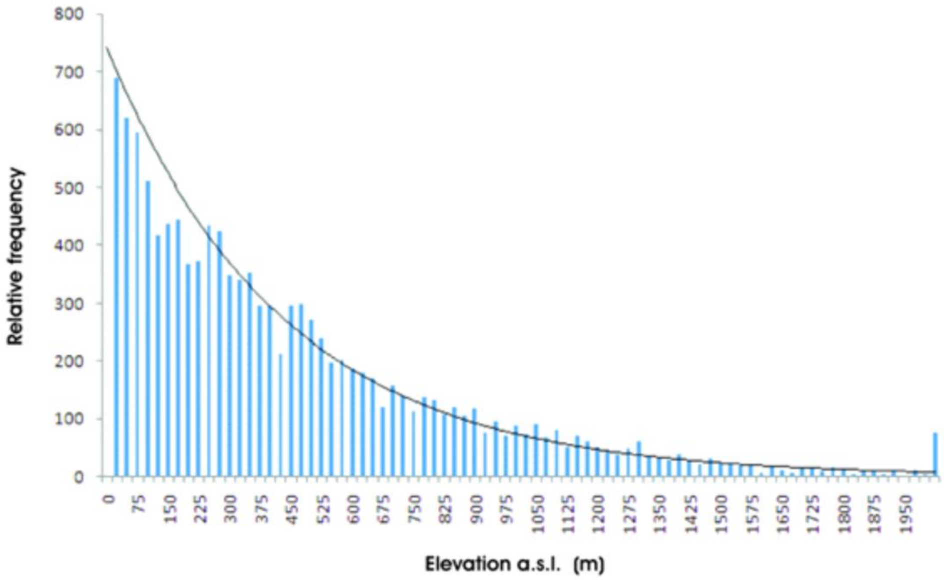


Figure 11: The altitudinal distribution histogram of beech based on the systematic grid sampling with a grid size of 5x5 km under the distribution map of *EUFORGEEN*. Elevation was derived from the digital elevation model of Europe (*GTOPO*).

2.3.2 Ecological and climatic constraints of the distribution of beech

European beech is a strong competitor with high shadow tolerance as seedling and sapling. Beech is therefore able to get to dominance on sites with a relatively broad spectrum of nutrient and hydrological regimes, from highly acidic to basic soils (*Leuschner et al., 2006*) and from dry to moist conditions. In the southern part of its range, and at low elevations, the competitiveness of beech is limited by increasing water stress, until finally it is replaced by forests consist of more drought-tolerant species (*Peters, 1997*), mainly *Quercus* and *Pinus* (*Horvat et al., 1974; Ellenberg, 1996*) (*Figure 12-13*).

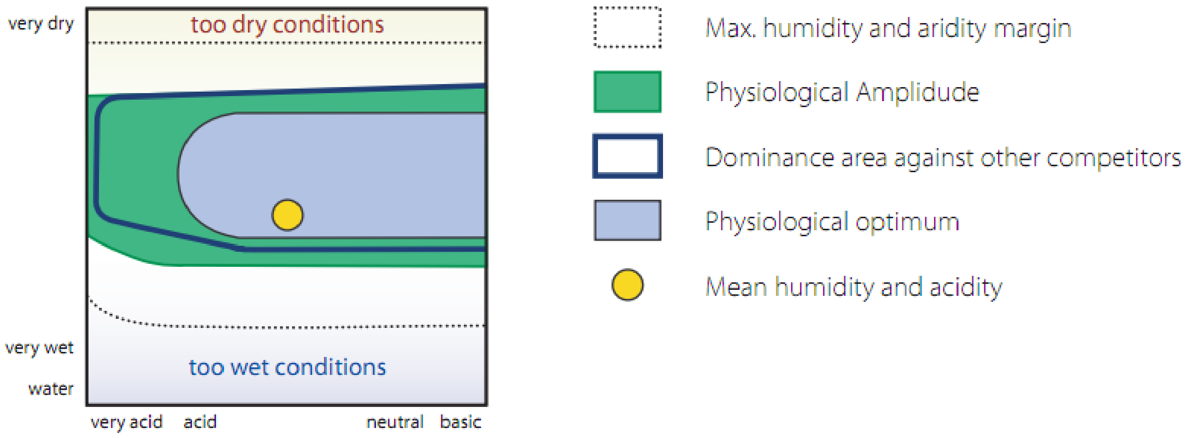


Figure 12: Natural humidity and acidity niche of beech under temperate sub-oceanic climate (*Ellenberg, 1996*).

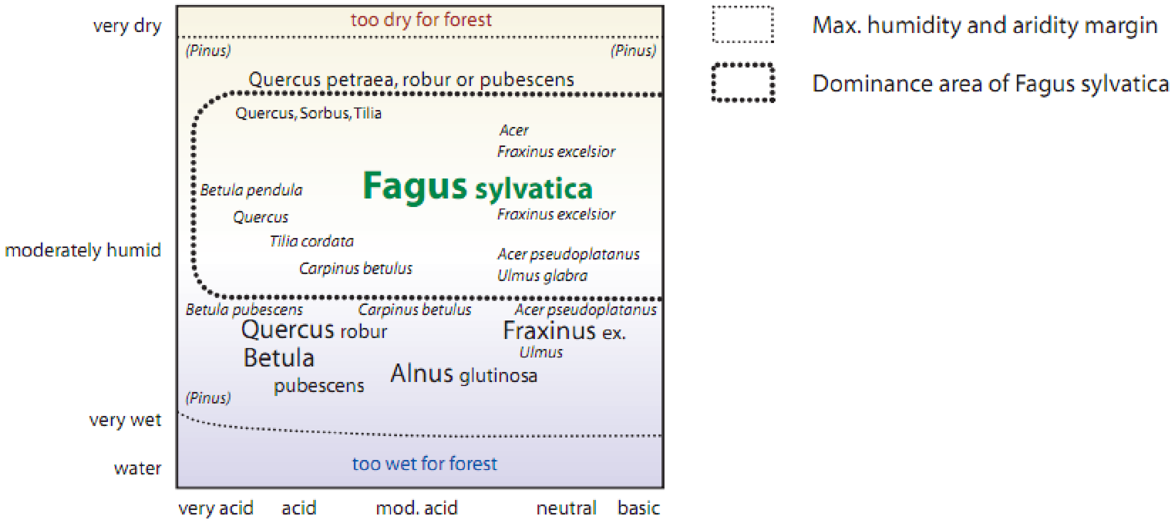


Figure 13: Dominance and competition between different species of beech in Central-West European forests at present. (*Ellenberg, 1996*).

Minimum temperature

Beech is not found in places where the mean temperature of the coldest month is less than -3°C (*Huntley et al., 1989*). This is due to its intolerance against late frosts (*Sykes et al., 1996*). Beech can be characterised with a distinctive response to the length of the chilling period (*Crawford, 2000*). This suggests that the budburst of beech definitely needs a not too cold and not too long chilling period (*Crawford, 2000*).

Drought

The water use of beech

Fagus sylvatica can get dominance on sites with a relatively broad spectrum of hydrological conditions, because beech can maintain the transpiration close to the cavitation induction point (*Bréda et al., 2006*). This makes beech very sensitive to drought-induced xylem embolism (*Backes and Leuschner, 2000; Cochard et al., 2001*).

The water use of beech is regulated conservatively (*Backes and Leuschner, 2000*). In case of a moderate water shortage, the stomatal regulation system prevents dramatic reductions in turgor, leaf water potential, and photosynthesis, but during severe droughts this system cannot adequately prevent the loss of hydraulic conductivity (*Geßler et al., 2001*). Thus decrease in predawn leaf water potential (*Backes and Leuschner, 2000*), canopy conductance (*Granier et al., 2000; Schipka et al., 2005*), photosynthetic capacity (*Bergh et al., 2003*), stem diameter growth (*Lebourgeois et al., 2005*), height growth (*Frech, 2006*), and net primary production (*NPP*) (*Ciais et al., 2005*) is expected. Short term dry and hot conditions during summer can also lead to a direct reduction of canopy leaf area index (*LAI*) or to dieback of the canopy (*Berki et al., 2009*; *Bréda et al., 2006*).

Effects of elongated water shortage (drought stress)

Drought stress happens, when the available water for plants drops below a limit inducing restrictions to growth and transpiration. This elongated water shortage leads to dysfunctions but rarely results in direct and immediate tree die-off. Water shortage causes decrease in leaf area index not only seasonally but also on an inter-annual period and hence assist to decline of gross primary productivity in beech forests (*Bréda et al., 2006*).

Tree ring width and leaf area is often smaller during several years following drought event. Moreover, physiological disorders increase tree vulnerability to stresses like insect damages, which leads eventually to mortality. If trees have been predisposed to stress because of poor growing conditions, site disturbance or damage, they may die this year or next year without showing visible warning signals.

Lower growth rate and poor crown condition are frequently reported before death, but it is not responsible for that. The probable explanation is that growth is an indicator of tree carbon balance dysfunction and mortality is very likely caused by reserve depletion (*Bréda et al., 2006*).

Very little is known about the response of the root system of mature beech trees to water shortage, which might respond more sensitively to drought than aboveground organs.

Effects of extreme heat and drought

Extreme heat and drought could have a direct effect on transpiration causing xylem embolism. Direct heat damage to trees was observed in 2003, since trees with closed stomata were unable to cool via transpiration (*Bréda et al., 2006*).

The net ecosystem exchange (*NEE*) measured above beech stands showed reduced CO_2 uptake and transpiration during the severe drought period in 2003, mainly due to stomatal closure. Carbon uptake reached a maximum between days of year (*DOY*) 150 and 170 (depending on site), and thereafter rapidly decreased. At peak drought intensity (around DOY 220-240), NEE turned to positive, i.e. carbon was released by the ecosystems to the atmosphere (*Figure 14*) (*Bréda et al., 2006*).

Fine-root length is also influenced by weather extremes, i.e. rainfall is one of the major environmental factors controlling fine-root dynamics of beech. The fine root biomass was much less in a dry beech stand as compared to stands with higher rainfall due to the large mortality of fine roots during extreme drought (*Eissenstat et al., 2000*).

Beech regeneration exhibits reduced growth and nitrogen uptake from the soil when subjected to severe drought (soil water potential < -0.4 MPa) throughout several weeks (*Fotelli et al., 2004*).

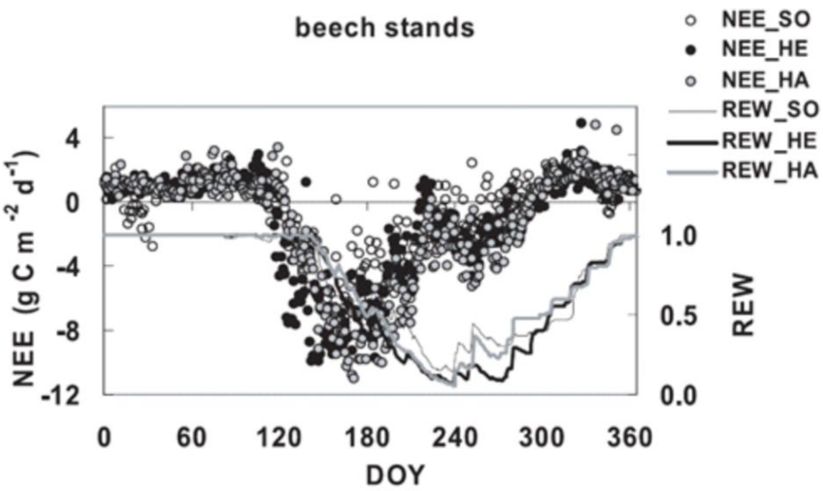


Figure 14: Time course of net ecosystem exchange (NEE, daily data) and relative extractable soil water (*REW*) in beech stands in Germany (*Bréda et al., 2006*).

2.3.3 Beech provenace trials

In common garden experiments, the transfer to the planting "test" site is interpreted as simulation of sudden (within one generation) environmental change. Quantitative, adaptive responses (growth, phenology, health and survival) measured in comparative tests could be utilized to forecast the effects of climatic change.

Initially, a series of beech field trials was established in the early 1980s, but because of the political situation at that time, the sample of provenances neither included stands representing the whole species range nor did the trial locations represent all the habitats inhabited by beech. Therefore, following political changes in Europe another series of 49 trials were designed. In 1995 a series of 23 trials, and in 1998 26 trials were established. In Hungary, one test of the international series of 1998 has been outplanted in Bucsuta, Zala hills, Southwest Hungary.

The consequence of climatic selection, differentiation in phenological behaviour is well reflected by field test results. For example, budbreak of beech shows a clinal East-West pattern: Atlantic coast provenances are late, while Alpine and SE-European continental sources are early flushing (*Wühlisch et al., 1995; Gömöry, 2009*).

Beech provenance trials could provide valuable information on growth, phenology, health and survival for simulation of climate change, but data available at this time from the provenance trials are for the juvenile state!

2.4 Beech in Hungary

Beech is one of the main stand-forming tree species in Hungary. Out of the 20.3 % of land covered by forests, beech currently occupies 107.940 ha, which amounts to 5.9 % of the forest area. Beech is widely spread on zonal sites, where summer precipitation is significant and the humidity is high. The distribution of beech is suspected to be wider in the past centuries, especially in the Western half of Transdanubia. While beech forests were often replaced by agricultural land use at low elevations, in less accessible areas beech forests remained in close to natural state.

While the altitudinal occurrence is stretching from the lowlands up to 1.000 metres above sea level, the vast majority of the beech stands in Hungary can be found between 200 and 500 m (*Figure 15*). The lowest elevation is an extrazonal site in the upper valley of the Drava river, due to favourable microclimatic conditions (Southwest Hungary, altitude ca. 120 m asl.).

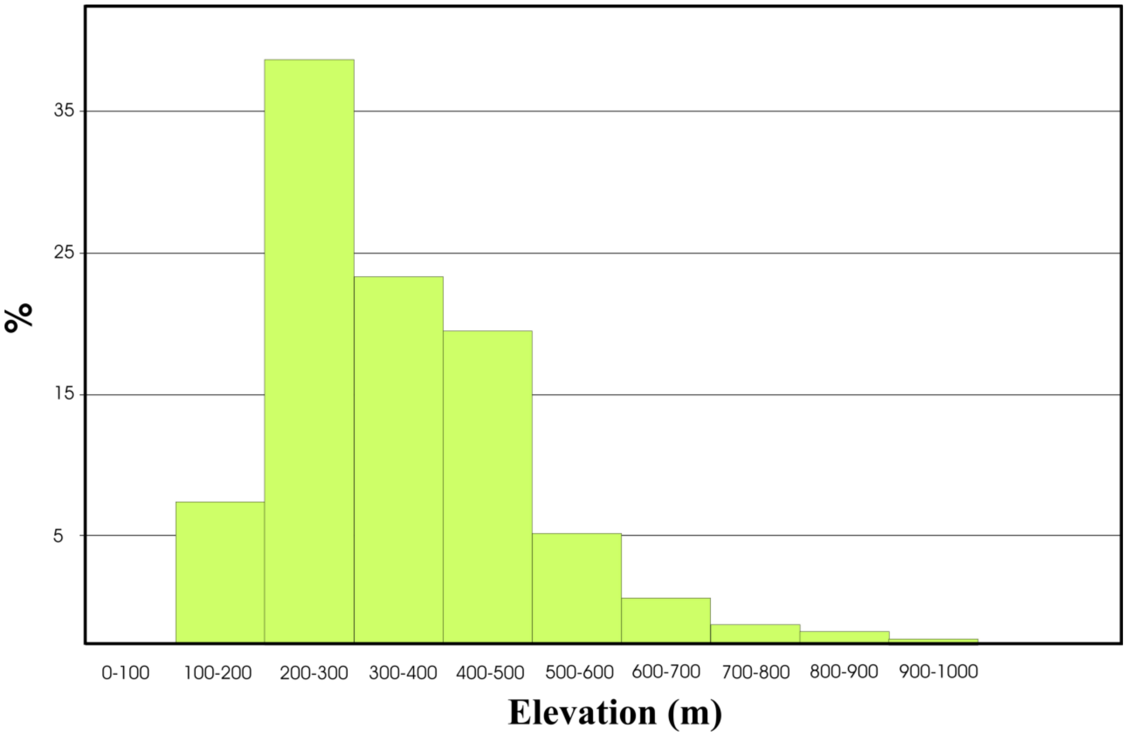


Figure 15: The altitudinal distribution of beech in Hungary.

Due to its climate sensitivity, beech is used in forestry practice as an indicator species for the beech forest belt, providing the most favourable growing conditions in the country. The climatic envelope of beech can be well characterized using summer mean temperature and precipitation of the growing season (*Figure 16*).

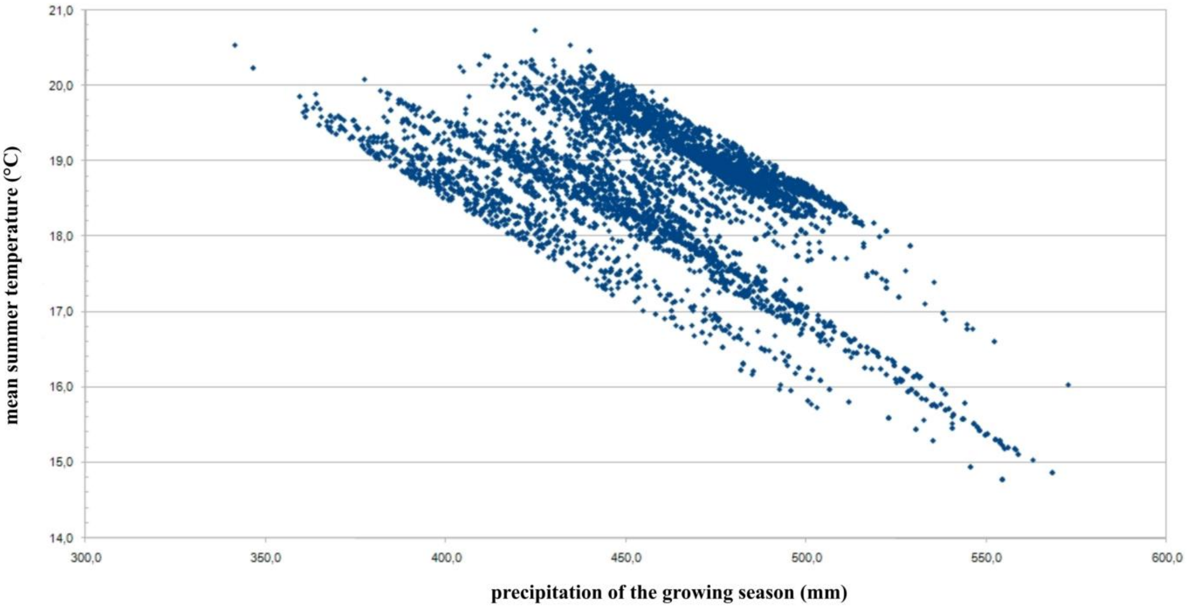


Figure 16: The 2 dimensional (precipitation of the growing season/mean summer temperature) climate envelope of beech subcompartments in Hungary.

2.4.1 Beech associations in Hungary

Typical mountain beech forests (*Aconito-Fagetum*) are found only at higher elevations of the North-Hungarian Middle Mountains. Their presence is restricted to the Bükk and Zemplén Mountains, and to smaller occurrences in the Mátra and Börzsöny Mountains. These are highly productive forests mainly growing on lessivated brown forest soils. Beside beech, common ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*), European rowan (*Sorbus aucuparia*) and mountain elm (*Ulmus glabra*) are admixed species (*Borhidi, 2003*).

Only isolated, small fragments represent the mixed fir-beech forests (*Abieti-Fagetum*) in the Sopron and Kőszeg Mountains (*Borhidi, 2003*).

The largest occurrences are submontane beech forests (*Melitti-Fagetum*) occupying the lower elevations of the Hungarian Middle Mountains crossing the country from NE to SW (first of all in the Zemplén, Bükk Börzsöny, Bakony and Kőszeg Mts.). Westward, in Southwest Transdanubia beech occupies more frequently collinal sites under 400 m a. s. l. The latter region receives more precipitation and is under moderate sub-Mediterranean influence, therefore floristically distinguished as Illirian beech forests (*Vicia oroboidis-Fagetum*). Submontane beech forests are mixed with hornbeam (*Carpinus betulus*) and sessile oak (*Quercus petraea*) indicating higher temperatures and less favourable humidity conditions (*Borhidi, 2003*).

Regarding specific site conditions, beech is a dominant tree species on humid-acidophilous sites (*Deschampsio flexuosae-Fagetum*). It is also present as admixed species beside common ash (*Fraxinus excelsior*) and large-leaved linden (*Tilia platyphyllos*) on the comparatively dry sites of calcareous ravine slopes of the Transdanubian Middle Mts. (*Mercuriali-Tilietum*). A relict-type occurrence with yew (*Taxus baccata*) in the Bakony Mts. has been described as *Taxo-Fagetum* (*Majer, 1980*).

2.4.2 Beech decline in Hungary

A considerable part of beech stands are situated close to the xeric limit, i.e. at the drought-related (trailing, or retreating) end of their warm-temperate distribution range in Southwest-Hungary (*Mátyás et al., 2009*).

Background

During the last century there have been unfavourable changes in the climate conditions for the beech forests in Southwest Hungary. The summer mean temperature has increased while the annual rainfall showed a decreasing trend. This has lead to a significant aridification, which could be also expressed by the shift of the isolines of the Ellenberg quotient (*EQ*) computed at the beginning and at the end of the last century (*Figure 17*). *Jahn* (*1991*) and *Czúcz et al., (2011*) proposed the *EQ=29* value as threshold for the lower distribution limit for beech.

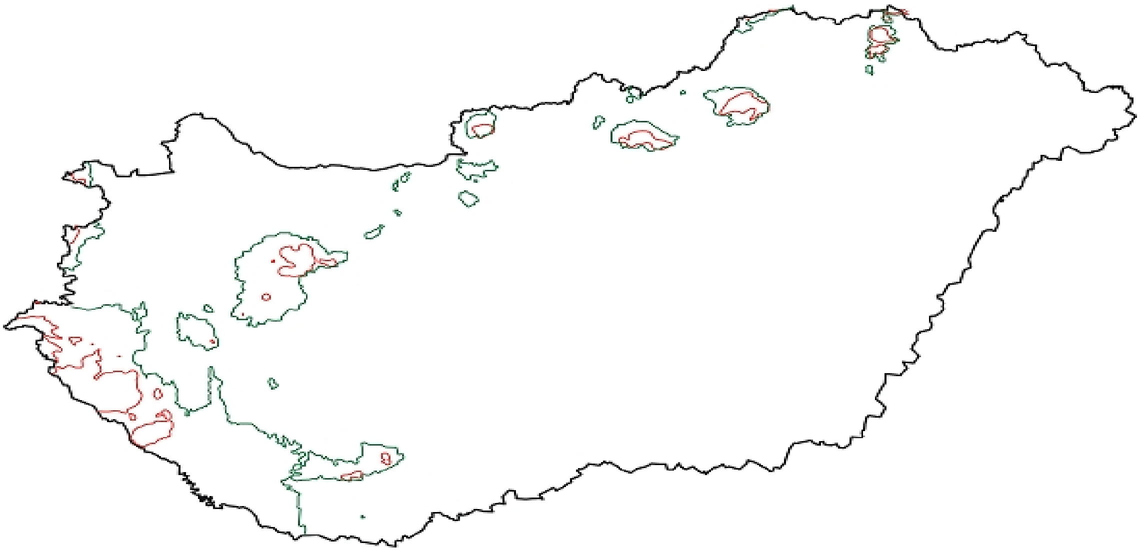


Figure 17: The distribution limit *EQ=29* for the period 1901-1930 (green) and for 1975-2004 (red).

Besides the long term trends, the fluctuation of precipitation on a finer temporal scale could be also observed especially in Southwest Hungary by comparing the decadal rainfall sums (*Figure 18*).

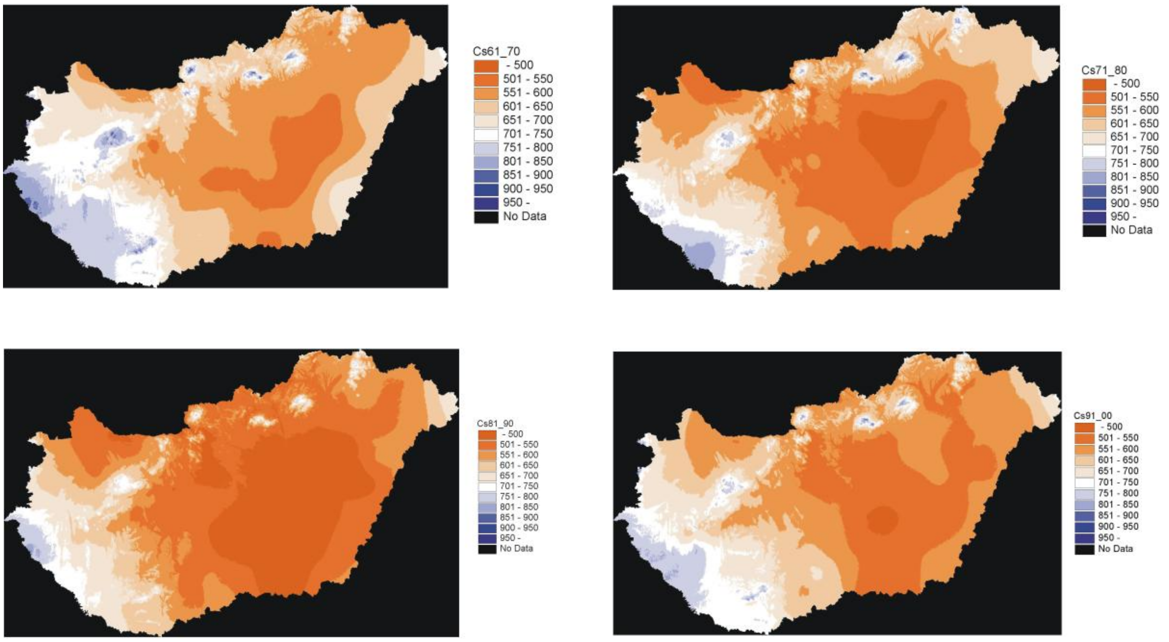


Figure 18: The decadal rainfall sums in Hungary.

A long drought period has occurred already during the 90's, which has hit mostly beech forests, standing at the trailing edge (*Leskó, 1995*). The next mass mortality of beech occurred in the early 2000's in Southwest Hungary. Due to the prolonged drought, the soil water storage has been almost completely depleted and the air humidity was often under the climatic mean.

Symptoms, secondary pest and diseases during the 2000-2003 droughts

The mass mortality of beech in the early 2000's was the result of a typical damage chain (*Lakatos and Molnár, 2009*). Drought has weakened the trees and favoured the development of different pests and pathogens. The weakened trees were ideal places for mass reproduction of different pests and heavy infestation of pathogens (*Csóka et al., 2007*; *Lakatos and Molnár, 2009*). Similar symptoms were only recorded in the 1880s (*Piso, 1886*).

Figure 19: Mortality caused by drought in late summer 2003 in a beech stand in Balatonszárszó (admixed oaks showed no damage!).

The direct causes of mortality were insects, the green jewel beetle (*Agrilus viridis*), the beech bark beetle (*Taphrorychus bicolor*) and the fungus species of *Biscogniauxia nummularia*. *Agrilus viridis* was the main pest species, while *T. bicolor* attacked only the weakened trees. Both insects damage the phloem and cambium thus sap flow occurred on the infested trees (*Lakatos and Molnár, 2009*). The physiological disorder has led often to direct dieback of trees, which can last for years. Other xylo- and phloeophagous species had no importance in the damage chain, since their presence can be explained by the large amount of dry trees to be optimal for their development (*Lakatos and Molnár, 2009*).

The affected area

Symptoms were first observed in Balaton highlands and Bakony Mountains, but the most severe damage occurred in the Southwest part of Hungary.

The most damaged beech stands were situated mainly in mixed forests with significant ratio of hornbeam and sessile oak. The following forest were affected by the mass mortality in Zala county: Csács, Kapornak, Kalamászos, Almás, Ligetfalva, Csáford (Zalaegerszeg Forest Office), Kondora, Irsa and Csöde (Lenti Forest Office).

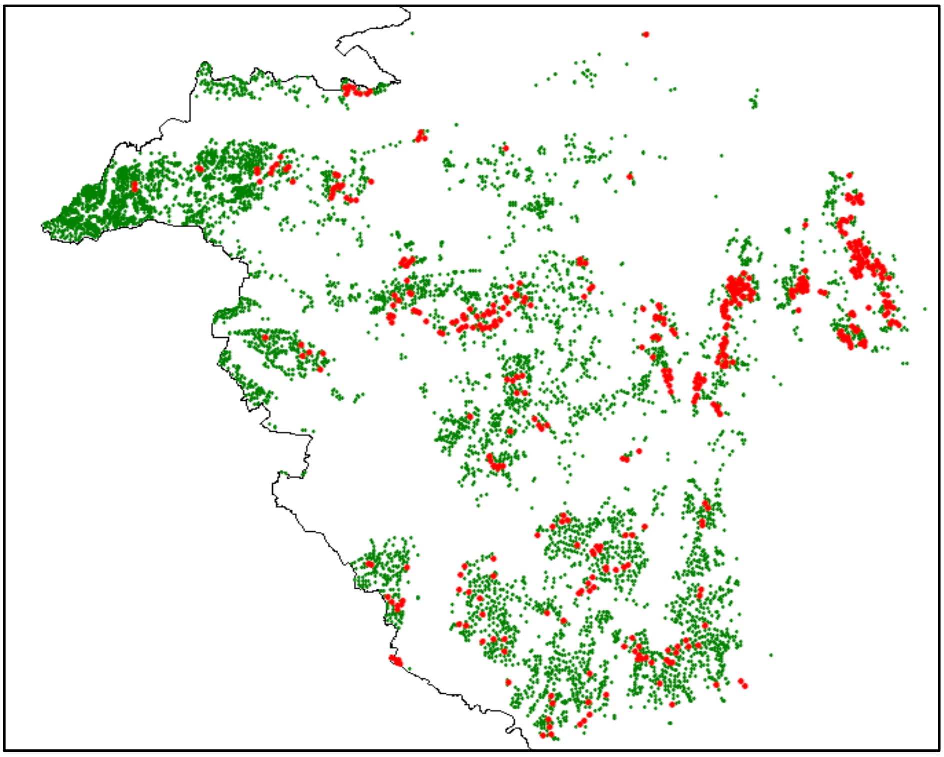


Figure 20: The affected (red) and healthy (green) beech subcompartments in Southwest Hungary.

Sporadic beech dieback was observed in Vétyem, Istvánd, Barkócás (Letenye Forest Office), Szentpéterfölde (Csömödér Forest Office), Templom forest, Alsóváros forest (Nagykanizsa Forest Office).

The affected area and the amount of sanitary felling per forest offices in 2004 can be found in *Table 2*.

Table 2: The affected area and the amount of sanitary felling per forest offices of the Zalaerdő Zrt. in 2004 (*Góber, 2005*).

Forest Office	Affected area (ha)	Volume of beech sanitary logging (m^3)
Nagykanizsa	63.3	7338
Bánokszentgyörgy	23.9	3578
Letenye	48.2	2639
Lenti	51.2	6602
Zalaegerszeg	212.0	56548
Csömödér	12.2	3192
Total	**410.8**	**80077**

Economical consequences

After the drought period more than 140 000 m^3 sanitary felling had to be undertaken in 2004-2005 (*Góber, 2005*), which affected approximately 411 hectares in Zala county in 2004. This amount constituted about 30% of the total volume of logged trees and caused approximately 400 million HUF (1,6M EUR) direct loss for the forest owners. The ratio of sanitary logged trees reached 67% in the Zalaegerszeg Forest Office. The canopy closure of the declining beech stands has often reached the limit of 70%, thus obligation for regeneration followed. The regeneration of the declined stands will be an important question of the future. After 2008 the health condition of the survived beech forests has improved slightly due to more humid years (*Kolozs, 2009*).

2.5 Distribution modelling

Early works of species distribution modelling (*SDM*) in the late 1970s concentrated mostly on the development of new methods to model effectively the shape of a species' response to environmental gradients (*Austin, 1987*). Recently spatiotemporal predictions of species distributions have become an increasingly important tool to address various issues in ecology, biogeography, evolution and, more recently, in conservation biology and climate change research.

It is difficult to classify distribution models as they all share some theories, concepts or assumptions. "Habitat models'' relates the environment (biotic and abiotic) of a region with respect to a species, without direct empirical links necessarily occurring between those descriptors and the species. They are purely descriptive and relate to a particular space and time frame (*Guisan and Zimmermann, 2000*). Static distribution models can be improved by integrating different interactions (combined or hybrid models).

"Process-based models'' use mechanistic links between the growth and fitness of species, or more abstract plant functional types, and a range of environmental or biological (e.g. competing species) variables. Examples range from dynamic vegetation model (*Woodward, 1992*), population viability analysis (based on population dynamics, *Possingham and Davies, 1995*), plant population modelling (*Jeltsch et al., 2008*) phenological models (based on phenology; *Chuine et al., 2000*), or diffusion/spread models (*With, 2002*).

The integration of statistical and more mechanistic, process-based models may lead to improved prediction efficiencies, yet few such attempts are available and it is still unclear which environmental and ecological processes necessitate the incorporation of dynamic mechanisms.

2.5.1 Distribution models

Distribution models apply statistical relationship between observed presence/absence or abundance of a given species (or population) to a relevant set of limiting environmental factors (typically climatic variables for plants) controlling the distribution of the species.

A striking characteristic of the distribution models is their reliance on the "niche concept" (*Guisan and Zimmermann, 2000*). The environmental niche is usually considered as all of the suitable habitats occupied by a species (*Grinell, 1917*). This is called fundamental niche. Biotic interactions can exclude the species from a part of their fundamental niche, resulting in the realized niche that is actually observed in nature. The potential niche is originally defined as that part of the fundamental niche available to species, as constrained by the realized environment. It considers that not all possible combinations of some given environmental variables exist in the study area, and thus differ from the realized niche.

A useful framework for clarification was recently proposed by *Pulliam (2000*), who proposed four theoretical views of the relationship between niche and distribution:

1. the *Grinellian* niche, where a species occurs wherever the environmental conditions are suitable (i.e. fundamental niche, with a population growth rate ≥ 1);
2. the realized niche of *Hutchinson*, where a species is excluded from part of its fundamental niche by a competitor or a predator,
3. the source-sink dynamics, where a species commonly occurs in a sink habitat where its population growth rate is < 1, and thus where it would disappear without constant immigration from source habitats, and
4. the dispersal limitation situation, where a species is frequently absent from suitable habitats because of recurring extinction events and limited dispersal ability preventing full recolonization.

Traditionally, plant ecologists have relied on niche concepts (*1*) and (*2*). The multidimensional envelope created by the niche based models is usually described as an approximation of the realized niche described by *Hutchinson (1957)*.

Modelling methods

A wide range of environmental niche models have been proposed for studying species distributions such as BioClim (*Busby, 1991*), Domain (*Carpenter et al., 1993*), linear, multivariate and logistic regressions (*Mladenoff et al., 1995; Felicisimo et al., 2002; Fonseca et al., 2002*), generalized linear modelling and generalized additive modelling (*Frescino et al., 2001; Guisan et al., 2002*), discriminant analysis (*Livingston et al., 1990; Manel et al., 1999*), classification and regression tree analysis (*De'ath and Fabricius 2000; Kelly 2002*), genetic algorithms (*Stockwell and Peters, 1999*), artificial neural networks (*Manel et al., 1999; Moisen and Frescino, 2002*), and support vector machines (*Guo et al., 2005*).

Recently modelling methods are grouped and applied in packages. There are many environmental niche modelling packages available; for example: GRASP, ModEco, BIOMOD, or Openmodeller. These platforms support consistent use and evaluation of the different modelling methods (*Table 3*).

Table 3: Some published SDM packages (based on *Thuiller and Münkemüller, 2010*).

Platform	**Reference**	**Modellig method(s)**	**source**
BIOCLIM	*Busby (1991)*	CE	http://www.arcscripts.esri.com
BIOMAPPER	*Hirzel et al. (2002)*	ENFA	http://www.unil.ch/biomapper
BIOMOD	*Thuiller (2003)*	GLM, GAM, CART, ANN	http://r-forge.r-project.org/projects/biomod/
DIVA	*Hijmans et al. (2001)*	CE	http://www.diva-gis.org
DOMAIN	*Carpenter et al. (1993)*	CE	http://www.cifor.cgiar.org/docs/_ref/
GRASP	*Lehmann et al. (2002)*	GLM, GAM	http://www.cscf.ch/grasp
DISMO	*Hijmans and Graham (2006)*	GLM, GAM, RF	http://cran.r-project.org/web/packages/dismo/dismo.pdf
MARS	*Friedman, 1991*	Multivariate Adaptive Regression Splines	
Open Modeller	*Munoz et al. (2009)*	ANN, CE, CSM, ENFA, GARP, RF, SVM	http://openmodeller.sourceforge.net/
ModECo	*Guo et al. (2005)*	ANN, CE, SVM, GLM	http://gis.ucmerced.edu/ModEco/

ANN: artificial neural networks;

CE: climatic envelope;

GAM: generalized additive models;

SVM : Support Vector Machines

CSM - Climate Space Model

ENFA: ecological niche factor analysis;

CART: classification and regression trees;

GLM: generalized linear models

GARP: Genetic Algorithm for Rule-set Production

RF: Random Forests

Modelling methods can be classified as “profile”, “regression”, and “machine learning”. Profile methods only consider presence data. Regression and machine learning methods use both presence and absence or background data.

Profile methods are the classic climate envelope models. The algorithms of these methods usually compute the similarity of a location by comparing the values of environmental variables at any location to a percentile distribution of the values at known locations of occurrence. Although they generally do not perform as good as some other modelling methods (*Elith et al., 2006*), particularly in the context of climate change (*Hijmans and Graham, 2006*), they are still used.

The most important regression methods are the generalized linear model and the generalized additive model. A generalized linear model is a generalization of ordinary least squares regression. Depending on how a generalized linear model is specified it can be equivalent to (multiple) linear regression, logistic regression or Poisson regression (*Guisan et al., 2002*). Generalized additive models (*Wood, 2006*) are an extension to generalized linear models. The linear predictor is the sum of smoothing functions. This makes them very flexible, and they can fit very complex functions.

Machine learning methods can take advantage of examples to capture characteristics of interest of their unknown underlying probability distribution. A major focus of machine learning research is to automatically learn and recognize complex patterns and make decisions based on data. The difficulty lies in the fact that the set of all possible behaviours given all possible inputs is too large to be covered by the set of observed examples (training data). Machine learning methods must generalize from the given examples, so as to be able to produce a useful output in new cases. There is a variety of algorithms like Artificial Neural Networks, Random Forests, Boosted Regression Trees and Support Vector Machines among others.

Uncertainties and limitations of SDMs

The main drawback of the approach lies in its correlative nature, which makes it not causal and not based on real processes. Correlation is not causation, so the reality of the relationships and the causal mechanisms responsible should be pursued by experiment, by theoretical analysis or by repeating the study at a different location.

One of the fundamental assumptions is that the current range of species is in equilibrium with the explanatory environmental variables. This assumption of equilibrium has been criticized, and several authors have demonstrated that conclusions made under this assumption can be wrong (*Pearson and Dawson, 2003*).

Niche based models usually ignore factors such as biotic interactions, transient dynamics, migration, and nitrogen deposition. Most of the models are calibrated under the assumption that biotic interactions do not influence species range patterns (*Huntley et al., 1995; Bakkenes et al., 2002*), or only affect patterns at small spatial scales (*Dormann et al., 2007; Heikkinen et al., 2007*). Examples demonstrated how the incorporation of biotic interactions into SDMs enhances species' distributions models and responses to environmental change (*Araújo and Luoto, 2007; Meier et al., 2010*).

Further limitations of these models are, that the present distribution of tree species (in Europe) are human induced therefore often different from the realised niche.

The interpolation of the controlling environmental factors is not sufficiently solved in all cases (temporal or spatial resolution).

Application of SDMs

The geographic representation of the estimated realized niche can be projected into the future according to climate change scenarios (*Heikkinen et al., 2006*). This approach has been widely applied, including in studies investigating the potential impacts of climate change on

- biodiversity (e.g. *Peterson et al., 2002; Midgley et al., 2003; Thomas et al., 2004; Hannah et al., 2005; Thuiller et al., 2006*).
- conservation priorities (e.g. *Araújo and Williams, 2000; Ferrier et al., 2002; Raxworthy et al., 2003; Williams et al., 2005*),
- niche evolution (*Peterson et al., 1999; Martínez-Meyer and Peterson, 2006*), and
- geographical ecology of invasive species (*Higgins et al., 1999*)

Although extensively used and also criticized (*Bahn and McGill, 2007*), some analysis having thoroughly tested their predictive power have shown relatively good performance to predict the current distribution based on independent data (*Araújo et al., 2005*).

2.5.2 Process based models

Process-based dynamic vegetation models for forests are often based on the 'gap dynamics' concept. These models have been used relatively successfully to reproduce past and current species composition of temperate forests and therefore are powerful tools for simulating the effects of global change on temperate tree species. There are currently a variety of efforts to improve the representation of the functional response of trees to global change and to simulate mortality and migration in gap-dynamic models (*Rickebusch et al., 2007*).

Dynamic Global Vegetation Models (*DGVMs*) are used to simulate the distribution of plant functional groups at (larger) regional scale. They are based on mechanistic descriptions of plant and ecosystem functioning (physiology, competition, disturbance, mortality). The strength of this approach is that it simulates the distribution of major plant types and the functioning of plants and ecosystems, but the small number of plant functional types (often less than 10 for the entire planet) currently prohibits their use for directly modelling distributions of species or species richness.

2.5.3 Hybrid models

Recently a new generation of models have been developed, termed ‘‘hybrid’’ models, like the joint application of LPJ-GUESS (*Smith et al., 2001*), BIOMOD (*Thuiller, 2003*), ECO-GENE (*Degen et al., 1996*) and ForGem (*Kramer et al., 2008*; *Kramer et al., 2010*). These models try to achieve a compromise between realism–accuracy and complexity– simplicity. One of the limitations of these approaches is that they are highly sophisticated, data demanding, and require detailed knowledge of ecological and physiological processes that is usually not readily available.

2.5.4 Empirical models

Current SDM applications focus on long-term climate predictors. The demographic signal of extreme adverse and favorable events may lead to both positive and negative effects locally; this is called source-sink dynamics. It is widely accepted in SDMs that the resulting pattern of overall range limits may well reflect climatic means. This association of range margin and climatic mean may not hold when climatic extremes occur with an increasing frequency (future climate change), or when the fluctuation of weather overrides the tolerance limit of a species (Liebig minimum role). This later addition could be especially important for predicting the trailing edge of a tree species.

SDMs assume that the modelled species is in equilibrium with its environment. Although this is a required assumption for projecting the model in space, a few critical considerations have been raised in the recent literature on how close a system really is to an equilibrium, and how long it would take to reach a new equilibrium, e.g. after an environmental change. *Svenning and Skov* (*2004*) measured low range filling (*RF*) for many European tree species (RF < 50% for 36/55 species), suggesting that many of these species might not be in equilibrium with their environment throughout their whole range. The non-equilibrium consideration is a critical issue in modelling the distribution of invasive or retreating species.

EMs concentrates in space and time on the specific momentum, when the modelled system is tipped out from its equilibrium state. The environmental change forcing the system to tip out from this equilibrium and the response of the selected species to that change is measured to establish the model.

EMs have several disadvantages. A drawback of EMs is that ecological data limiting the distribution are not available for most species, as this tip-out is rarely observed. Secondly, EMs establishing the response of a species with the environmental forcings is usually restricted to a certain region; therefore the extension of the response to the whole range in case of a widespread species needs special attention.

In general EMs are considered superior for understanding the relationship between climate and the distribution of species (*Woodward and Rochefort, 1991; Malanson et al., 1992; Prentice et al., 1992; Guisan and Zimmermann, 2000*) and have been used to study the effects of climate change on distribution and production of crops (*Rosenzweig and Parry, 1994*).

2.5.5 Critical evaluation

A trade-off in modelling species' responses to environmental changes is between generality and specificity. Distribution models (*Guisan and Thuiller, 2005*) fit species environmental niches explicitly, ignore all mechanisms driving species' demography and species' interactions. These models are simplistic but they focus explicitly at the species level, allowing the modelling of numerous species, and can thus be used to estimate patterns of current and future diversity (*Peterson et al., 2002; Thuiller, 2004; Ferrier and Guisan, 2006*).

Process-based dynamic global vegetation models are generalized to such an extent that they can simulate global patterns of vegetation distribution, as well as carbon, nutrient and water cycling from existing knowledge of the mechanisms driving these processes (*Thuiller et al., 2006*). The drawback is that primary producers are classified into a small number of functional types, which provide a coarse classification.

Tree species-specific responses have been extensively explored with ''forest gap models'' (*Bugmann, 2001*). These models have been criticized for being highly parameterized for particular species and sites, but there has been considerable progress in the development of generalized forest gap models, which can now be applied across different regions, at least in the temperate zone, and account for population demographics, species' interactions and physiological (*Hickler et al., 2004*).

2.6 The problem of modelling the xeric limit

SDMs often do not differentiate between the "leading" and "trailing" edge, although the processes are fundamentally different (*Mátyás and Nagy, 2005; Aitken et al., 2008*). The upper limit is mostly determined by temperature conditions (i.e. "thermic limits") with relatively accurate measurability and predictability. Assessments of climate change impacts deal predominantly with the response of forest stands at the thermic limits (e.g. *Crawford, 2008*).

Low elevation and low latitude distributional limits (xeric limits) are generally determined by the water availability. Strong biotic interactions such as pest and diseases can also play an important role at xeric range limits (*Mátyás et al., 2008*). Changes in water availability are more difficult to forecast than temperature conditions, which increases uncertainties. Colonisation at the thermic limits also responds better to climatic changes than loss of vitality and retreat at the xeric limits, because the latter is buffered by persistence and plasticity (*Mátyás et al., 2008*). Furthermore, aridity conditions, determined by both temperature and precipitation regime, and modified by local topography and hydrology, leading to a patchy distribution pattern. Due to higher human population density land use intensity is increasing towards lower latitudes and altitudes, and this also contributes to the difficulties in the predictive modelling of xeric limits as compared to that of thermic limits (*Mátyás et al., 2008*). It is of no surprise that forest growth/performance studies at the xeric limits are scarce (*Hampe and Petit, 2005*) and are often restricted to montane-(Sub-) Mediterranean regions (e.g. *Penuelas et al. 2001; Jump et al. 2006*).

2.7 Distribution modelling of European beech

2.7.1 Distribution modelling of beech on European scale

Europe-wide distribution modelling of beech is rare, because it needs an accurate database about the spatial distribution of beech and about the limiting climatic factors. *Thuiller et al., (2003*) modelled first the habitat suitability of beech for the end of the century in Europe using the statistical framework of BIOMOD (*Figure 21*). The BIOMOD framework (*Thuiller, 2003; 2004; Thuiller et al., 2009*) is implemented under the R-software. BIOMOD fits the following statistical models: artificial neural networks, classification tree analysis, generalized additive model, generalized boosted model, generalized linear model, multiple adaptive regression spline, mixture discriminant analysis, and RandomForest. Thuiller has taken the presence and absence of beech in Europe from the Atlas Florae Europaeae (*Lahti and Lampinen, 1999*) at a resolution of 50 x 50 km. He used mean annual temperature, mean winter temperature, growing degree-days up to April and August and the average fraction of plant-available soil water-holding capacity in the first (0–0.5 m) and second (0.5–1.5 m) soil layers, during the growing season.

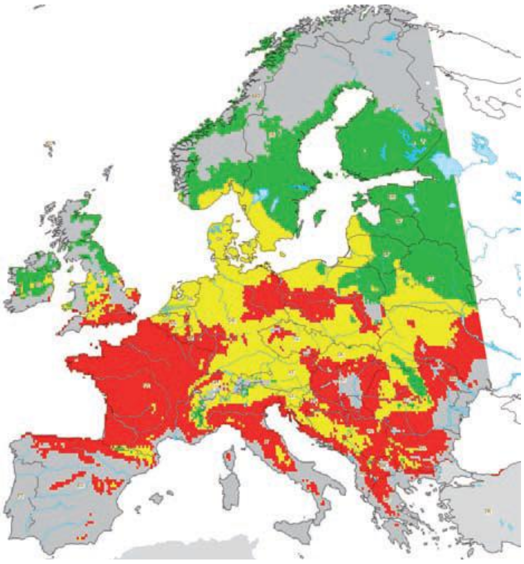


Figure 21: Projected response of European beech to 21st century climate change using the IPCC A1 emissions scenario and the BIOMOD niche-based model (*Thuiller et al., 2005*). Red = current portion of range where climate becomes unsuitable by 2080, Green = new areas where climate becomes suitable, Yellow = climate suitable now and in 2080.

The results of the statistical species area modelling have shown a northward shift of the southern limit of the distribution of beech and a northward extension of the northern limit. Under the A1 climate change scenarios beech could lose about 29% of its current suitable habitats, and could gain 12% of additional new suitable habitats in Northern Europe. Most of the current habitats which could become unsuitable by 2050 are located in the South of France, Italia, the Balkan half-island, and Greece.

Later *Kramer et al. (2010*) explored impacts of climate change on the geographic distribution of European beech by combining the same statistical (*Figure 22*) and a process-based model (LPJ-GUESS) using the IPCC A2 and B1 scenarios.

Figure 22: Simulated current and future (scenario A2 and B1) potential distributions of beech in Europe using statistical distribution models. The maps indicate the average presence value across models, evaluation methods and scenarios (A2 and B1), weighted by the models' evaluation scores: 1 (black) = suitable, 0 (light grey) = unsuitable according to all models. (A) Current climate, (B) A2 climate change scenario, and (C) B1 climate change scenario. (*Kramer et al., 2010*)

The LAI simulations of LPJ-GUESS process-based model has also shown decreasing dominance in southern Europe. The magnitude of range shifts, however, is substantially less. Both climate models have given similar changes in the projected distribution and dominance of beech by the end of the century (*Figure 23*).

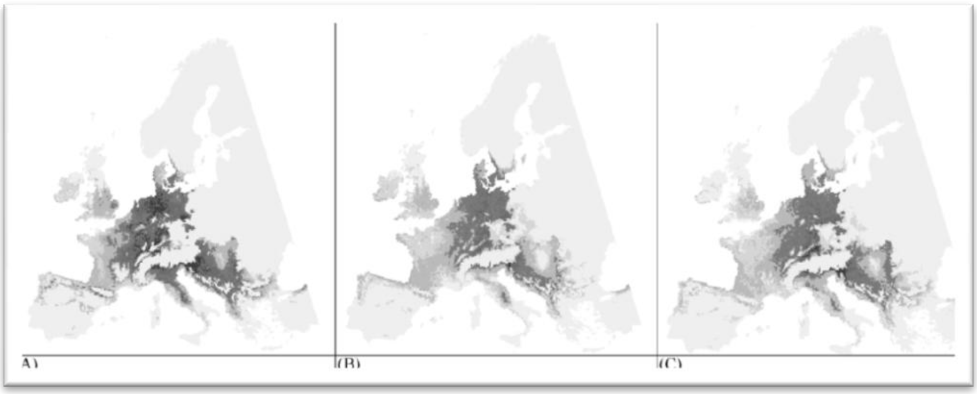


Figure 23: Current and future leaf area index (LAI) of beech in Europe using a process-based dynamic vegetation model (*Kramer et al., 2010*). (A) Current climate (averaged for 1961–1990). (B) HadCM3 scenario (averaged for 2071–2100). (C) NCAR-PCM scenario (averaged for 2071–2100).

2.7.2 Distribution modelling of beech on national level

Mediterranean countries like Spain, France and Italy are highly interested in modelling the future changes of beech cover.

Badeau et al. (2005) published beech suitability predictions for France (*Figure 24)*

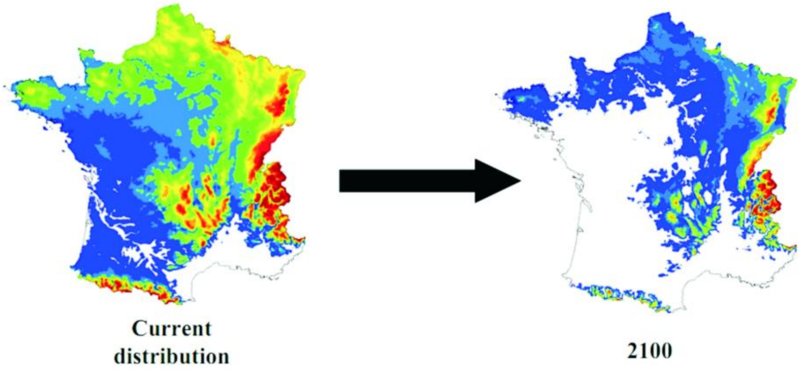


Figure 24: Shift of climate envelope for beech in France based on the work of *Badeau et al. (2005)*. White colour is unsuitable, blue to red indicates suitable habitat for beech.

The project “BioRefigio” analysed of the potential effects of climate change on tree species’ distribution and abundance in two Italian regions (Lazio and Abruzzo) in Central-Italy (*Attorre et al., 2008*). Forest Inventory Data of Italy (3x3 km grid) and simple bioclimatic indexes were used by a regression tree analysis to define the ecological niche. The analysis found, that *Fagus sylvatica* is mainly found in areas with an average temperature of less than 24 °C for the hottest month. In areas above this limit, the species can only be found in very small areas characterised by a high amount of summer precipitation (above 200 mm). This ecological niche was projected into the future by applying the IPCC A1 climate change scenario to 2080 (*Figure 25*).

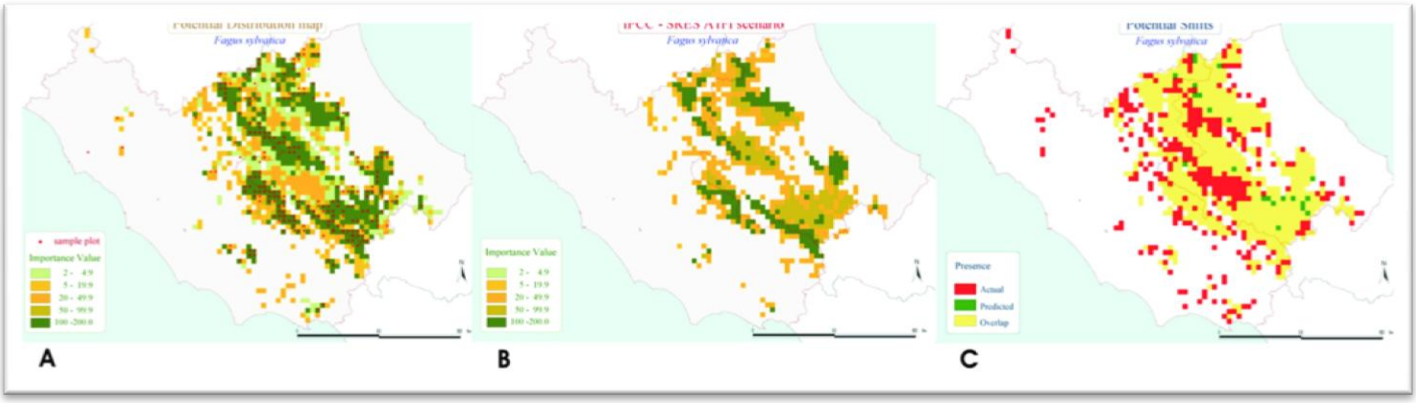


Figure 25: The (A) current, the (B) future potential area and the (C) shift of beech in Central Italy. The importance of the plots are also indicated by colours (Importance Value=Density+Dominance) (*Attorre et al., 2008*).

Thuiller et al. (2003) used classification tree analysis to explore the environmental correlates of the realized niches of tree species in Spain (Catalonia). In the analysis *Fagus sylvatica* appeared mainly restricted to areas with > 950 mm of annual rainfall. Within this, in areas with less than 1050 mm, the distribution was related to winter and summer precipitation (*Figure 26*).

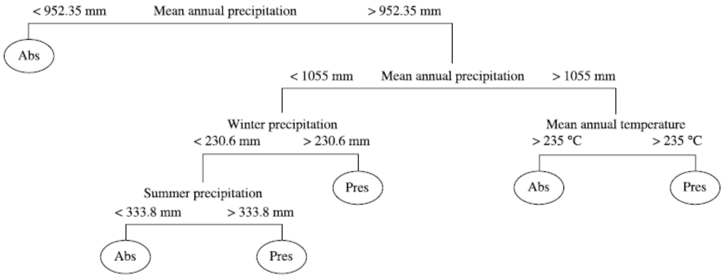


Figure 26: Main predictors of *Fagus sylvatica* distribution in Catalonia (Spain) by classification tree analysis. *Pres*: presence, *Abs*: absence *Thuiller et al. (2003)*

Maps of potential tree distributions were applied to define suitable habitats and to highlight areas where species have been planted outside their natural distribution (*Figure 27*).

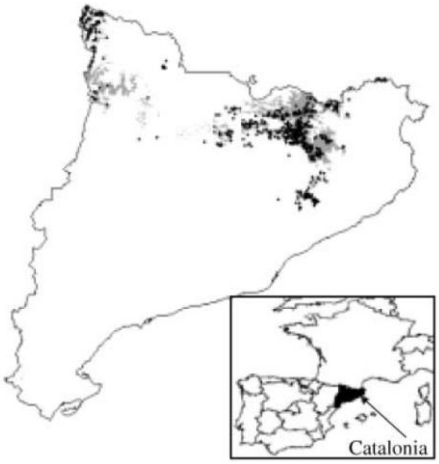


Figure 27: Potential distribution map of *Fagus sylvatica* for Catalonia (Spain). Points represent the sampling plots where the species was present and shaded areas are the areas modelled as suitable (*Thuiller et al., 2003*).

The analysis of *Thuiller et al. (2003*) confirmed that species at the edge of their range were predicted only moderately well with the classification tree analysis model.

The resulting patterns of overall range limits may well reflect climatic means, however, when the variability around means is very high, then a species may not be able to compensate in good years the losses that occur during adverse years. *Zimmermann et al., (2009*) used interannual variability to explain and predict spatial patterns of 11 tree species in Switzerland.

They analysed forest inventory data on a regular 1 km grid and a climate predictor set containing long-term (1961–2006) averages of monthly, seasonal, or annual predictors and standard deviations of the mean values. The statistical analysis was carried out using a general additive model (*GAM*) (*Figure 28*).

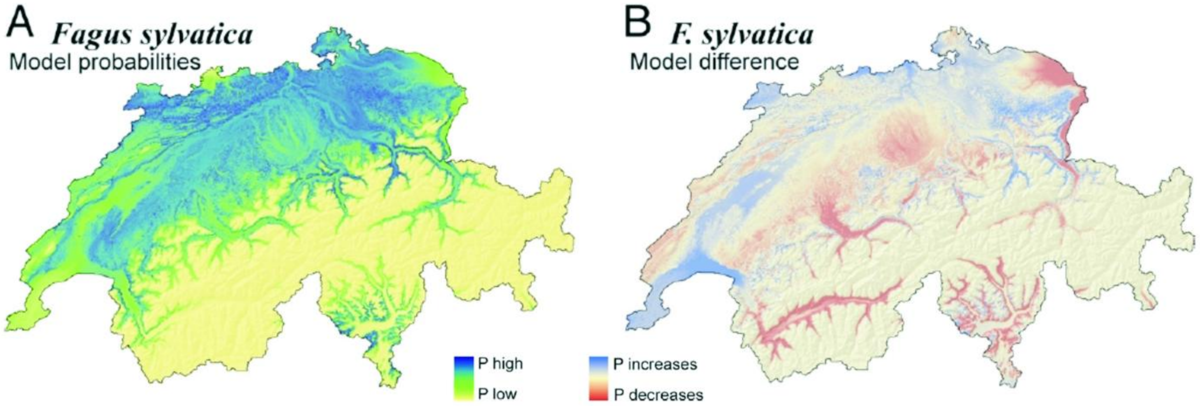


Figure 28: Effect of adding climatic variability on predicted spatial patterns. (A) Simulated probabilities of *F. sylvatica* from GAMs using climatic means and variability as predictors with no statistical interactions added. (B) The effect of adding variability calculated as the difference between predicted probabilities of the more complex model using means and variability and the model using means alone. Red and blue colours indicate the forcings of the standard deviations as predictors to decrease and increase the probabilities of the species model (A) compared with the simple model consisting of climatic means alone (*Zimmermann et al., 2009)*.

They found clear, although comparably small, improvement in models that use variability in addition to means.

2.7.3 Distribution modelling of beech in Hungary

The distribution modelling of beech in Hungary started with the work of *Berki et al. (2009)*. In this first approach the health status and weather conditions were investigated on selected zonal beech stands. As the author of this work was also involved and the results influenced the latter work, detailed description will be given about the methods and results.

Materials and methods

Study sites

To define the xeric limit zonal sites were needed, where the relationship of the vitality loss and climate could be analysed, excluding as many disturbing factors as possible (soil deficiency, effect of slope and aspect, seeping water). More than 30 stand situated near the xeric limit of beech was investigated. After analysing the results, six sites in strictly zonal positions were selected for further investigation, where the individual beech trees showed clear signs of a chronic decline (*Figure 29*) – (*Table 4*).

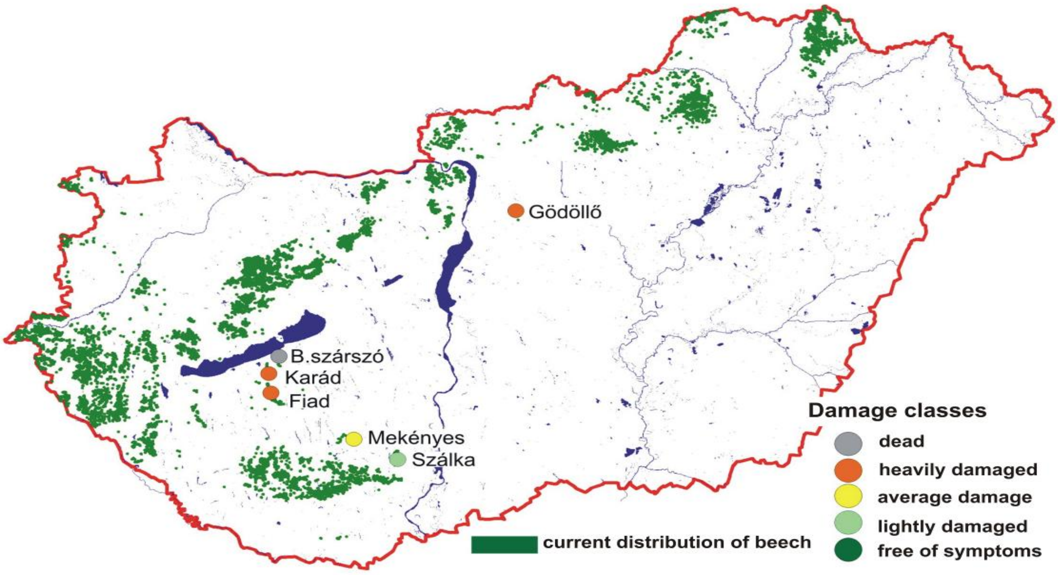


Figure 29: Geographical location and average damage classes of the investigated beech sites.

Table 4: Site conditions of the investigated beech sites.

Site	Elevation amsl (m)	Avg annual precip 1975-2004 (mm)	Avg annual precip 2000-2003 (mm)	Mean summer temp 1975-2004 (°C)	Mean summer temp 2000-2003 (°C)	Soil type	Mixture ratio of beech (%)	Canopy closure (%)	Age (year)
Szálka	238	676	594	19.7	21.4	BF	50	90	92
Mekényes	230	699	658	19.5	21.3	LBF	26	85	74
Fiad	241	684	561	19.5	21.2	LBF	21	75	82
Karád	234	670	576	19.7	21.3	BF	74	80	81
Balaton-szárszó	208	649	547	20.0	21.7	BF	12	70	65
Gödöllő	229	577	524	19.7	21.3	RBF	100	60	144

Soil: *BF*: Brown forest soil, *LBF*: Lessivated brown forest soil, *RBF*: Rusty brown forest soil

Definition of the beech tolerance index

A climate index (Q_{BTI}) for beech was introduced based on the weighted spring and summer precipitation and mean summer temperatures:

$$Q_{BTI} = \frac{0.2 \cdot P_{III} + 0.5 \cdot P_{IV} + P_{V} + P_{VI} + P_{VII} + 0.8 \cdot P_{VIII}}{(T_{VI} + T_{VII} + T_{VIII})/3}$$

where:

P_{III} : precipitation in March

P_{IV}: precipitation in April

P_{V}: precipitation in May

P_{VI}: precipitation in June

P_{VII}: precipitation in July

P_{VIII}: precipitation in August

T_{VI}: mean temperature in June

T_{VII}: mean temperature in July

T_{VIII}: mean temperature in August

The humidity conditions of the last 30 years of the six selected sites was characterised using the climate index Q_{BTI} fed by interpolated meteorological data (*Figure 30*).

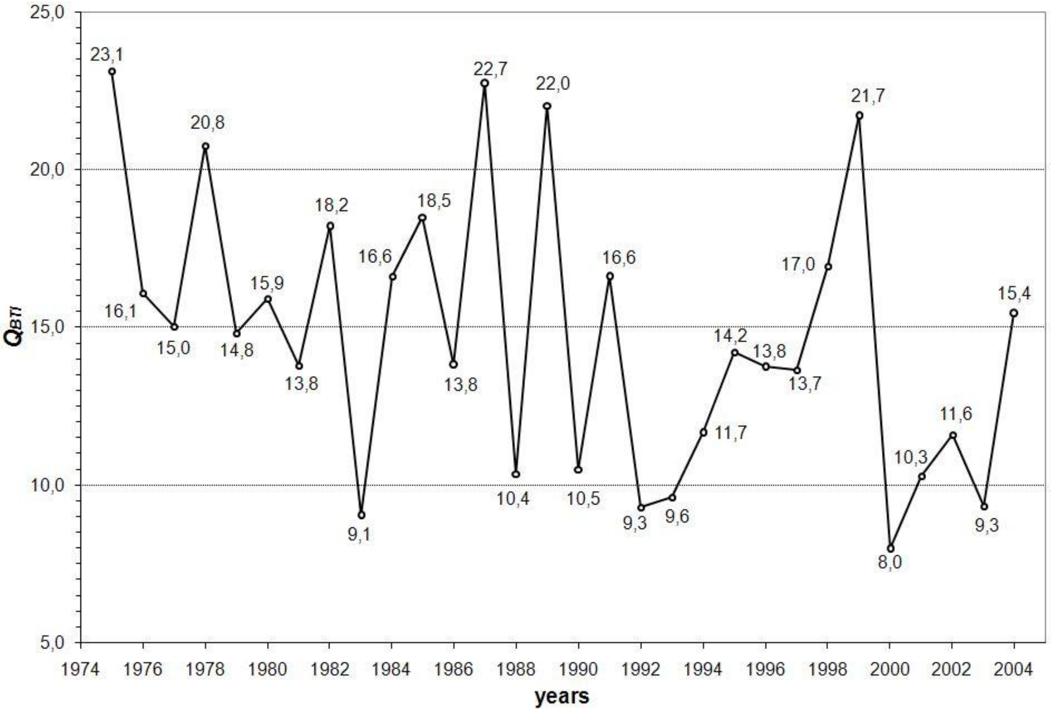


Figure 30: Temporal change of the tolerance index of beech (Q_{BTI}) between 1975 and 2004 in Balatonszárszó.

Assessment of vitality condition

Beech vitality condition was determined at each stand by setting up a 50x50 m sample square in 2004. The assessment and quantification of the vitality of individual trees were based on canopy density (transparency) which was similar to the method used on the ICP Forest Monitoring plots. All the trees within the sample area were investigated (leaf loss, leaf colouring and crown dieback). The damage status was defined by considering the social status of the trees and by setting the ideal crown condition to 100%. Five damage categories were defined (*Table 5).* The mean damage condition was computed for each sample plot.

Table 5: Vitality status of the crown and related damage categories.

Vitality status of the crown (%)	Damage categories
90 – 100	Healthy
75 – 89	Slightly damaged
61 – 74	Medium damaged
1 – 60	Heavily damaged
0	Died

Defining the drought tolerance limit of beech and predicting the future distribution

Vitality condition of the investigated sites and the four year mean (2000-2003) of Q_{BTI} was assessed to obtain the lower tolerance limit of beech at the selected sites.

Using climate change scenarios, the future distribution of beech could be predicted. The downscaled values of the PRUDENCE project (Prediction of Regional scenarios and Uncertainties for Defining European Climate change risks and Effects) were applied to the predictions. The expected climatic changes in the Carpathian Basin compared to the period of 1961-1990 can be found in *Table 6*.

Table 6: Change of the average precipitation and temperature in the Carpathian Basin for 2050 compared to the period of 1960-1990, based on PRUDENCE.

	2050				**2085**			
A2 scenario	winter	spring	summer	autumn	winter	spring	summer	autumn
Precipitation change (%)	14.8	**1.5**	**-13.4**	-3.1	28.6	**2.9**	**-26.1**	-6.0
Change in temperature (°C)	2.1	**1.8**	**2.8**	2.5	4.1	**3.5**	**5.4**	4.8
B2 scenario	**2050**				**2085**			
Precipitation change (%)	14.8	**1.5**	**-13.4**	-3.1	21.4	**2.1**	**-19.5**	-4.5
Change in temperature (°C)	2.1	**1.8**	**2.8**	2.5	3.1	**2.6**	**4.0**	3.6

Results

Drought tolerance limit of beech

The driest site was Balatonszárszó, where almost all tree had already died by the summer of 2004. Only few heavily damaged individuals remained and more than two-third of their upper canopy was already dead. The climate at this site has exceeded the tolerance limit of beech during the period 2000-2003.

The forest management plan at the Balatonszárszó site indicated some sanitary cutting in 1996, so the first event of mortality was most likely the result of the drought period of 1992-1994, when the less drought tolerant individuals died. As an effect of the extremely dry period of 2000-2003, the rest of the beech trees have died.

The climate of the other five stands showed similar pattern. The relationship of the health status and the tolerance index in the six investigated sites is shown in *Table 7*.

Table 7: Average damage class of the investigated beech stands and the average tolerance index between 2000 and 2003.

Name of the site	Average damage classes of beech trees	Average of the tolerance index for the time period 2000-2003
Szálka	lightly damaged	12.6
Mekényes	medium damage	13.3
Fiad	heavily damaged	**10.6**
Karád	heavily damaged	**10.5**
Balatonszárszó	dead	9.8
Gödöllő	heavily damaged	**10.8**

The results indicate the value of the Q_{BTI} based drought tolerance limit of beech in Hungary is about 10.8 as an average over a short term period of 4 years.

This threshold value has been mapped (spatially extended for the whole country) for the period 2000-2003 (*Figure 31*). The spatial pattern of the experienced beech dieback concured well with the modelled map.

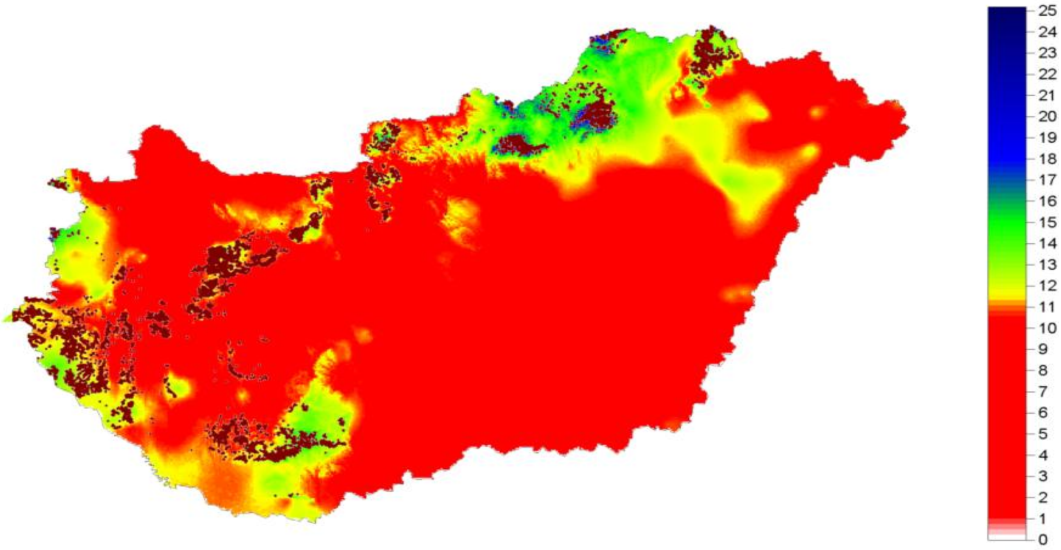


Figure 31: Spatial pattern of tolerance index of beech between 2000 and 2003 (brown colour shows the current distribution of beech).

It is also necessary to emphasize, that one single year below 10.8 (Q_{BTI}) is not enough for mass mortality. Trees react to drought in many ways (shoot length and morphology, tree ring width), but they are able to fully recover, if the following years are not extremely dry.

Projection of future distribution of beech

Based on the defined tolerance limit, future distribution of beech was predicted in Hungary for the middle and end of this century. The red colour indicates the climatically unsuitable areas for beech (values of Q_{BTI} is under 10.8).

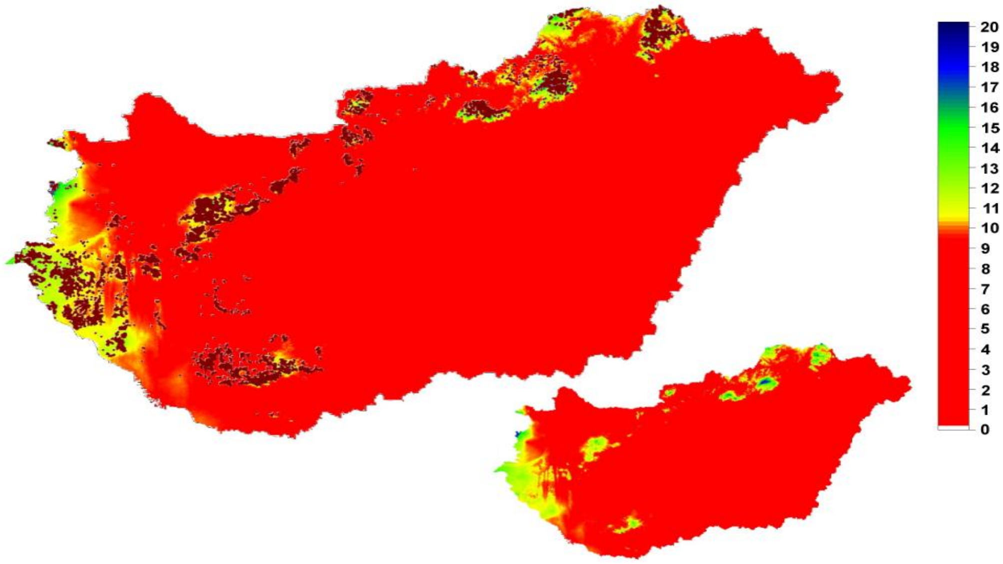


Figure 32: Expected spatial pattern of tolerance index of beech in 2065 (Brown colour on the big left map shows the current distribution of beech in Hungary, the inset on the right is without distribution data. Red colour indicates the climatically unsuitable areas; areas marked with green are pessimum sites with light or medium damage and blue means optimum).

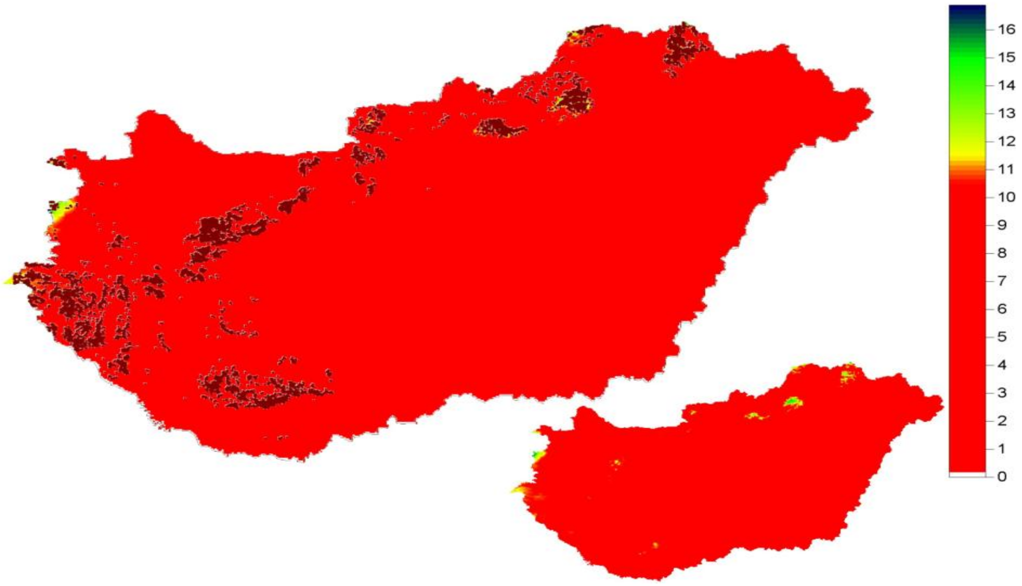


Figure 33: Expected spatial pattern of tolerance index of beech in 2100 (Brown colour on the big left map shows the current distribution of beech in Hungary, the inset on the right is without distribution data. Red colour indicates the climatically unsuitable areas; areas marked with green are pessimum sites with light or medium damage and blue means optimum).

Discussion of the results

This first approach had several limitations.

1. The relationship between beech vitality condition and weather condition was based on field observations at the selected six sites. The low number of the sites increases the possibility that the relationship of weather and vitality is biased by local (often hidden) biotic or abiotic interaction. Thus the spatial and temporal (for prediction) extension of this model shared high level of uncertainty.
2. For the prediction results of the PRUDENCE model were used. This was the best available model at that time, which was not able to handle regional differences in Hungary.
3. This model was calibrated under the assumption that the distribution of beech is formulated only by the climate (macroclimate) and therefore the results were only valid for forest stands in strictly zonal positions.

However this first modelling approach had several limitations the research highlited some important ecological theories tested later in SDMs and in the EM, namely:

- the distribution of beech is determined by short-term dry periods rather than by long-term climatic means close to the trailing edge,
- 4-5 consecutive extreme dry years are enough for mass mortality in beech stands situated near to the xeric limit and
- for reliable spatial and temporal extension empirical relationship should be obtained from relatively big sample size.

Czúcz et al. (2011) applied a different approach to identify the most influential macroclimatic factors and to predict climatic risks for beech forests in Hungary. They used Forest inventory data with a grid size of approx. 1.5×1.9 km, and climatic means of the period 1961-1990. In addition to basic climatic variables they also considered two simple aridity indices; the Ellenberg's climate quotient (*Ellenberg, 1988*), and the Forest aridity index (*Führer et al., 2011*). To establish the relationship between climatic conditions and the presence of beech, conditional inference-based regression trees were used as the main modelling tool.

Czúcz et al. (2011) laid special emphasis within the modelling process on screening of the database in order to limit modelling to plausible climate-dependent (i.e. zonal) occurrences.

For beech the Ellenberg's climate quotient (*EQ*) was found to be superior as predictor variable. Moreover, in almost all cases EQ appeared repeatedly at different levels of the classification tree, suggesting that this climate index has, by itself, a good potential to describe the aridity limitation of beech forest stands in Hungary (*Figure 34*).

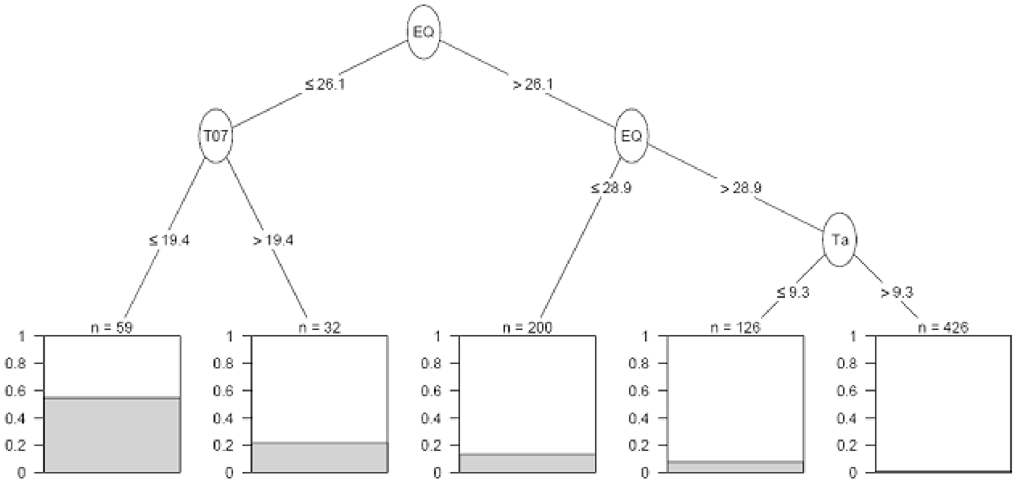


Figure 34: The decision tree of the zonal beech forest with EQ among the predictors - *Czúcz et al. (2011)*. EQ: Ellenberg's Climate Quotient; T07: Mean July temperature; Ta: Annual mean temperature.

The results show that climate change may lead to extensive reduction in macroclimatically suitable areas for beech forests: applying the calculated thresholds to the probabilistic projections reveals that 56–99% of present-day zonal beech forests will be outside their optimal bioclimatic niche by 2050 (*Figure 35*).

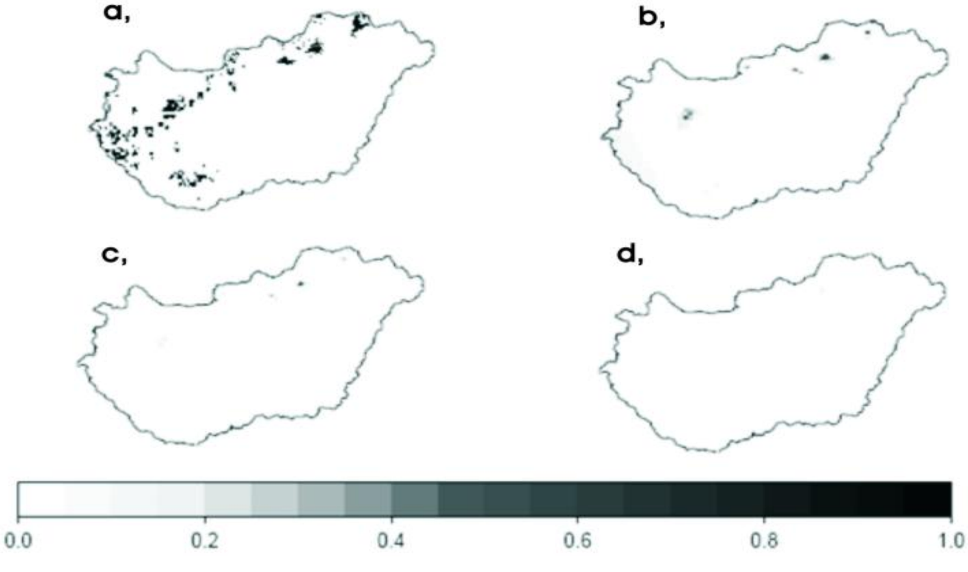


Figure 35: Actual distribution of beech (*Fagus sylvatica*) stands in Hungary (a), consensus projection maps for the probability of presence (b-d). Time horizons for the mean projections: 2025 (b); 2050 (b); 2085 (d). The intensity of shading indicates the probability of the location to be above the xeric limit for stable zonal stands (*Czúcz et al., 2011)*.

1.1.1. Gaps

The short overview of the above mentioned models suggest the followings gaps:

- Studies at European and national level apply data on a coarse scale (some 10 km), which makes the use of the results on practical level impossible.
- Most of the studies apply only one statistical algorithm to establish the relationship between environmental variables and occurrence data. As all methods have its strength and weaknesses, multimodel application are more reliable. The integration of different algorithm or different approaches could strengthen the reliability of the results.

3 Materials and Methods

3.1 Climate database

3.1.1 Climate data for current conditions (1950-2000)

For current conditions, the WorldClim database (*Hijmans et al., 2005*) was used. This dataset has a spatial resolution of approximately 1 km and was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude, and elevation as independent variables.

This database has been selected to characterise the climate conditions, as this database had access to stations' data series not available for public.

3.1.2 Meteorological database (1975-2006)

Precipitation

Monthly precipitation data were obtained from the hydrological annals, published by the Water Resources Research Centre (VITUKI). The scanned precipitation data was checked with the original data. Additional station data were obtained from the Hungarian Meteorological Service (OMSz). The dataset included 608 rain gauge stations in monthly resolution for the years 1975-2006 in Hungary (*Figure 36*). The number and the location of the rain gauges changed frequently in the given period, thus only stations with continuous dataseries could be included in the database. To achieve this, a representative radius of 5 km was set to each station. If translocation happened within this radius time series was considered as continuous. Raw rain gauge station observations underwent a series of quality tests to identify obvious anomalies and remove false values.

Figure 36: Spatial distribution of precipitation gauges used for the interpolation.

Precipitation maps were created by the kriging interpolation method. Kriging is a geostatistical gridding method that has proven useful and has been applied extensively for the interpolation of climate data (*Dingman et al., 1988; Hevesi et al., 1992; Garen et al., 1994*).

The kriging interpolation

Kriging produces visually appealing maps from irregularly spaced data. It attempts to express trends suggested in the data, so that, for example, high points might be connected along a ridge rather than isolated by bull's-eye type contours. Kriging is a very flexible gridding method, which can be custom-fit to a data set by specifying the appropriate variogram model. It can be either an exact or a smoothing interpolator depending on the user-specified parameters and incorporates anisotropy and underlying trends.

The prediction obtained by ordinary kriging is a linear combination of measured values, with weights depending on the spatial correlation between the data. The mathematical description of the method is the following:

The ordinary kriging model for spatial stochastic process $Z(s)$ is:

$$Z(s) = \mu + \delta(s)$$

where μ is unknown expected value of random process, independent on location s, $\delta(s)$ is a zero-mean intrinsically stationary random process with existing variogram $2\gamma(r)$. The predicted value $Z'(s_0)$ can be expressed as:

$$Z'(s_0) = \sum_{i=1}^{n} \lambda_i Z(s_i)$$

Linear coefficients λ_i, $i=1,\ldots.,n$ are calculated under the condition for uniformly unbiased predictor as:

$$E(Z'(s_0)) = E(Z(s_0)), \sum_{i=1}^{n} \lambda_i = 1$$

and under the constraint of minimal prediction error variance (kriging variance) $\sigma^2(s_0)$ at location s_0 as

$$\sigma^2(s_0) = E(Z(s_0) - Z'(s_0))^2$$

The details of the theory can be found in *Cressie (1991)* and *Isaaks et al.* (*1989*).

For the spatial process $Z(s)$ intrinsic stationarity is assumed. The predictions are weighted linear combinations of the available data. Linear coefficients are calculated under the condition of a uniformly unbiased predictor and under the constraint of minimal prediction error variance (kriging variance).

A disadvantage of this method using meteorological variables is that they can rarely be considered as an intrinsic stationary random process. In some cases we can use different size and shape of the search neighbourhood to eliminate this problem. The ordinary kriging gives prediction errors, called kriging standard errors (square root of kriging variance).

Ordinary kriging is offered by all high-level GIS software products (ArcGIS, Surfer, S-Plus Spatial module). We used Golden Software Surfer 8 by applying a spatial resolution of 1000 m. A search radius of 50 km was set to use the nearby stations for estimation of each grid cell with minimum number of eight stations. Due to the high spatial density of stations, dependence of the precipitation on elevation was not considered.

Cross-validation

The reliability of the precipitation maps were assessed using the cross-validation method. Generally, it can be considered an objective method of assessing the quality of a gridding method or to compare the relative quality of two or more candidate gridding methods. Cross validation results can also be used to assess the spatial variation in gridding quality. Given the known values at "N" observation locations in the original data set, cross validation assesses the relative quality of the grid by computing and investigating the gridding errors. In Surfer 8, these errors are calculated by removing the first observation from the data set, and using the remaining data and the specified algorithm to interpolate a value at the first observation location. Using the known observation value at this location, the interpolation error is computed as:

$$\textit{error} = \textit{interpolated value} - \textit{observed value}$$

Then, the first observation is put back into the data set and the second observation is removed from the data set. Using the remaining data (including the first observation), and the specified algorithm, a value is interpolated at the second observation location. Using the known observation value at this location, the interpolation error is computed as before. The process is continued in this fashion for all observations up to "N". This process generates "N" interpolation errors.

The mean of the deviations from the observed values was 49.4 mm, which was 8.2 % of the observed mean annual precipitation in Hungary.

Temperature

Mean monthly 2 meter air temperature data were obtained from the monthly weather reports published by the Hungarian Meteorological Service (OMSz). The temperature dataset included 31 weather stations in Hungary for the period of 1975-2006 (*Figure 37*).

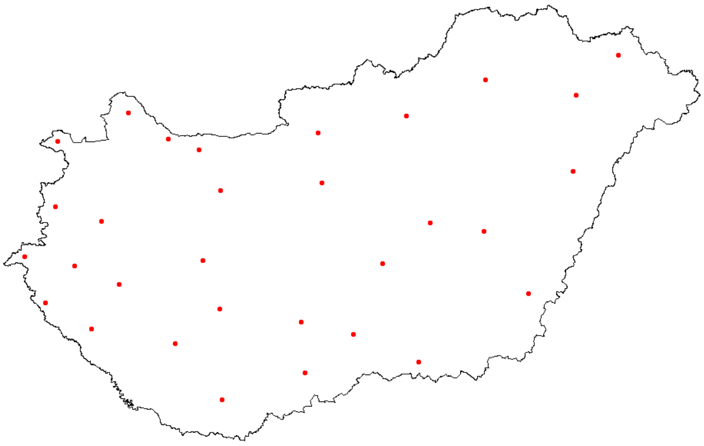


Figure 37: Spatial distribution of the temperature stations used for the interpolation.

Temperature maps were created using the same kriging interpolation method. The elevation dependence of temperature was taken into account by applying a monthly vertical gradient (*Table 8*) according to *Péczely (1979)*:

Table 8: Mean monthly 100 m vertical temperature gradient (^{0}C) for Hungary (*Péczely, 1979*).

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
0.24	0.37	0.56	0.63	0.66	0.65	0.63	0.61	0.55	0.46	0.42	0.31

The effect of slope and aspect on air temperature was considered by global radiation using the solar radiation analysis tool of the ArcGIS software.

The solar radiation analysis tool calculates insolation across a landscape or for specific locations, based on methods from the hemispherical viewshed algorithm, developed by *Fu and Rich (2000)*. It accounts for atmospheric effects, site latitude and elevation, steepness (slope) and compass direction (aspect), daily and seasonal shifts of the sun angle, and effects of shadows cast by surrounding topography.

The solar radiation tools in ArcGIS Spatial Analyst include the direct (Dir_{tot}) and diffuse (Dif_{tot}) radiation, but reflected radiation is not included in the calculation of the total radiation ($Global_{tot}$):

$$Global_{tot} = Dir_{tot} + Dif_{tot}$$

The solar radiation calculations involved four steps:

1. The calculation of an upward-looking hemispherical viewshed based on topography
2. Overlay of the viewshed on a direct sunmap to estimate direct radiation
3. Overlay of the viewshed on a diffuse skymap to estimate diffuse radiation
4. Repeating the process for every location of interest to produce an insolation map

Since radiation can be greatly affected by topography and surface features, a key component of the calculation algorithm requires the generation of an upward-looking hemispherical viewshed for every location in the digital elevation model. The amount of visible sky plays an important role in the insolation at a location.

During the insolation calculation, the viewshed raster is overlaid with the sunmap and skymap rasters to calculate diffuse and direct radiation received from each sky direction.

Since the tool is developed for landscape scale, the country was segmented into ten latitude zones. Solar radiation maps were created using the 90 m resolution SRTM digital elevation model for each month of the year and later resampled to 1000 m.

Solar radiation influences significantly air temperature. Air temperature differences on variable slopes and aspect is in close relationship with the received global solar radiation (*Xin et al., 2007*). An improved model is put forward as follows:

$$T' = T + \Delta T$$

where T' is the air temperature after correction, T is temperature on flat terrain and ΔT is the temperature difference between the slope and flat unit.

A close relation between global radiation and air temperature was confirmed by *Xin et al. (2007)* using TM6 thermal infrared images to validate the results. According to their analysis, the relationship between temperature and global radiation, as well as slope and flat can be expressed as follows:

$$\frac{Q_{slope}}{Q_{flat}} = \frac{T_{slope}}{T_{flat}}$$

where Q_{slope} and Q_{flat} stands for global radiation amount (MJ/m^2) at slope and flat unit, respectively. T_{slope} and T_{flat} is the temperature of slope and flat unit.

Hence, temperature difference ΔT between slope and flat is:

$$\Delta T = \frac{Q_{slope} - Q_{flat}}{Q_{flat}} T_{flat}$$

Q_{flat} and Q_{slope} denotes astronomical global radiation on terrain. Temperature difference (ΔT) between slope and flat was calculated according to this equation and was subsequently added to T_{flat} to get the terrain corrected temperature.

This very attractive trait of the temperature maps allowed me to characterise forest stands even in non-zonal positions (*Figure 38*).

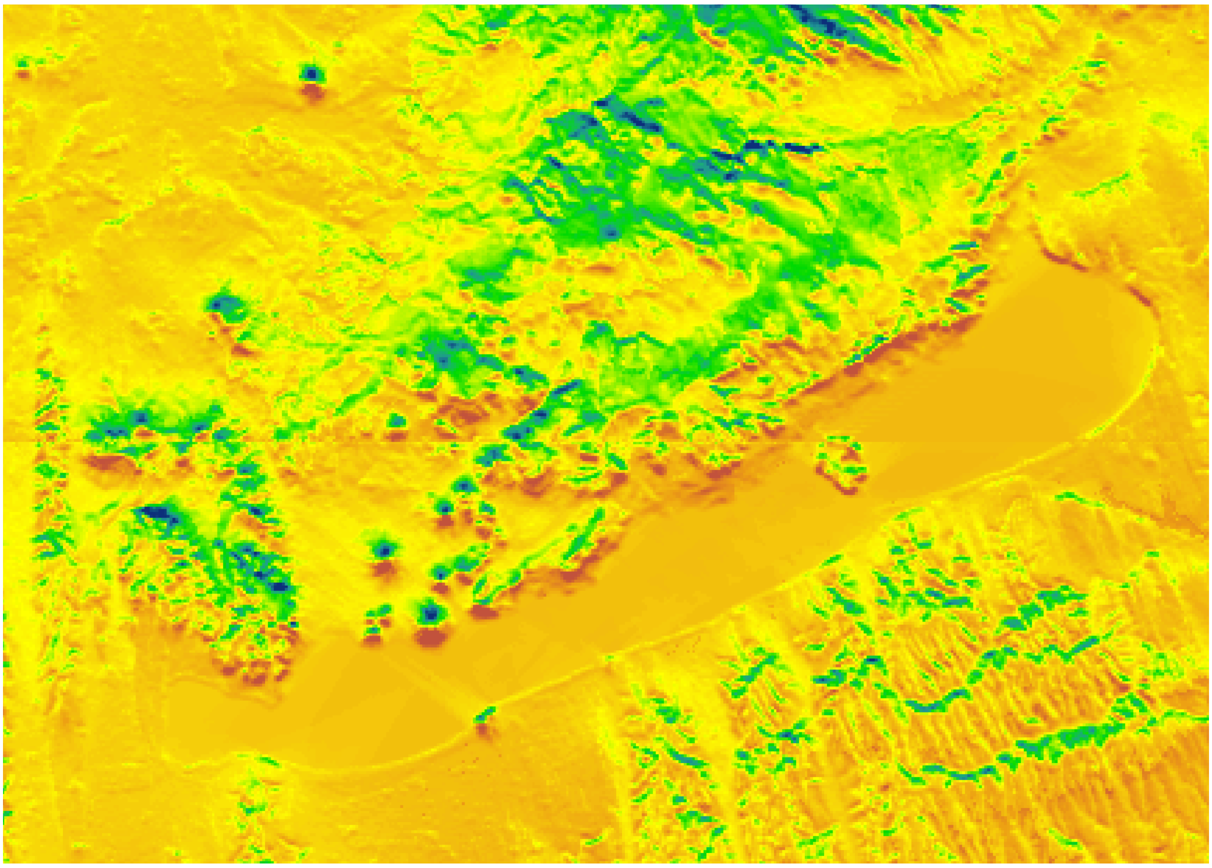


Figure 38: An example of the effect of slope, aspect and global radiation on air temperature at higher resolution near the Lake Balaton in November 2002 (lowest temperature is indicated with blue and the highest with orange).

3.1.3 Scenarios for the future

The past and future of climate are described by global and regional numerical climate models. In climate models a spatial grid is put over the Earth surface and the atmosphere (and ocean) is divided into vertical discrete layers. Within each grid box of these three dimensional grid the new climate variables are computed for each time step. Climate models are essential tools for providing insight into the atmospheric processes. They can be applied for simulation of the present and future climate tendencies.

Regional climate models differ in complexity and character from the general circulation models. To make detailed climate simulations for a selected region, a regional model is nested within a GCM. Such nested models are the regional climate models (*McGregor, 1997*).

Regional climate models are complementary to global climate models. A typical use of regional climate models is to add further detail to global climate analysis or simulations, or to study climate processes in more detail than global models allow. Over the past 20 years, the development of regional climate models has led to increased resolution, longer model runs, and steps towards regional climate system models. During recent years, community efforts have started to emerge in earnest, which can be expected to further advance the state-of-the-art in regional climate modelling. Applications of regional climate models span both the past and possible future climates, facilitating climate impact studies, information and support to climate policy, and adaptation.

RCMs work by increasing the resolution of the GCM in a small, limited area of interest. An RCM might cover an area typically 5000 km x 5000 km. The full GCM determines the very large scale effects of changing greenhouse gas concentrations, volcanic eruptions etc. on global climate. The climate (temperature, wind etc.) calculated by the GCM is used as input at the edges of the RCM. RCMs can resolve the local impacts given small scale information about orography (land height), land use etc., giving weather and climate information at resolutions as fine as 50, 25 or 10 km (*Figure 39*).

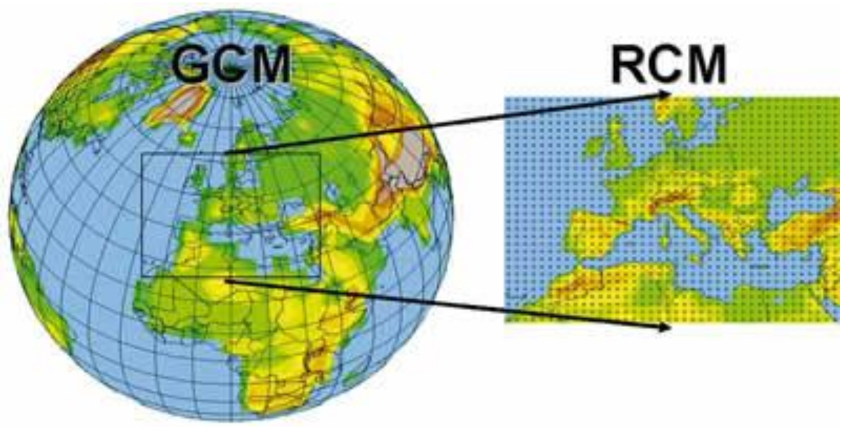


Figure 39: Illustration of the concept of regional climate models with finer resolution.

The CLM regional climate model

The ClimateLimited-areaModelling (CLM) regional climate model was applied for simulation of future health conditions of beech in Hungary using the A1B scenario (*Table 9*).

Table 9: Important features of the CLM model.

Data compilation	Model and Data Group (MandD) at MPI for Meteorology, Hamburg
Model	CLM 2.4.11(Climate mode of the Local Model of the DWD) Dynamic model; drive: ECHAM5/MPIOM, non-hydrostatic
Model region	Europe
Simulation period	From 1960 to 2100
IPCC (Intergovernmental Panel on Climate Change) emission scenarios	A1B, B1 (from 2001)
Resolution	0.165° (data stream 2), 0.2° (data stream 3); approx. 20 km
Structure	Rotated model grid (data stream 2 = DS2) or Regular lat/lon grid (data stream 3 = DS3); Extraction of subregions possible
Data format	NetCDF or ASCII format

The Model and Data Group (*MandD*) at the Max Planck Institute for Meteorology, Hamburg has made climate simulations, which are made available via the Climate and Environmental Data Retrieval and Archive (*CERA*) database of the World Data Centre for Climate (*WDCC*). The climate simulations were carried out at the request of the Federal Ministry for Education and Research (*BMBF*) and in consultation with the group of German regional climate modellers. The cooperation project provides free access to the model data to the scientific and application-oriented community. The climate data intends to enable the work of climate impact research projects and to stimulate and support the development of adaptation strategies to climate change.

Monthly mean temperature and precipitation sum were downloaded from the WDCC (*http://cera-www.dkrz.de/CERA/jblob/)* in NetCDF format for all model pixels, contained any beech subcompartment (*Figure 40*).

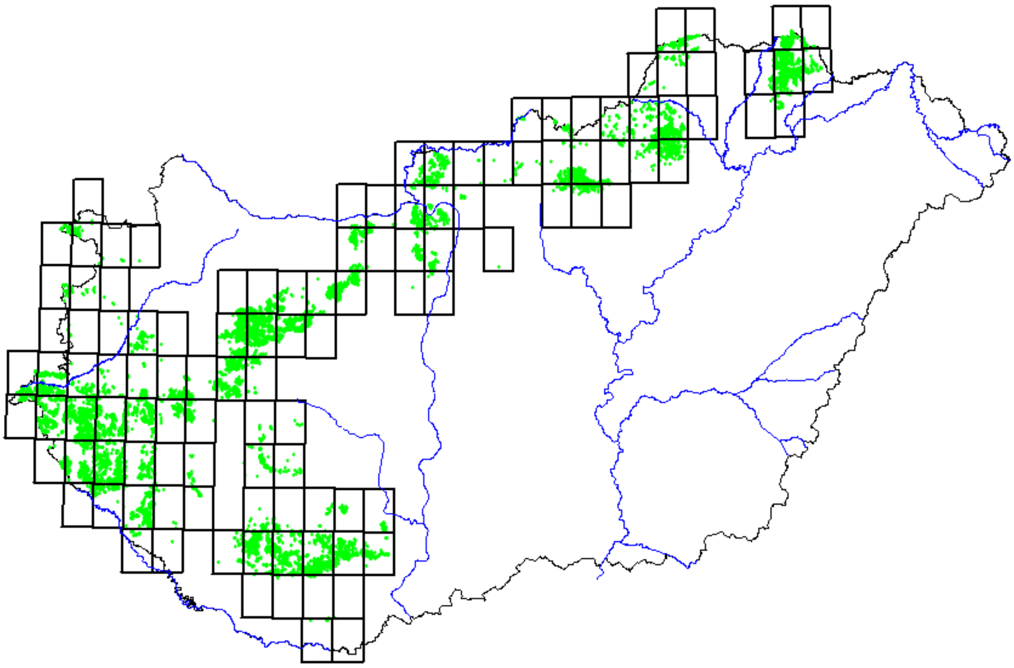


Figure 40: The grid boxes of the CLM model and beech subcompartments in Hungary.

NetCDF files were converted into plain ASCII text files by using two packages (NetCDF, FAN). Since the observed and simulated data or the past has deviated considerably from each other, CLM model data were corrected using the delta change approach (*Hay et al., 2000*). The correction was based on the mean deviation of the observed and simulated variables between 1960 and 2000 for each grid box.

Since climate variables are given in the CLM model for the mean altitude of each grid box, the consideration of altitude was essential. Long-term precipitation and air temperature differences were computed between the observed mean of the grid boxes and each beech subcompartment for the period 1960-2000. The differences were added to the mean-altitude simulation values corrected previously by the delta change approach.

3.2 Species distribution models (SDMs) using long-term climate data

3.2.1 The ModEco platform

The primary reason to choose ModEco was because it contains models for dealing with presence-only and presence/absence data. Further advantage of ModEco is that it has feature analysis, model performance evaluation and accuracy assessment tool. As ModEco incorporates several modelling methods, the training, analysis and assessment can be carried out on the same platform supporting consistent comparisons.

Disadvantage of the platform is that a trained model needs new environmental surfaces for climate change predictions, which slows down the process.

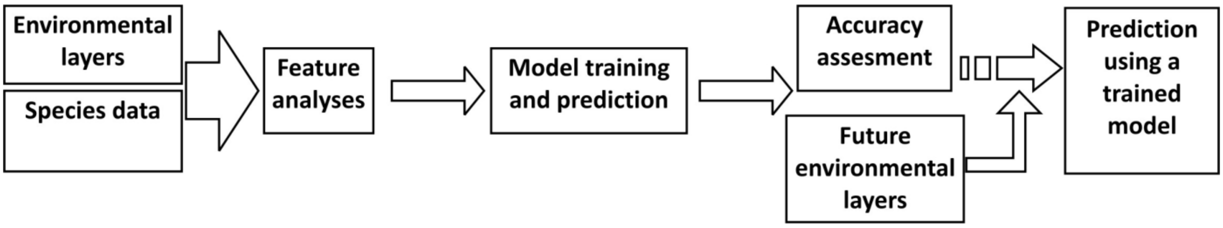


Figure 41: General workflow of the distribution modelling using the ModEco platform.

3.2.2 Environmental layers

96 different environmental predictor surface maps were used as input, all with a spatial resolution of 0.0083^{o} (approx. 1x1 km).

Environmental variables were selected according to their relevance to tree survival and growth. Climatic variables were taken as surrogates for variables having more direct physiological roles in limiting the ability of plants to survive.

Although the main environmental data used for the analysis were climate data (derived from the WorldClim database), soil and geomorphological factors were also included. Soil texture and moisture regime is an indirect variable and was considered as surrogates for soil type, with direct impacts on nutrient and water availability for plant growth (*Austin and Smith, 1989*). Geo-morphological factors were used as surrogates for sites in non-zonal positions. The predictors included:

Soil

Two soil variables were selected from the Hungarian Agrotopography Database (*AGROTOPO, 2002*):

- soil texture with 7 classes (sand, sandy loam, loam, clay loam, clay, organic soils, coarse fragments -gravel, rocks, etc.) and
- soil moisture regime with 9 classes:
    - high IR, P, HC, low FC, very poor WR;
    - high IR, P, HC, good FC, good WR;
    - good IR, P, HC, FC, WR;
    - moderate IR, P, HC, high FC, good WR;
    - moderate IR, poor P, HC, high FC, WR;
    - low IR, very low P, HC, high WR;

- very low IR, extremely low P, HC, very high WR;
- good IR, P, HC, very high FC;
- extreme moisture regime due to shallow depth

where: IR = infiltration rate, P = permeability; HC = hydraulic conductivity; FC = field capacity and WR = water retention

Both layers were used as nominal (categorical) layers.

Geo-morphological factors

3 geo-morphological factors derived from the SRTM digital elevation model were used:

- mean altitude,
- slope and
- dominant orientation (aspect).

Climate data

The dataset included monthly maximum, minimum, and mean temperatures, and monthly precipitation; and a set of 19 climate-derived variables (*Table 10*).

Table 10: Variables of the climate database used for the modelling.

Climatic predictors	**Formula**
average monthly mean temperatures (°C)	
average monthly minimum temperatures (°C)	
average monthly maximum temperatures (°C)	
average monthly precipitation (mm)	
Annual Mean Temperature (°C)	
Mean Diurnal Range (°C)	= (Mean of monthly (max temp - min temp))
Isothermality	= (Mean Diurnal Range / Temperature Annual Range) * 100
Temperature Seasonality	= (standard deviation *100)
Max Temperature of Warmest Month (°C)	
Min Temperature of Coldest Month (°C)	
Temperature Annual Range (°C)	= Max Temperature of Warmest Month - Min Temperature of Coldest Month
Mean Temperature of Wettest Quarter (°C)	
Mean Temperature of Driest Quarter (°C)	
Mean Temperature of Warmest Quarter (°C)	
Mean Temperature of Coldest Quarter (°C)	
Annual Precipitation (mm)	
Precipitation of Wettest Month (mm)	
Precipitation of Driest Month (mm)	
Precipitation Seasonality	= (Coefficient of Variation)
Precipitation of Wettest Quarter (mm)	
Precipitation of Driest Quarter (mm)	
Precipitation of Warmest Quarter (mm)	
Precipitation of Coldest Quarter (mm)	

Bioclimatic indices

Bioclimatic indices are important elements of drought monitoring and assessment since they simplify complex interrelationships between many climate and climate-related parameters. The advantage of these indices is that temperature and precipitation are well measured parameters and could be easily interpolated over large areas but the simplification of the connection between temperature and evapotranspiration limits the wider applications. They are classified mostly based on their complexity or input parameters (*Tuhkanen, 1980*).

12 bioclimatic factors and indices computed from minimum and maximum monthly averaged temperatures and monthly precipitations were used. The bioclimatic predictors include: Thermicity index, Ombrothermic index (*Rivas-Martinez, 1990*), de Martonne aridity index (*de Martonne, 1942*), Ellenberg quotient (*Ellenberg, 1988*), monthly and annual potential evapotraspiration (*Thornthwaite, 1948*), Box moisture index of precipitation/evapotranspiration (*Box, 1981*), continentality index, the forest aridity index (*Führer et al., 2011*) and the beech tolerance index (*Berki et. al, 2009*).

Beside the 11 bioclimatic indices indicated in *Table 11* the mean monthly and mean annual potential evapotranspiration [PET] was also calculated according to the Thornthwaite equation.

Table 11: Bioclimatic indices.

Bioclimatic predictors	Formula or reference
Gorczinski's Continentality Index [GCT]	$= ((1.7\ A)/(\sin L)) - 20.4$
De Martonne aridity index [DMI]	$= [(P/T+10)+12p/(t+10)]/2$
Continentality index [CONTINENTY]	$= T_{max} - T_{min}$
Box Moisture Index [BMI]	$= P/PET$
Ellenberg Index [EQ]	$= (T_{max}/P)1000$
modified Ellenberg Index [EQm]	$= (T_{max}/P_{veg})\ 1000$
Forest Aridity Index [FAI]	$= 100(T_{7-8})/(P_{5-7}+P_{7-8})$
Beech tolerance index [BTI]	$= (0.2P_3+0.5P_4+P_5+P_6+P_7+0.8P_8) / T_{6-8}$
Ombrothermic Index [Io]	$= (P_p/T_p)10$
Ombrothermic index of the summer quarter [Iosq]	$= (P_{6-8}/T_{6-8})/10$
Thermicity Index [It]	$= (T + m + M)\ 10$

Tmax: mean temperature of the hottest month [°C]

Tmin: mean temperature of the coldest month [°C]

P: annual precipitation [mm]

T: mean annual temperature [°C]

Pi: precipitation sum of the given month [mm]

Pii: precipitation sum of the given months [mm]

Ti: mean temperature of the given month [°C]

Tii: mean temperature of the given months [°C]

p: precipitation of the driest month [mm]

t: mean temperature of the driest month [°C]

PET: annual accumulated potential evapotranspiration calculated by the Thornthwaite equation [mm]

A: mean annual air temperature amplitude [°C]

L: latitude of the site [absolute value]

Pveg: precipitation sum of the vegetation period [mm]

Pp: Yearly Positive Precipitation [mm] (total average precipitation of those months whose average temperature is higher than 0°C)

Tp: Yearly Positive Temperature [°C] (sum of the monthly average temperature of those months whose average temperature is higher than 0°C)

m: average minimum temperature of the coldest month of the year [°C]

M: average maximum temperature of the coldest month of the year [°C]

Beech occurrence data

Beech occurrence data for the distribution modelling were derived from the Hungarian Forest Inventory database provided by the Central Agricultural Office. The database incorporates every forest subcompartment containing beech. (A tree species is registered in a forest subcompartment, if the mixture ratio of the given tree species exceeds the 5% threshold limit.) These subcompartments were considered in the model as “true presence” observation points (in total 11.332 subcompartments). As the environmental data were given in a 1x1 km grid, occurrence points were also converted to a raster with the same resolution.

At this point I would like to outline, that forests in Hungary are managed forest, and therefore the presence/absence of beech is human influenced (see Literature review, Beech in Hungary section).

3.2.3 Factor analysis

As models deal with large datasets it makes sense to reduce the number of the predictors. Removing could improve the overall model accuracy and speed up the prediction. To detect less important features three methods has been applied before the model training.

To determine which variables to include, redundant environmental layers were identified via pairwise correlations. Values of environmental variables at 5000 randomly selected points were used to calculate the Pearson correlation between variables. Variables showing a correlation >0.80 were considered redundant. Between any two redundant variables, those related to climate extremes were preferred because based on the field observations they are more important for limiting the distribution of beech.

Secondly the factor histogram analysis was applied to compare the frequency distributions of environmental variables between the observed species localities and the whole study area. If the environmental factor histograms follow a pattern similar to the background distribution, it could indicate that this environmental variable may not be relevant to determine the species distribution at the scale of interest.

After the histogram comparisons the factor importance analysis was carried out to examine the contributions of different environmental factors to the overall classification accuracy of a specific model. Different measures can be used to evaluate the quality or accuracy of a prediction (*Fielding and Bell, 1997*). Some measures emphasize the weight of false absences; others give more weight to false presences. Here the Cohen's kappa values were used to evaluate the model performance (*Forman, 2003*).

The equation for κ is:

$$\kappa = \frac{Pr(a) - Pr(e)}{1 - Pr(e)}$$

where *Pr(a)* is the relative observed agreement among raters, and *Pr(e)* is the hypothetical probability of chance agreement (the probability of random agreement). If the raters are in complete agreement then κ = 1. If there is no agreement among the raters other than what would be expected by chance (as defined by *Pr(e)*), κ = 0.

This importance analysis is designed to evaluate the change of classification accuracy of with-only or without a specific environmental factor on the model (*Phillips, 2006*). It is important to note that factor importance analysis is algorithm-sensitive analysis; i.e. different models are sensitive to different predictors, there is no single best predictor (see Results).

3.2.4 Modelling methods

Modelling techniques used in this work can be grouped into three categories according to their kinds of adjustment to data: (1) techniques that use only species presence data to seek relationships with the environmental predictors (e.g. DOMAIN, BioClim, One-Class SVM); (2) techniques that focus on general trends of species' response (e.g. parametric models such as GLM); (3) techniques that give priority to the empirical behaviour of species' response to environmental variables (e.g. non-parametric models such as classification trees and neural networks).

The first approach is expected to provide models with high sensitivity (low misclassification of true presences). The second approach is expected to provide reasonable models for species responding to environmental gradients as predicted by simple response curves. The third approach is expected to provide better models for species with complex distribution patterns, i.e. where occurrences do not respond to environmental variables according to a predefined 'shape'.

In ModEco eight models were used and compared:

- Support vector machine (*SVM*)
- BioClim
- Domain
- Generalized linear model (*GLM*)
- Maximum likelihood classification (*MLC*)
- Artificial neural network trained using back-propagation algorithm (*BP-ANN*)
- Maximum entropy (*Maxent*)
- Classification Tree (*CTree*)

Support Vector Machines

Support vector machines originally developed by *Vapnik* (*1995*), are considered to be a new generation of learning algorithms.

SVMs are designed for two-class problems where SVMs seek to find a hyperplane in the feature space that maximally separates the two target classes. *Guo et al. (2005*) applied one-class SVM in modelling a newly found tree disease in California and found that one-class SVM is a promising addition to environmental niche modelling approaches.

BioClim

BioClim (*Busby, 1986*) is a classic climate-envelope model. The BioClim algorithm computes the similarity of a location by comparing the values of environmental variables at any location to a percentile distribution of the values at known locations of occurrence. The closer to the 50th percentile (the median), the more suitable the location is.

Although it generally does not perform as good as some other modelling methods (*Elith et al., 2006*), particularly in the context of climate change (*Hijmans and Graham, 2006*), it is still used because it is very straightforward and often provides reasonably good results (*Rissler et al., 2006*). Another advantage is that it only requires one free parameter (i.e. percentile).

Domain

The Domain model is considered an improvement over the BioClim model (*Carpenter et al., 1993*). The Domain algorithm assigns each cell in the output layer an average multivariate distance, termed the Gower metric, between that cell and the closest presence cell in the training set (*Carpenter et al., 1993*). These distance values are than rescaled from zero to one. The similarity metric is the only free parameter needed in the Domain model. Essentially, the Domain model is analogous to nearest neighbour classification which is commonly used in spatial interpolation or image classification. On a recent method comparison (*Rissler et al., 2006*), the Domain model has been demonstrated to be a very competitive model based on its performance and relatively easy implementation.

Generalized Linear Model

GLM is a generalization of linear models. By using a link function that transforms the scale of the dependent variable, a GLM is able to relax the distribution and constancy of variances assumptions that are commonly required by traditional linear models (e.g. linear regression). The GLM is commonly used to model dependent variables that have discrete distributions and are nonlinearly related to independent variables (*Guisan et al., 2002*). Consequently, the GLM model is particularly suitable for predicting species distributions, and has been proven to be successful in various ecological applications (*Guisan et al., 2002; Latimer et al., 2006*).

Maximum Likelihood Classification

MLC is one of the most popular classification methods in remote sensing (*Richards and Jia, 1999*). The idea of the MLC is to label an unknown location to the class (either presence or absence) of the maximum likelihood. The likelihood is defined as the posterior probability of the unknown location belonging to either presence or absence. The MLC method relies heavily on a normal distribution of each environmental factor, and it takes into consideration the variance and covariance of environmental factors of presence and absence data by using a covariance matrix. The MLC method is considered to be one of the most accurate classifiers if the data meet the assumptions.

Artificial Neural Network

ANNs were originally inspired by the central nervous system. ANNs have been commonly used to model complex relationships between dependent variables, and independent variables or used to mine patterns in data. The idea of ANNs is to extract linear combinations of the input variable as derived features, and model the output as a nonlinear function of these derived features. The strength of ANN is the ability to 'learn' underlying (non-linear) patterns of correlation between observed input (environmental/climatic variables) and target (species presence/absence) data. ANNs have been already used with great success in a variety of species habitat/bioclimatic suitability analysis (*Araújo et al., 2005; Pearson et al., 2002; Thuiller 2003*).

In ModEco, I implemented a 4 layer feed-forward ANN (one input layer, one output layer, and two hidden layers) that can be trained using backpropagation algorithm and Particle Swarm Optimization (*PSO*) algorithm. Given the heuristic nature of ANN, each simulation gives slightly different results. For this reason, ANN solutions were calculated 10 times and the mean was used to provide predictions.

Maximum Entropy

Entropy is a fundamental concept in information theory; it measures how much choice is involved in the selection of an event. The principle of maximum entropy indicates that the distribution model that satisfies any given constraints should be as uniform as possible (*Phillips, 2006*). This agrees with everything that is known, but carefully avoids assuming anything that is not known.

Classification Trees

CTree seeks to recursively partition the response variable into increasingly pure binary subsets with splits and stop criteria. Trees can overgrow to exactly fit the training data, but this form of overfitting can be avoided by using pruning rules to find the most parsimonious combination of predictor variables. The method has two main advantages:

- it can handle any combination of categorical (classification) and continuous (regression) data. (For example, in my case, I could use the aspect directly into the classification tree)
- it has the ability to capture hierarchical and nonlinear relationship among predictor variables (*De'ath and Fabricius, 2000*).

3.2.5 Accuracy assessment

Traditional measures of fit used in regression, such as R^2 and p-values have little relevance in species distribution modelling.

Cross-validation, the Receiver Operating Characteristic (*ROC*), the Area Under the Receiver Operator Curve (*AUROC*, generally further abbreviated to *AUC*), and maximum Kappa values were used to assess the accuracy. These assessments are commonly used as standard measures to evaluate the performance of environmental niche models (*Elith et al., 2006*).

Cross-validation accuracy assessment was implemented as follows: first, the training data was randomly split into 10 subsets of equal size. Second, each subset was used for accuracy testing and the remaining 9 subsets for training. Finally, the total accuracy was estimated by averaging the accuracy of each test.

The receiver operating characteristic (ROC), or simply ROC curve, is a graphical plot of the sensitivity, or true positive rate, vs. false positive rate (1 − specificity or 1 − true negative rate), for a binary classifier system as its discrimination threshold is varied. The ROC can also be represented equivalently by plotting the fraction of true positives out of the positives (TPR = true positive rate) vs. the fraction of false positives out of the negatives (FPR = false positive rate).

The area under the ROC curve is the "AUC" ("Area Under Curve"). This area could characterise the “goodness” of the prediction. If the ROC curve is a 45^0 line it is equal with a random guess (AUC=0.50). A rough guide for classifying the accuracy based on the AUC (*Swets, 1988*) is:

0.50–0.60 = fail;

0.60–0.70 = poor;

0.70–0.80 = fair;

0.80–0.90 = good;

0.90–1 = excellent.

For presence-only data, the above mentioned measures are not applicable therefore the true positive rate (*TPR*) vs. the fractional prediction area (*FPA*) as a proxy for true positive rate vs. false positive rate and the area under TPR vs. FPA (*Guo et al., 2005; Phillips et al., 2006*) was used.

3.3 Extreme drought event based empirical model (EM)

The theoretical assumptions of an EM fundamentally differ from those of an SDM. SDMs share theoretical assumptions that may not hold during modelling the potential future distribution of beech near the xeric limit (1: modelled species is in equilibrium with its environment; 2: resulting pattern of overall range limits well reflect climatic means). Although SDMs are widely used for prediction of species distribution, it was believed that comparing SDMs with an empirical approach could provide more reliable results necessary for conservation and management strategies.

Beech sanitary logging information - as a proxy of vitality condition - was coupled with meteorological data in a selected study area to obtain the vitality response of beech. The future vitality status of beech to different terms of this century was simulated using the response function and the same regional climate model projection used by the SDMs (*Figure 42*).

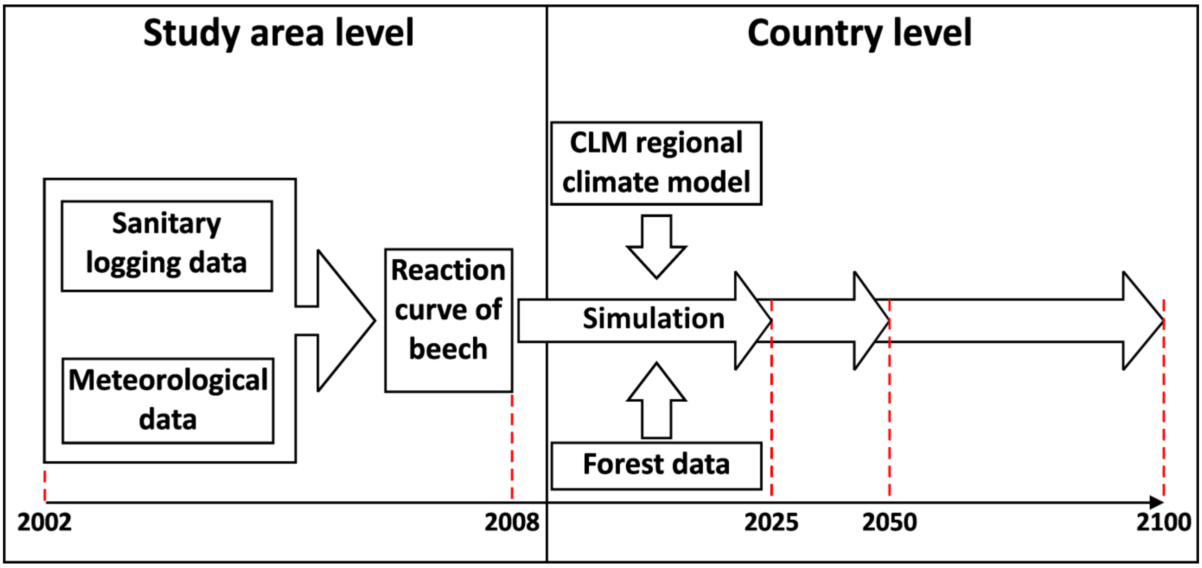


Figure 42: Flow chart of the work in the empirical model.

3.3.1 Study area

General description

A considerable part of beech forests are situated close to the xeric limit, i.e. at the drought-related (trailing, or retreating) end of their warm-temperate distribution range in Hungary (*Mátyás et al., 2008*).

The latest drought event during the early 2000's has induced extensive decline of health condition and mortality of beech especially in Southwest Hungary (*Berki et al., 2009*). The gradually growing moisture deficit has led to the emergence of serious pests and diseases (*Lakatos and Molnár, 2009*).

Due to the specific ecological and climatic conditions six forest regions were chosen as study area for the EM in Southwest of Hungary (*Figure 43*).

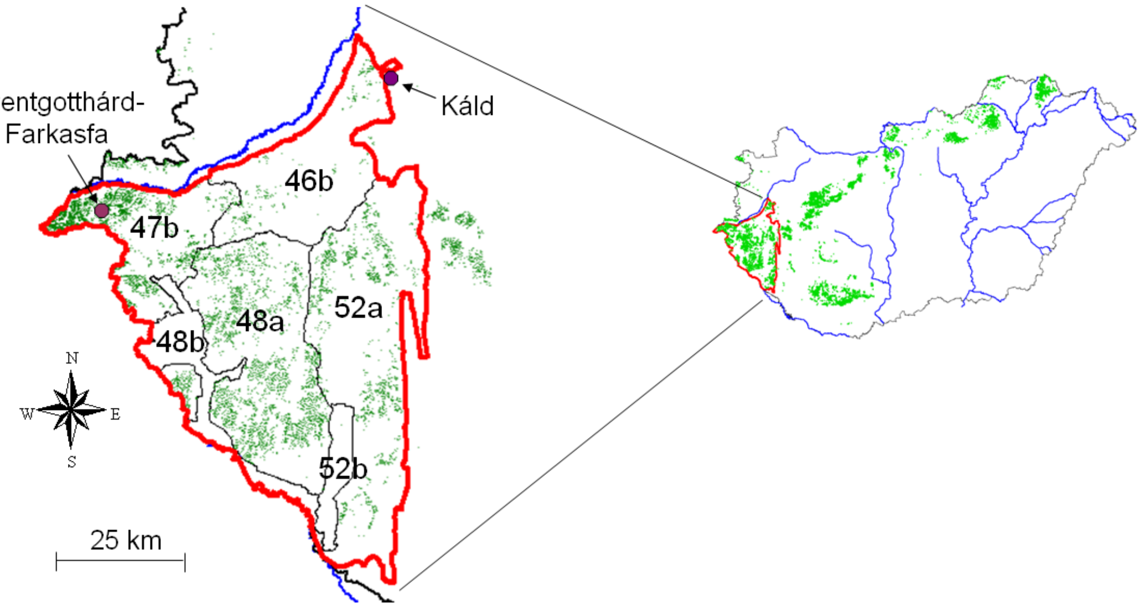


Figure 43: Study area (highlighted in red) and beech forests (47b: Lower Őrség, 46b: Lower Kemeneshát, 48a: Göcsej Hills, 48b: Kerka-Mura Plain 52a: East-Zala loess region, 52b: Sandy region of Nagykanizsa. Meteorological stations (Szentgotthárd-Farkasfa and Káld) are highlighted.

Although the forest region 48b and 52b are not typical beech regions, they are geographically enclave and therefore considered to be part of the stud area. (As the analysis uses only beech subcompartments, it has no influence on the results). Beech subcompartments east from the 52a region were excluded, as sanitary logging information was not available for that region.

Topography, geology

The elevation of the hilly landscape varies between 120 and 380 m above sea level. The western part of the study area was erstwhile one of the gravel-terrace of the river Rába. This landscape is splitted by stream-valleys and covered by clayey loam, originated from the last ice age. This Pleistocene gravel-terrace stretches long northeastwards, situated in the northern part of the region, covered by watertight clayey gravel. The central part of the study region is mainly a hilly region, dominated by numerous ridges and valleys with steep slopes. Soils are formed on loess sediments at the eastern part and on loam at the western part of this region. The eastern part of the study area is characterized by north-south range of hills and valleys. Hills are mainly covered by loess on Pannon sediments while peat soils are more common in the valleys.

Climate conditions

The climate of the study area is humid continental, warm summer subtype (Dfb - *Köppen, 1918*) with moderate Mediterranean characteristic. The summer is slightly cooler, while winter is milder than the climatic mean in Hungary. Since there is a North-East – South-West climatic gradient in the study area, we have chosen two meteorological stations (Szentgotthárd-Farkasfa and Káld), situated at opposing end of this gradient.

The climate can be visualized using the Walter-Lieth (*Walter and Lieth, 1964*) diagram. The temperature scale of the diagram always corresponds to the double of the rainfall amount on the precipitation scale. Months are considered arid when the temperature curve runs above the precipitation curve. The larger water demand of forests is taken into account using the reduced precipitation curve, where the monthly precipitation amounts are reduced to the third (*Figure 44*).

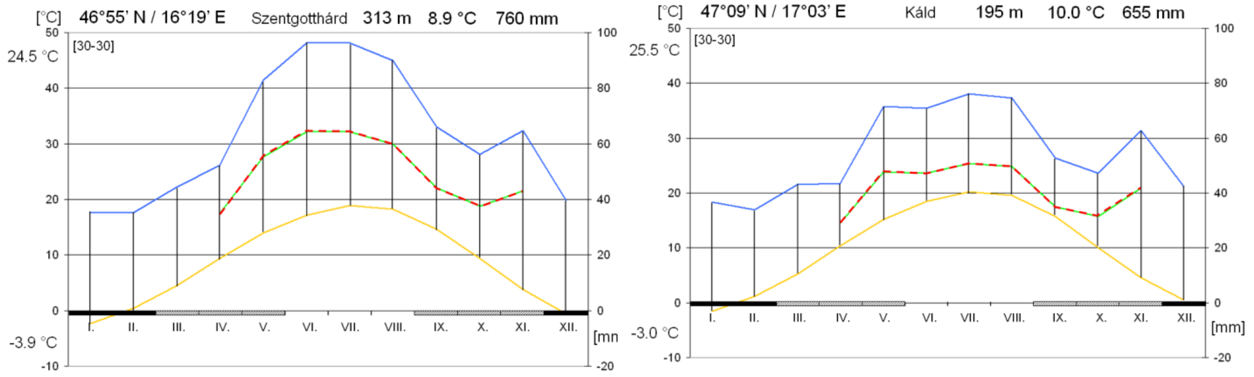


Figure 44: Walter diagram of Szentgotthárd-Farkasfa (left) and Káld (right) meteorological station (1961-1990).

Since the reduced precipitation line runs significantly above the temperature curve, typically there are no water-shortage periods in the western part of the study area. Near the North-Eastern part of the region the climate is drier, but the reduced precipitation curve only approaches the temperature curve.

Annual precipitation shows a strong North-East – South-West gradient with increasing rainfall towards Slovenia and Croatia. Mean annual precipitation (1961-1990) reach values from 620 mm in the North-East up to 780 mm at the South-West.

The time series of annual precipitation sum and mean annual temperature were provided by the Hungarian Meteorological Service (*Figure 45*).

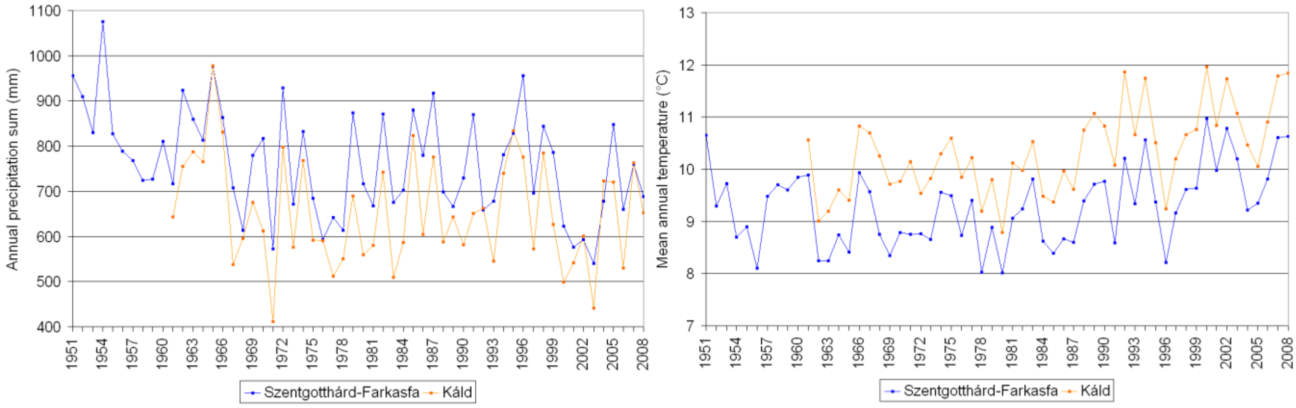


Figure 45: Annual precipitation sum (a) and annual mean temperature (b) of Káld and Szentgotthárd-Farkasfa meteorological stations (Hungarian Meteorological Service).

The annual precipitation shows a slow, but not continuous long-term decrease during the past 60 years. There was a severe drought period between 2000 and 2003, accompanied with rather high annual temperatures. The annual temperature shows a significant upward trend from around 1985.

The annual precipitation was above 700 mm during the 50s and 60s across the whole study area. There was a large decrease in the 70s, since then the annual precipitation has risen slightly in the study area.

Forest cover

In the central and southwest part of the study region the potential vegetation is beech and in smaller part Scotch pine and hornbeam oak forests. In the northern and eastern part the horn-beam and turkey oak forests are dominant potentially.

As the consequence of land use the extent of Scotch pine forests have increased substantially. In the valleys of rivers the common associations are alder and edaphic forests, but the proportion of black locust is also noteworthy. The proportion of each species are 31.2% for Scots pine, 17.4% for beech and 12.4% for black locust. 15.4% of the total forested area in the study area can be considered as water-dependent (*Halász, 2006*). The proportion and area of beech forests in the six forest regions shows high variability (*Table 12*).

Table 12: Beech area and areal proportion in the six forest regions (*Halász, 2006*).

Forest region	Beech area (ha)	Areal proportion of beech (%)
46b: Lower Kemeneshát	271.7	1.2
48a: Göcsej Hills	3446.3	6.9
48b: Kerka-Mura plain	4.2	0.1
47b: Lower Őrség	351.3	1.1
52a: East-Zala loess region	1940.4	5.9
52b: Sandy region of Nagykanizsa	0.0	0.0

Soil

According to the soil texture map of the Hungarian Soil Database (*AGROTOPO, 2002*), the loam texture prevails across the study area. Gravel is typical in the northern part of the study area and peat and clayey soils can be found along the stream valleys. According to the map, most of the beech stands (95.6%) are located over loam texture cover (*Figure 46*).

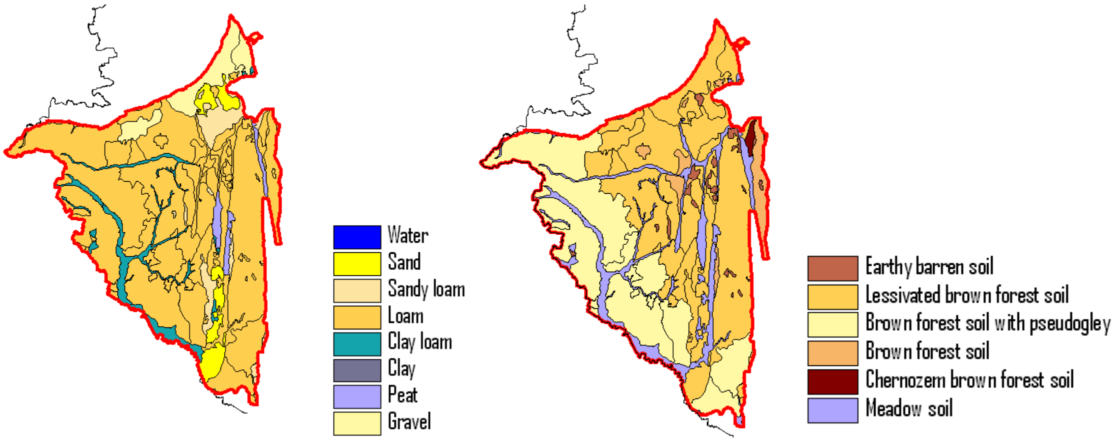


Figure 46: Soil texture (left) and soil type (right) map of the study area (*AGROTOPO, 2002*).

In the southwest part of the study area the most common soil type is the brown forest soil, formed mainly on loam texture type. In the central and eastern part of the study area various types of the brown forest soils are prevailing. Along the valleys meadow soils are characteristic. Beech sites are located mainly on brown forest soil with pseudogley (65.8 %) and on lessivated brown forest soil (28.4 %).

3.3.2 The extreme drought period of 2000-2003

Description of the drought

Significant drought event emerged between 2000 and 2003 in Southwest Hungary which was unprecedented in duration and strength since the beginning of the 50's. After this drought event large volume of declining or already dead beech was logged by forest managers under the control of the Forest Directorates. First, solitary trees showed the typical symptoms of reduced water availability (leaf yellowing, top drying) in 2002 (*Figure 47*).

Figure 47: Beech dieback in northern Zala.

The symptoms of xylo- and phloeophagous insect attack (*Agrilus viridis, Taphrorychus bicolor*) and fungal infection (*Biscogniauxia nummularia, Nectria coccinea*) appeared in 2003 and expanded rapidly after 2004 (*Lakatos and Molnár, 2009*). After 2006 the health condition of beech has improved slightly due to more humid years.

Delineation of the drought period

The annual aridity index (*Budyko, 1974*) was calculated for several meteorological stations for 1951-2010 to characterize the climate of the study area. The Chow's *F* statistics (*Chow, 1960*) were computed for potential significant (at 97.5% confidence limit) trend breaks using the "*R*" package "strucchange" (*Zeileis et al., 2002*). The year 2000 was denoted as optimal location for a break. Avoiding the statistical problems of having two breakpoints the same test was applied for the period 2000-2009 to delineate the end of the drought period. 2004 was found to be the second breakpoint. All meteorological station within the study area showed the same breakpoints, thus drought between 2000 and 2003 can be considered as one single extreme event, which is significantly different from the long-term trend in the study area. The Chow's *F* statistics of the meteorological station Szentgotthárd-Farkasfa is presented in *Figure 48*.

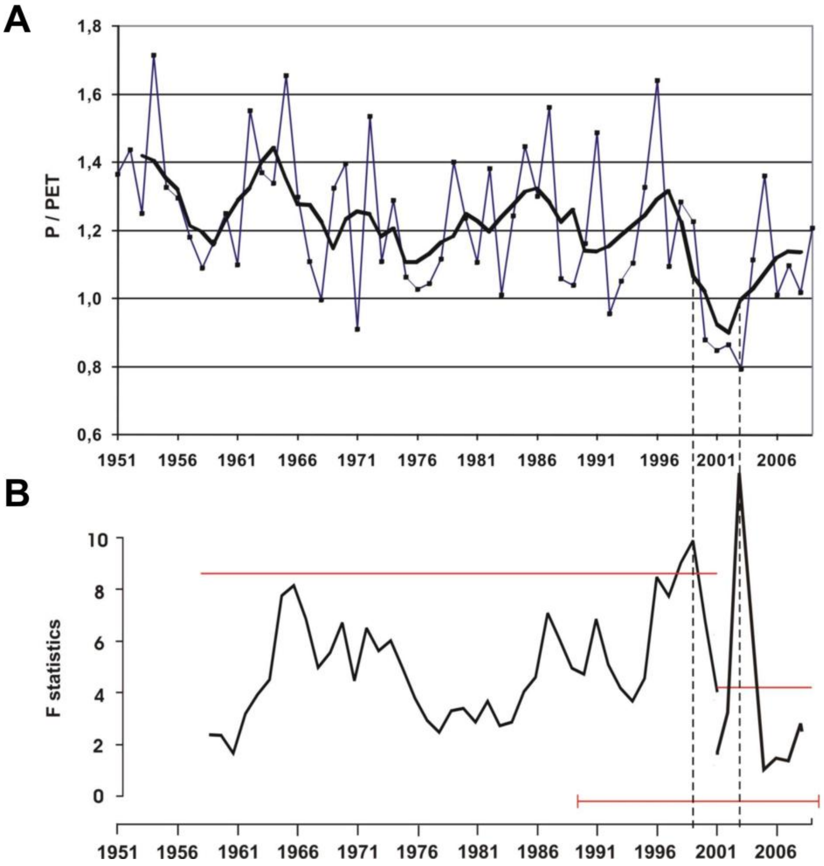


Figure 48: (A) Changes of the annual aridity index (*P/PET*) at Szentgotthárd-Farkasfa with 5-year moving average (solid line) and (B) optimal breakpoints in the aridity index (vertical dashed line), level of significance (red line) and confidence interval (red bracket) using the *Chow's F* statistic.

3.3.3 Forest data

General information

Information on the forest subcompartments in Hungary including the geographical location and the detailed site (area, elevation, topography, slope, aspect) and stand description (species, mixture rate, closure, age, production capacity, yield class, basal area, height, diameter, stand volume, current increment, felling age) was derived from the Forest Inventory Database of the Central Agricultural Office. For training the EM, 1372 beech subcompartments were used in the study area with an average size of 6.9 ha.

Sanitary logging data

The annual volume of beech sanitary logging was provided by the State Forest Companies (Szép Tibor - Szombathelyi Erdőgazdaság Zrt., Góber Zoltán - Zalaerdő Zrt) for each subcompartment of the study area for the period 2000-2008. Sanitary logging affected 14.3 % of the beech forest subcompartments with a total area of 4189 ha.

3.3.4 Vitality response of beech

Severity assessment

Originally the factor selection was planned to base on the factor importance analysis carried out only within the study area of the EM. Ideally this method could explain the importance of the different environmental factors, but SDMs in the study area failed. Results of the factor importance in the study area were hardly better than a random guess with low Kappa values; therefore the selection of the predictor for the EM was based on the factor importance analysis of the models applied for the whole of the country.

The modified Ellenberg's climate quotient (EQ_m) was chosen as predictor for the severity assessment in the EM, since the factor importance analysis (see Results) in the SDMs ranked this layer within the five most important (see *Table 13*). EQ_m was preferred compared to maximum temperatures, because this index includes also precipitation, which is known to be the minimum factor in the xeric limit.

The interpolated meteorological surfaces were used for computing the four year mean (2000-2003) of the EQ_m for each subcompartment.

Vitality response of beech

Before preparing the vitality response function of beech different "inciting factors" like age, mixture ratio, aspect and slope were also investigated. The analysis showed no clear relationship between sanitary logging data and any of the investigated parameters. Only in the case of the age could be stated, that subcompartments over 60 are more affected by sanitary logging.

Relationship between the EQ_m and the sanitary logging data was analysed to obtain the vitality response of beech. Sanitary logging data between 2000 and 2008 were pooled together, since the progress of sanitary cuttings couldn't always keep up with the decay.

First the distribution frequency of the beech subcompartments were investigated in the different EQ_m classes. To reduce the bias originating from the unequal distribution, the range of the predictor (EQ_m) was divided into 18 equal intervals interpreted as "drought classes".

Practically this means that beech subcompartments were aggregated into 18 drought classes based on their EQ_m values.

The vitality condition of the given “drought class” was characterised with the ratio of the area affected by sanitary logging to the total area of the related drought class. This ratio was subsequently plotted to obtain the response function.

Simulation the future vitality condition of beech

The defined vitality response of beech was used to simulate the future conditions until 2025, 2050 and 2100.

The model investigated with a “moving window” the EQ_m time series of each beech subcompartment until 2025, 2050 and 2100. Based on the mean value of the worst four year situation each subcompartment was evaluated.

4 Results

4.1 SDMs using long-term climate data

4.1.1 Performance of presence-only methods

Potential current distribution

Presence-only methods showed marked variation in modelling success. Although TPR was very similar the predicted area varied a lot among the models. Using the accuracy measures of presence-only data, the one-class SVM performed better (TPR: 0.794) for predicting current distribution than BioClim and Domain but, the predicted area was also greater. If we also consider absence data during the assessment and penalize the false negative predictions by using the ROC score (true positive rate vs. true negative rate), Domain showed the best performance (*Table 13*).

Table 13: Parameters and statistical performance of presence-only methods for predicting potential current distribution of beech in Hungary.

Models	Parameters	Number of layers	True positive Rate (TPR)	Predicted area	TPR vs. predicted area	ROC
BioClim	percentile: 96%	88	0.708	1.004	0.8924	0.898
Domain	similarity: 0.995	64	0.765	0.987	0.7264	**0.933**
One-class SVM	Nu: 0.064 Gamma: 27.6	65	**0.794**	**1.318**	**0.9046**	0.909

There were significant regional differences between the modelled potential and the actual distribution. However BioClim the simpliest climate envelope model predicted in total almost the same area as suitable, there were regional biases. BioClim notable overpredicted in the Southwest (Zala county, south from Szombathely) and in the Northeast (Cserhát, north from the Mátra mounteains), but also a smaller patch north form the lake Balaton (Balaton-felvidék) was predicted as suitable for beech. BioClim systematically excluded the marginal sites (Mátra, Bükk, Zemplén, Kőszeg, Soproni-hg., Börzsöny, Mura valley) and also failed in the Vasi-hegyhát and in Aggtelek. One-class SVM performed regionally similarly to BioClim, only the magnitude of the overprediction was greater. Domain predicted very precisely the current distribution of beech, almost all observation point were enclosed in the potential area (*Figure 49*).

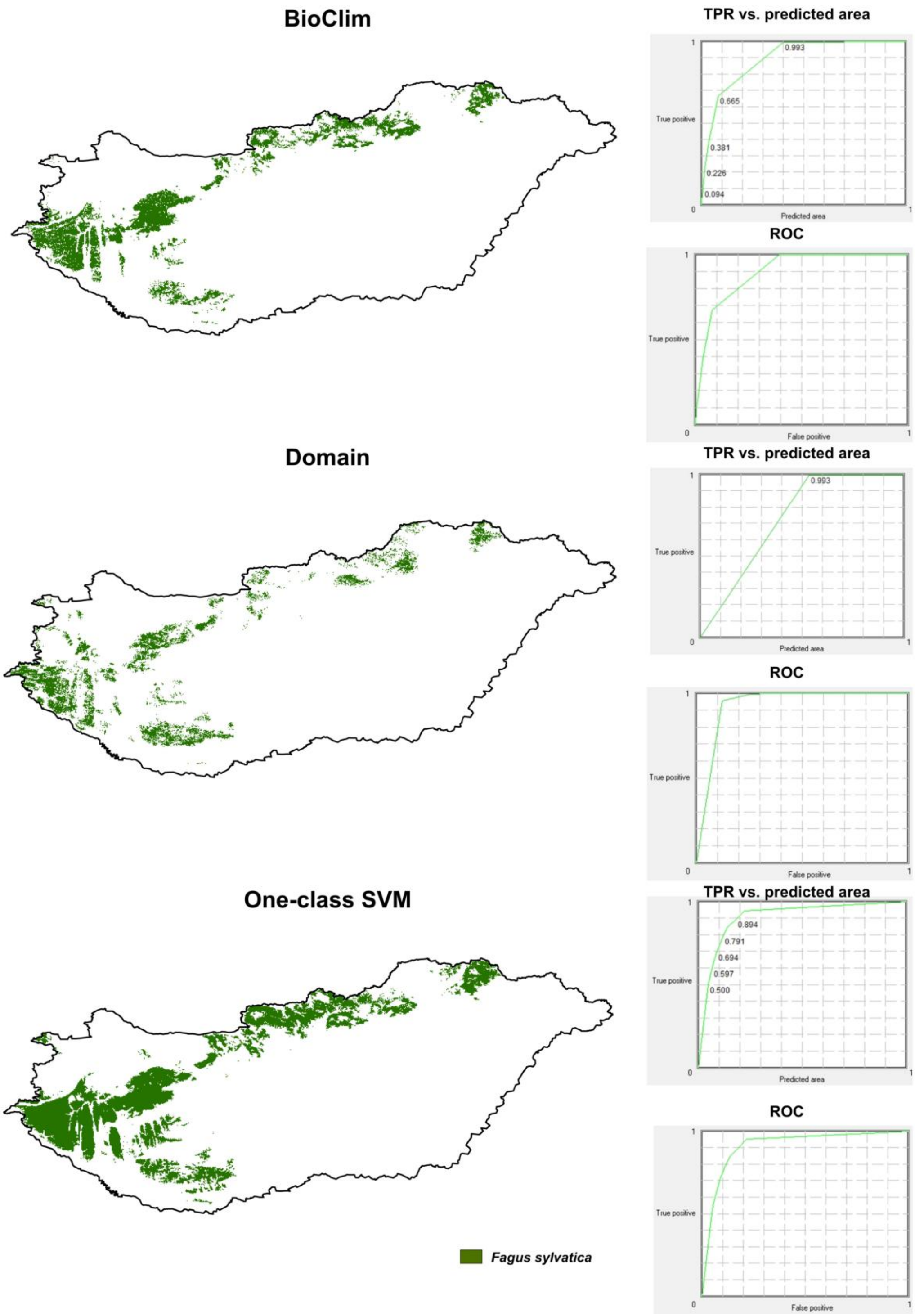


Figure 49: Potential distribution modelled by BioClim, Domain and One-Class SVM for present conditions and the related operating curves (TPR vs. predicted area; ROC). Green colour represents areas modelled as suitable for beech.

Potential future distribution

While the presence-only methods performed “fair” or “good” by describing the current distribution of beech all the three methods were unsuited for predicting climate change impacts. BioClim and Domain removed all beech even for the near future (2011-2040) while one-class SVM predicted potential occurrence only for regions under sub-Mediterranean and subcontinental influence.

Prediction with Domain and Bioclim was only possible when the number of the environmental predictors were strongly reduced.

4.1.2 Performance of presence/absence classification methods

Potential current distribution

Presence/absence classification methods outperformed presence-only models, the TPR and also the kappa score was higher in all cases (*Table 14*).

Table 14: Parameters and statistical performance of presence/absence models.

Models	Parameters	True positive Rate (TPR)	Predicted area	Kappa index
Artificial Neural Network with backpropagation (BPP-ANN)	Momentum: 0.3 Learning rate: 0.1	0.9425	1.2096	**0.8336**
Classification Tree (CTree)	Number of trials: 10 Window size: 20 Pruning confidence level: 0.25	0.9493	1.3196	**0.8431**
General linear Model (GLM)	Link function type: LOGIT Threshold: 0.426	0.9592	1.6237	0.8174
Maximum Entropy (MAXENT)	Omission rate: 0.05	0.9395	1.4362	0.8145
Maximum likelihood (MLC)	No parameter required	0.9415	1.5205	0.8076

MAXENT, MLC and GLM performed relatively poorly, only GLM had high TPR (0.959), which yielded from the strong overprediction (1.623). CTree and BP-ANN performed significantly better than the other models. The high TPR, the smaller predicted potential area and the high kappa score indicated that these models are able to capture non-linear responses and can handle interactions between the variables.

Visually, the CTree model created a more dispersed potential area, while the BP-ANN model produced a less fragmented distribution with more distinct boundaries (*Figure 50-51*).

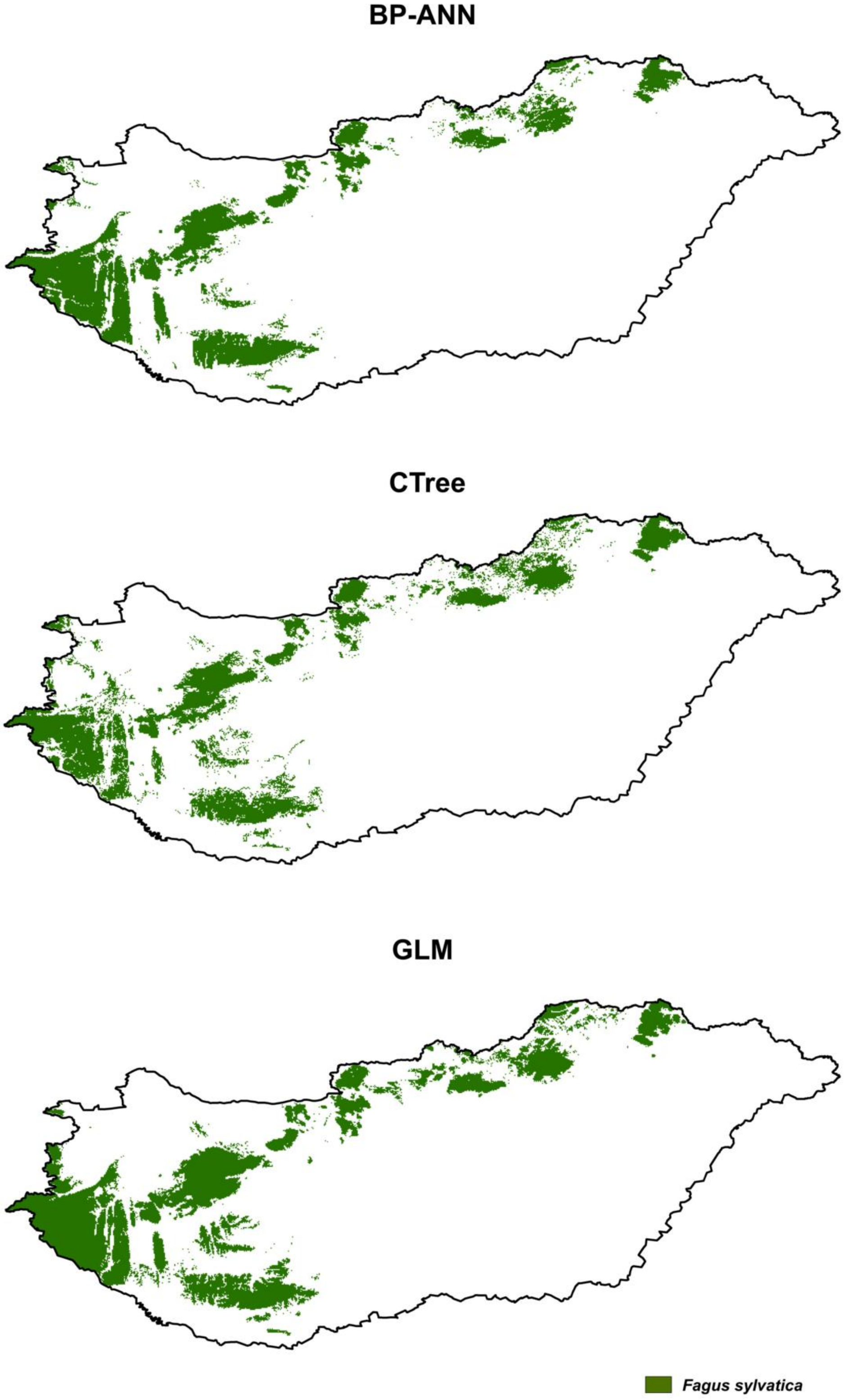


Figure 50: Potential distribution modelled by artificial neural networks with backpropagation algorithm (BPANN), classification tree (CTree) and general linear model (GLM) for present conditions. Green colour represents areas modelled as suitable for beech.

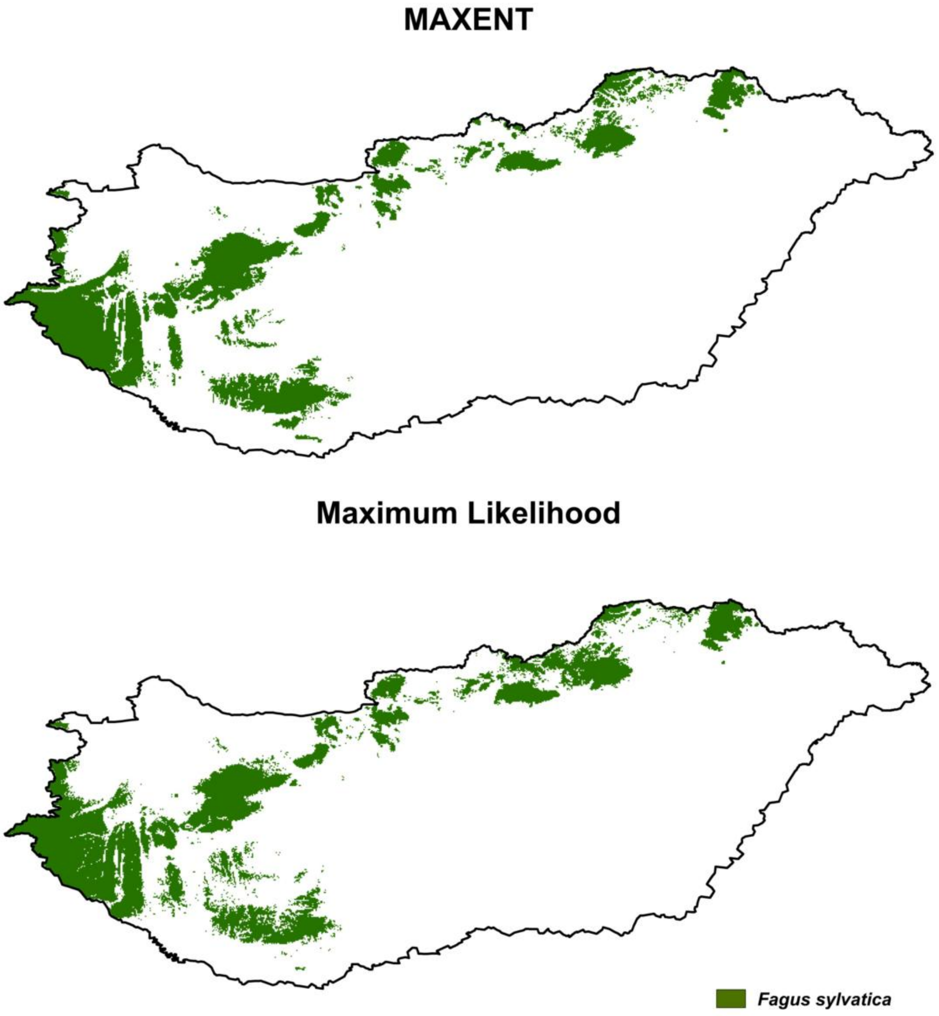


Figure 51: Potential distribution modelled by Maximum Entropy (MAXENT) and Maximum likelihood for present conditions. Green colour represents areas modelled as suitable for beech.

Potential future distribution

Maximum likelihood predicted complete extinction of beech for the whole country for the period 2011-2040. GLM overpredicted the distribution of beech in the near future, and marked regions as potential area, which are already out of the current distribution range. MAXENT predicted a considerable dieback even for the near future removing more than 91.6 % of the current stands. BP-ANN predicted almost no reduction in the potential area for the period 2011-2040 and a very slight (8.0%) for 2036-2065. A considerable shrinkage (56.8 %) of the potential area was predicted only to the end of this century which results that 45.2% of the current stands will be out of the potential area. Regionally the most serious decrease was predicted for the sub-Mediterranean region in the Southwest (*Figure 52*). CTree predicted a more pronounced shrinkage in all regions of Hungary by losing 37.3%, 67.5% and 74.7% respectively (*Figure 53*).

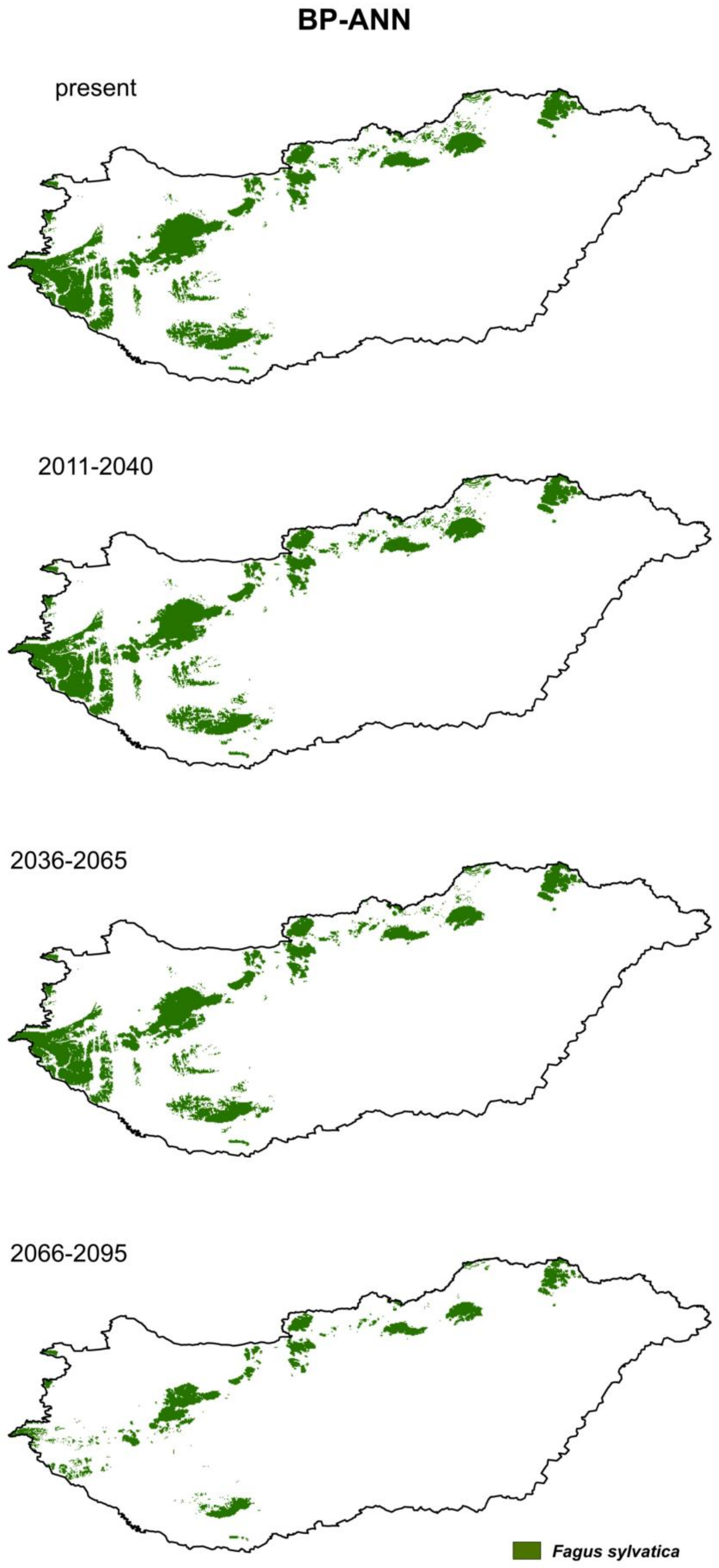


Figure 52: Potential distribution modelled by artificial neural networks with backpropagation algorithm (BPANN) for present and future conditions (2011-2040, 2036-2065 and 2066-2095) respectively. Green colour represents areas modelled as suitable for beech at the given period.

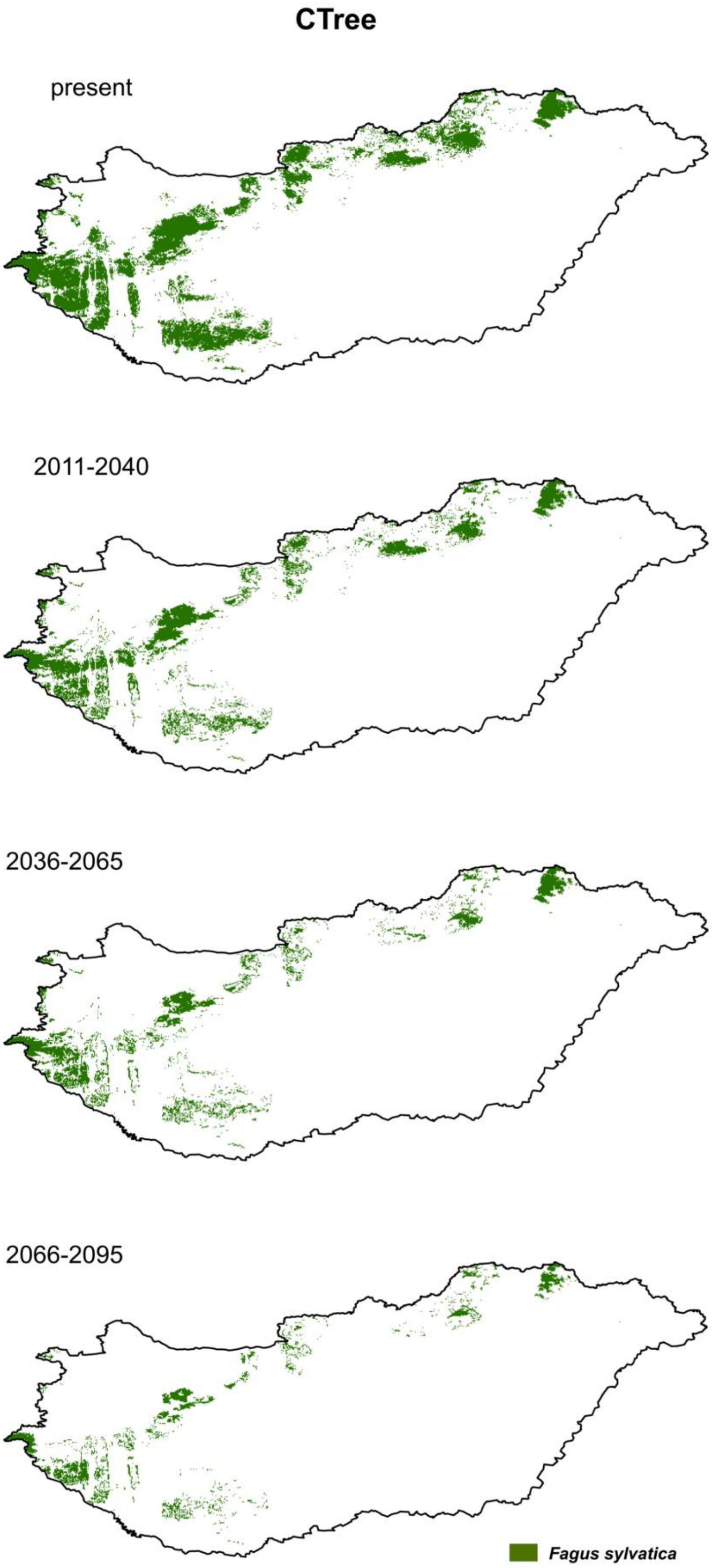


Figure 53: Potential distribution modelled by classification tree (CTree) for present and future conditions (2011-2040, 2036-2065 and 2066-2095) respectively. Green colour represents areas modelled as suitable for beech at the given period.

4.1.3 Factor importance analysis

Factor importance analysis is algorithm-sensitive, but among the environmental variables the maximum temperature of May (*Tmax_05*) and the *EQm* appeared repeatedly as the most influential predictor. In addition, maximum temperatures of summer and precipitation of late summer played a significant role in determining the presence of beech (*Table 15*).

Unfortunately in the case of the best performing model (artificial neural networks with backpropagation algorithm – BPANN) it is not possible to rank the predictors.

Table 15: The overall classification accuracy of the models and the most predictive five factors with the related kappa values resulted from the factor importance analysis.

Rank	Models							
	Bioclim		One-Class SVM		CTree		GLM	
	Predictor	kappa	Predictor	kappa	Predictor	kappa	Predictor	kappa
	overall	0.611	overall	0.788	overall	0.843	overall	0.817
1.	**EQm**	0.570	**EQm**	0.533	**Tmax_05**	0.717	**Tmax_05**	0.708
2.	**Tmax_05**	0.565	Prec_09	0.511	Tmax_06	0.707	Tmax_06	0.697
3.	BMI	0.555	**Tmax_05**	0.491	Tmax_08	0.704	Tmax_07	0.673
4.	Prec_09	0.544	Tmax_08	0.544	Tmax_04	0.704	**EQm**	0.670
5.	IO	0.534	Prec_08	0.451	**EQm**	0.673	Tmean_05	0.664

4.2 Extreme drought event based empirical model (EM)

4.2.1 Vitality response of beech

Vitality response of beech, described by the proportional damaged area of the dought classes area is shown in *Figure 54*.

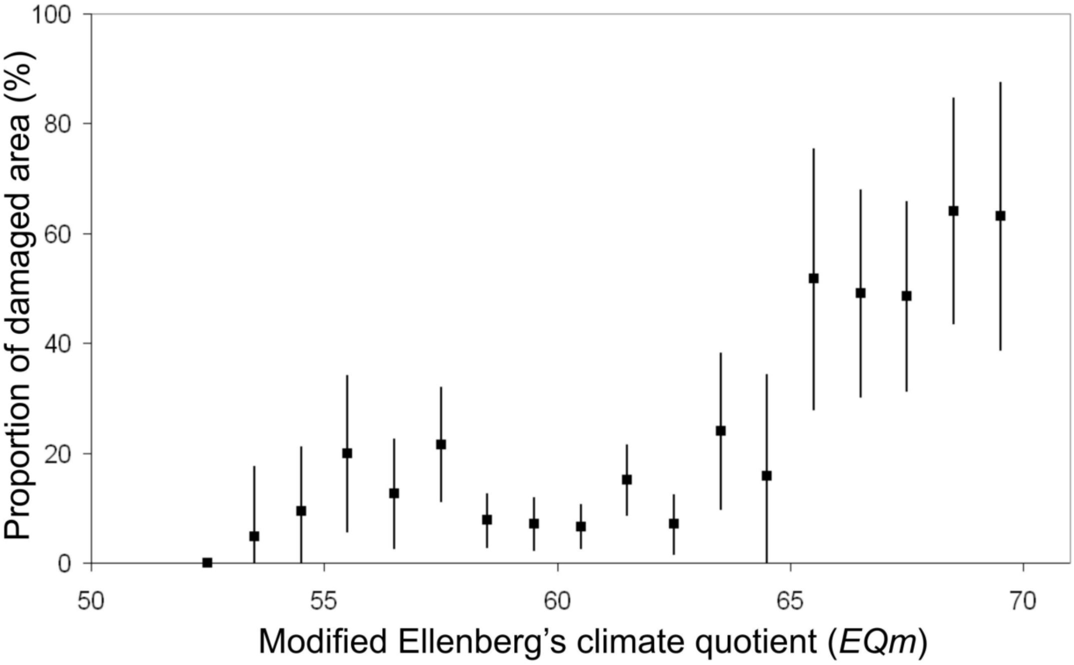


Figure 54: Relationship of the modified Ellenberg's climate quotient (EQ_m) and the proportion of damaged area (%) with 95% percentiles.

The relationship suggest an exponential shaped function, but shows an interesting abrupt change towards drier weather conditions, thus application of a continuous function was rejected. Instead, the range of the "response function" was divided into three categories:

1. *EQm* less than 53 with no damage,
2. *EQm* from 53 to 65 with moderate damage (mean: 12.7%) and
3. *EQm* above 65 with serious damage (mean: 55.4%).

Surprisingly, the 95% percentile intervals were separated quite well at the boundary of the moderate and serious damage class.

4.2.2 Simulation results of beech vitality in the future

Vitality of beech showed considerable changes only after 2025. Until 2025 significant drought events might cause only local damages along the xeric distribution limit of beech (*Figure 55a-c*).

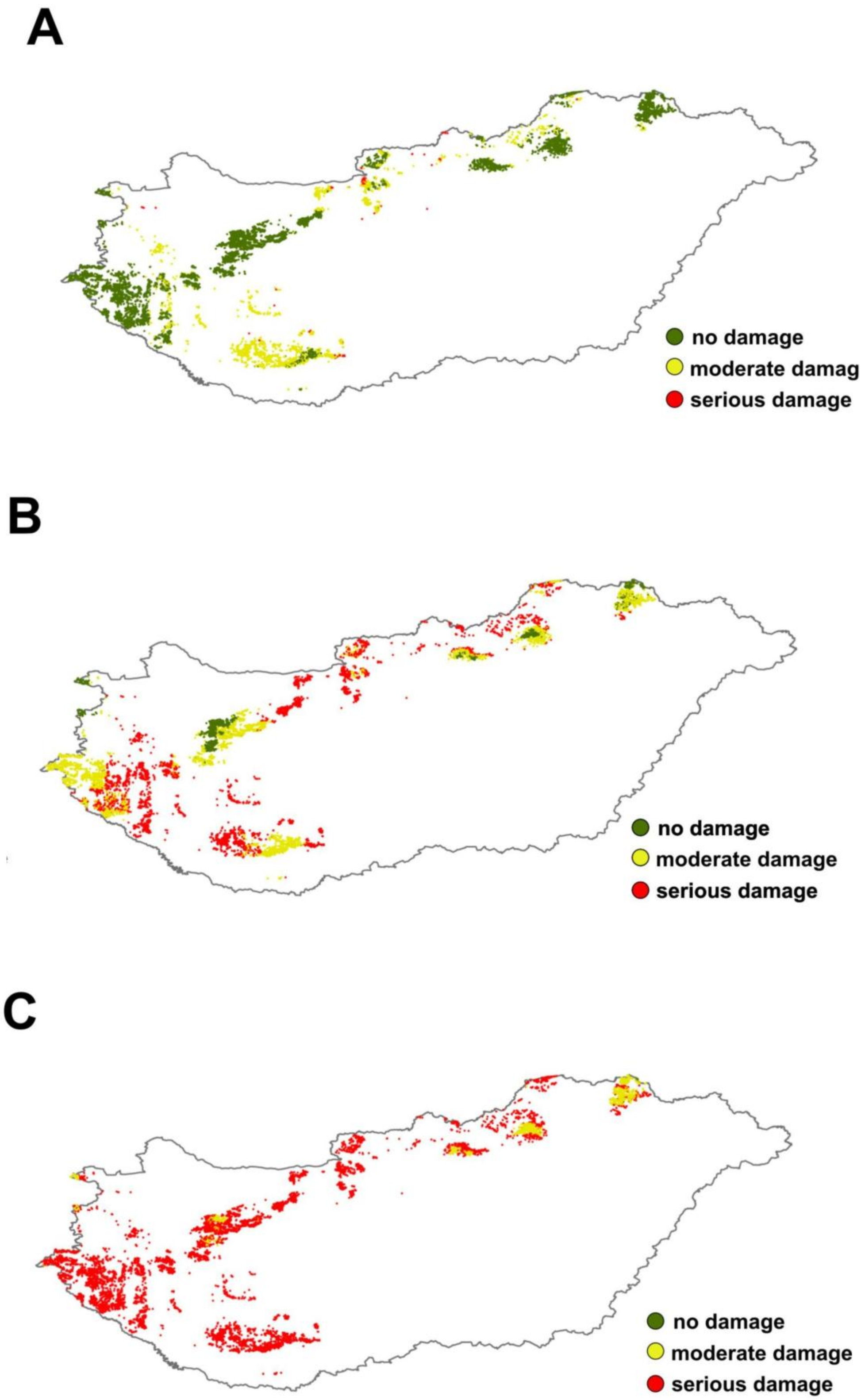


Figure 55: Beech vitality condition by 2025 (A), 2050 (B) and 2100 (C) in Hungary using the A1B scenario of the CLM model. Dark green indicates healthy stands, yellow indicates moderate dieback while red means serious decline.

Beech vitality condition is expected to decline significantly by 2050. Serious decline is expected regionally not only at the lower distribution range, but at optimal site conditions. Moderate damage is likely at almost all beech sites, except the mountainous regions approximately above 500-600 m.

Beech might not be sustained by the end of the century in most of the country, except above 700-800 m mainly in the Northeast.

5 Discussion

5.1 Performance of the SDMs

Overall, the ANN showed the highest model performance whereas similarity and ordination-based models (DOMAIN, BioClim, One-Class SVM) showed the lowest performances. While some authors (e.g. *Mastrorillo et al., 1997; Pearson et al., 2002*) also consider BP-ANN to be advantageous to model species occurrences, these observations are not supported by other studies, where BP-ANN showed overall performances comparable to GLM (*Manel et al., 1999*). Other studies also showed that similarity and ordination-based methods perform less well than advanced techniques, namely CTree and BP-ANN (*Elith and Burgman, 2002*). Since these studies did not always use the same parameterization, they are, however, not fully comparable.

5.1.1 Actual and potential current distribution

BioClim treats the environmental data values at the locations of species occurrence as multiple one-tailed percentile distributions. It creates hyperboxes to include a given percentile for each variable so that, for example, the fifth percentile is treated the same as the 95th percentile. This results that locations with extreme conditions (wettest – driest, hottest – coldest etc.) are considered as outliers. This is the reason, why BioClim obviously failed in the top of the mountains in the Northwest (coldest sites of Börzsöny, Mátra, Bükk and Zemplén Mountains) and at low elevation sites in Zala (Kerka-Mura valley).

BioClim in general is a very robust model, which concentrates on the “core areas” (96% percentile). This characteristic is advantageous by predicting rare or coarse sampled species using low number of predictors. The more predictor we have the more site is eliminated during creating the hyperbox (climate envelope), therefore BioClim is unsuitable for modelling range margins.

Domain is a similarity based model, which uses the Gower distance method to classify the suitability of any new site. The more variable we have, the more accurate the similarity assessment of a new site is. The calculation was very time consuming, but resulted a very precise prediction with high accuracy rate. Similarly to BioClim, with the “similarity value” during the parametrisation we define a certain amount, which is considered outlier during the classification. This means, that marginal sites (with a significantly lower rate than in BioClim) are eliminated in the model.

Method such as BioClim only use hyperboxes to contain the presence data, and are thus often unsuitable for other forms of data (that have e.g. irregular distributions in feature space), therefore one-class SVM was also applied. One-class SVMs seek to find an optimal hypersphere which contains all or most of the training points, at the same time tightly constraining the presence data in feature space. Originally SVMs are designed for 2-class problems (separating two types of data) and optimised for working with low number of predictors. The relatively high number of the environmental variables produced a very complex distribution pattern which resulted greater overprediction.

Although CTree has clear advantages over classic climate envelope methods, certain disadvantages emerged. CTree appeared to be very sensitive to the number of predictors. Even small changes produced highly divergent results. The dispersed potential map of CTree could be a sign of overfitting, which means, that the model is too specific (unbalance of specificity and sensitivity).

The larger amount of overprediction and the distinct boundaries in the potential maps of BP-ANN indicated that the generalization ability of BP-ANN was clearly superior to that of classification trees.

Except Domain all models predicted larger potential area than the current distribution. The systematic overprediction of the models could be explained mainly by the following factors:

- **Human influence**: After the post-glacial recolonisation as a result of deforestation and land use change a general reduction of the distribution of tree species has occurred. Due to the low-altitude occurrence of beech in the Southwest, beech forests were often transformed by human use of land (plough-land, populated places). In the mountainous areas human impact on beech forests has been traditionally low (cold and moist areas unsuitable for agriculture), however the low-elevation beech forests were often converted into oak forests (pasture).
- **The lack of soil data**: Beech can be found on a wide scale of soil types from acidic to calcareous but beech is not able to tolerate the quick changes of dry and wet soil conditions. Although, soil data were considered in the study, fine-scale soil information for forests was not available. Therefore some models (BioClim) assessed the macroclimate as suitable for beech in West-Hungary; the occurrence is often hindered by unfavourable water-air, physical and textural characteristics of the soil.
- **Competition and other biotic interactions**: Competition is an important mechanism that is absent from SDMs (already discussed in Chapter 5.1.2). One classical theory originally derived from Darwin, and later by MacArthur, predicts that, along a key environmental gradient, species appear to find one direction to be physically stressful and the other to be biologically stressful (*Brown et al., 1996*). The idea remains to be tested, and has been only rarely discussed in the literature (e.g. *Guisan et al., 1998*).

  As beech is very competitive inclusion of other tree species as predictors were not considered in this work. We hypothesised, that the loss of competitiveness or the occurrence of other tree species could be surrogated by using a wide range of environmental predictors.

  Other biotic interactions should also be considered, such as facilitation, pollination, herbivory, or symbiosis, however existence of such databases are not available.
- **Extreme events**: Most SDMs are calibrated under the assumption that range margins are formulated by climatic means. The association of range margin and climatic mean may not hold when climatic extremes occur with a skewed frequency distribution, thus predictions based on climatic means alone could overestimate ranges. The inclusion of real extreme measures could be especially important on the trailing edge of distribution (xeric limit).

5.1.2 Future potential distribution

The mathematical properties of the models can help to explain the differences in their predictive performance. The most important reason of the underprediction of Biclim is that the model is very sensitive to the occurrence of variables that are outside what was observed in the current climate, even if this is not truly a limiting factor (*Tsoar et al., 2007*).

In Domain all occurrence points are treated separately and, unlike in the other models, there is no generalization (creation of response functions). Contrary to BioClim Domain has a higher level of specifity but a low generalisation ability. Domain is therefore very sensitive to the occurrence of new combinations of environmental predictors and this negatively affects its predictive ability.

One-class SVMs is able to represent very irregular data distribution shapes without making assumption on the probability density of the data (*Tax and Duin, 2002*) which allowed better performance during prediction.

Presence-absence classification models seemed to be able to predict species distributions better under current and novel combinations of climate than presence-only methods. GLM performed relatively poorly due to the lack of flexibility (*Austin, 2002*). MAXENT (*Phillips et al., 2006*) uses an exponential model for probabilities, and therefore gave very large predicted values for environmental conditions outside the range present in the training set.

CTree provided the best statistical performance describing the current distribution among all models, although the predictions for the future showed regional inconsistency especially in the Southwest and in the Northeast. The relatively good predictive performance of CTree could be explained by the ability to find interactions and hierarchical relations among environmental variables (*Hastie and Tibshirani, 1990; Austin, 2002*).

BP-ANN significantly outperformed CTree in the domain of predicting the future potential distribution of beech. Although BP-ANN performed slightly poorer than CTree, the predictions for the future were more realistic without regional inconsistency. One possible explanation for the difference in the predictive performance is that complex features that are constructed allow non axis-parallel and nonlinear decision boundaries. The results of this investigation lend clear support to the preference for neural networks in at least this type of bio-informatics problem.

5.1.3 Regional differences

Model accuracy can be measured not only on country level (overall performance), but also on finer scale (Forest Regions). This breakdown of the accuracy indicates that false negative rates (overprediction) are higher in Mecsek, Western Zselic, Marcali ridge of hills, Göcsej Hills, Lower Őrség and East-Zala loess region (*Figure 56*).

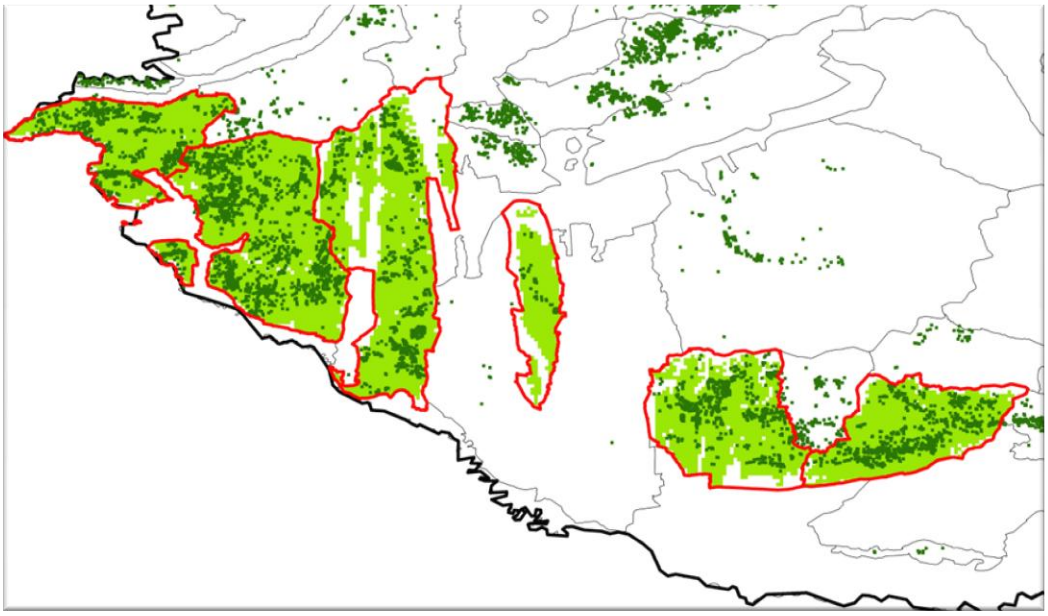


Figure 56: Forest regions with high false negative values (overprediction) in the artificial neural networks with backpropagation algorithm (BP-ANN). Potential area predicted by the BP-ANN model is coloured with light green, observed localities of beech occurrence is indicated with dark green.

False negatives typically reflect the inability of static models (*Guisan and Zimmermann, 2000*). This inability of SDMs suggests that beech in these regions is not in equilibrium with the climate and/or long-term climate means are unsuited to describe its distribution.

5.1.4 Correlates of beech distribution

The previous section described that even the best SDMs have failed in certain regions in Hungary, thus the model performance was evaluated using different tye of environmental predictors (climate, soil, geomorphological variables and extreme measures)

Using climatic predictors only, the current distribution of beech could be easily predicted under optimal conditions, but models failed in Southwest and Northeast Hungary. Including soil data and continentality indices improved model performance in these regions.

This suggests that beech at the edge of its distribution range is more restricted by weather extremes and soil conditions than long-term climatic means.

An example how the addition of soil parameters improved prediction accuracy can bee seen on *Figure 57*.

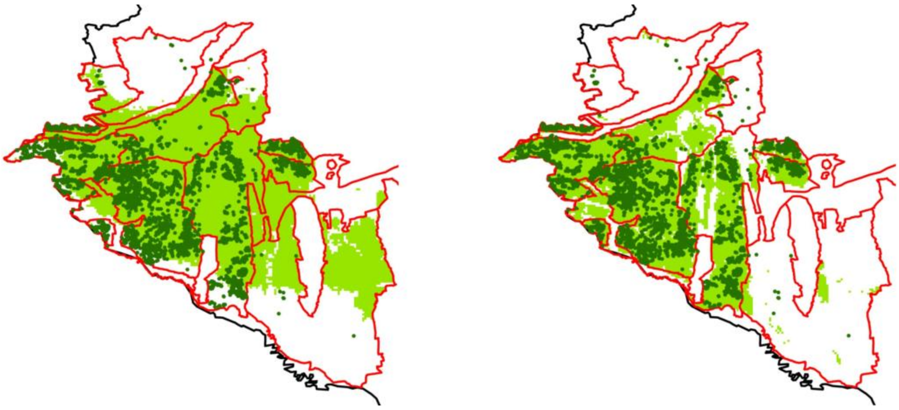


Figure 57: Predicted potential distribution of beech by artificial neural networks with backpropagation algorithm (BP-ANN) in Southwest Hungary using climate predictors only (left) and using climate, soil and geomorphological predictors (right).

5.2 Performance of the EM

The main advantage of the extreme drought based approach is that it uses real, empirical relationship of experienced damage and drought severity. Since our empirical model applies sanitary logging data, results can be interpreted as silvicultural rather than ecological. Furthermore it is important to emphasise that serious damage in the EM does not mean implicitly extinction. The aim of sanitary logging is first of all to extract valuable timber from the damaged compartments, thus healthy trees are also often logged, not only the declined ones. Regarding the reliability of sanitary logging data, it is based on forest management plans and controlled by Forest Directorates.

Past events have shown that decline of forests is triggered by extreme drought periods (*Zimmermann et al., 2009*). Spontaneous selection events and symptoms of decline due to prolonged drought appear usually rather abruptly. Our results also suggest, that drought induced mortality is strictly connected to a certain threshold and large scale decline develops rapidly with worsening climatic conditions. In addition to biotic factors such as pathogens and insects two physiological mechanisms have been advanced in the literature as a potential trigger of such mortality. (1) Embolism increases rapidly when soil water potential drops below a threshold value (cavitation) and there is no efficient stomatal limitation of water losses (*Cochard et al., 1992; Lemoine et al., 2002*). (2) The carbon (*C*) starvation hypothesis predicts that reduced *C* assimilation via photosynthesis as a result of drought-induced stomatal closure leads to an imbalance between *C* availability and *C* loss. Over time, if drought persists, such negative *C* balance can lead to an exhaustion of *C* reserves and, ultimately, to death. As beech trees have large stored *C* pools regardless of climate and past stress (*Sala et al., 2010*) the hydraulic failure could be the principal mechanism of the experienced drought induced mortality. Mortality resulting from hydraulic failure is extremely difficult to demonstrate in nature. Lower resistance to cavitation (*Rice et al., 2004; Pratt et al., 2008*) and lethal leaf dehydration (*Kursar et al., 2009*) have been related to increased mortality in the field, rendering hydraulic failure a very plausible mechanism for observed tree mortality under severe, acute drought.

Simulation results of the empirical approach have several uncertainties, concerning mainly the climate model simulations and biotic relationships. The occurrence of drought is random in climate models both in time and space, which could influence considerably the results at a specific location. The spatial uncertainty and temporal randomness of drought occurrence was reduced by using the mean of two runs of the A1B scenario and by using long periods for projections. Projection of precipitation changes in climate models is quite uncertain in the Carpathian Basin (*Christensen et al., 2007*). Minor changes of precipitation trends influence considerable the future vitality of beech, especially close to the xeric limit.

Soil physical properties were not considered as key environmental factor due to its relative spatial homogeneity across the study area. However, the soil water holding capacity of sites could be critical during severe drought periods (*Gärtner et al., 2008*) thus it contributes to the uncertainty of the results. Several attempts has been done to further develope this empirical model to a "bucket model" by including soil properties and physiological factors like rooting depth etc., but the limited available soil information foiled this extension.

Biotic uncertainty results from the limited understanding of the mainly ecological factors. Climate change affects also consumers and pathogens, thus previously unknown pests may appear. The effect of such changes in virulence cannot be predicted. The persistence of forest ecosystems is the main source of uncertainty of distribution modelling, which is supported by the wide phenotypic plasticity of beech proven by comparative field tests (*Mátyás, 2007*). The persistence of beech forests is further supported by planned forest management, which may assist to maintain beech forests in the future (*Mátyás et al., 2009*).

5.3 Comparison of stochastic (BP-ANN) and empirical model

The BP-ANN and the EM model showed considerable regional differences, and as expected the EM predicted more severe dieback for the middle and the end of this century.

There was almost no difference between the two model predictions for 2025. BP-ANN predicted only a very slight (0.1%) reduction in the potential area. As BP-ANN slightly overpredicted the current distribution of beech, this reduction by 2025 did not affect the current stands. Only some subcompartments in Western Zselic and in Heves-Borsod Hills were affected. The EM predicted serious damage on 0.7% and medium damage on 23.1% of the current stands, mainly close to the margins.

The difference between the two approaches got visible only in 2050. The BP-ANN predicted only minor shrinkage (15.0%) in the potential area, but this shrinkage did not affect the current distribution. The EM reported damage on 84.3% of the stands. Serious damage was predicted for Eastern Zselic, Western Zselic, Geresd Hills, Baranya Hills, Outer Somogy, Marcali ridge of hills, East-Zala loess region, the northern part of Göcsej Hills, Vértes, Gerecse, Börzsöny, Heves-Borsod Hills, Visegrád Mountains, Pilis-Buda Mountains. Only forest of Central-Bakony, Southern Bakony, Sopron Mountains, Kőszeg Mountains, Mátra, Central Bükk and Zemplén Mountains remaind healthy.

According to the predictions made with EM to the end of this century almost all beech forest in Hungary showed stability problems (99.9%). The potential area reduced only to 43.2% by the BP-ANN method. This shrinkage affected subcompartments of Outer Somogy, Marcali ridge of hills, East-Zala loess region, Göcsej Hills, Geresd Hills, Heves-Borsod Hills and Lower Kemenshát.

Although the stochastic and empirical models showed temporal and spatial differences, both methods identified the most vulnerable regions like: Heves-Borsod Hills, Eastern Zselic, Western Zselic, Göcsej Hills, East-Zala loess region and Outer Somogy.

5.4 Outlook

The results of this study confirmed that different modelling methods using the same input data could produce highly divergent results. As other authors used different models with different parametrisation, spatial scale, number of predictors and different climate scenarios, thus detailed comparison of the results is limited.

A regional modelling analysis in Hungary, using conditional inference-based regression trees analysis showed already extensive beech decline by 2025, mainly at the xeric limit of the distribution range (*Czúcz et al., 2011*). This analysis was based on long-term climatic means and not on climatic extremes, thus its results were significantly different, since expect of one scenario, 92–99% of present-day zonal beech forests would be outside their optimal bioclimatic niche by 2050. It should be outlined that *Czúcz et al.* (*2011*) used climate means of the 1961-90 period and the A2 scenario for future conditions.

The future distribution pattern of beech was modelled by *Führer et al. (2011*) using the forest aridity index (FAI), based on phenological patterns of growth. The simulation showed similar results to ours; by 2050 large beech areas are not sustained in the Southwest of Hungary, except of a narrow area near the Slovenian border and the high mountainous region in the Northeast.

Future distribution of beech at European scale was explored also by *Kramer et al. (2010)* using a general process-based dynamic vegetation model and a statistical species distribution model. According to the distribution maps using the A2 emission scenarios, climate could become unsuitable for beech by 2050 in Hungary, except the high mountainous regions in the Northeast.

Impacts of climate change on beech was modelled in Europe by *Thuiller et al. (2005)* using the BIOMOD niche-based model. The model was applied using the A1 emission scenario of the IPCC by 2080. Except of the highest mountainous regions beech is not considered to be sustained in Hungary.

6 Summary

6.1 Introduction

A significant drought event emerged between 2000 and 2003 in Southwest of Hungary which was unprecedented in duration and strength since the beginning of the 50's. After this drought event large volume of declining or already dead beech was logged.

Several studies suggest extensive beech dieback (*Berki et al., 2009; Czúcz et al., 2011*) with worsening climatic conditions consequently modelling the vitality response of beech to predicted changes of climate is a critical issue (*Mátyás, 2009*).

For management and conservation issues species distribution models (SDMs) have been extensively used. SDMs connect the species' environmental requirements of the localities where it is currently known to occur but it is not tested whether models that are successful in predicting current distributions are equally powerful in predicting distributions under different climates. Furthermore the multidimensional climatic envelope created by SDMs is often described by long-term means, but long-term climatic means do not express the importance of extreme drought events, which act as triggering effect on growth decline and pests or diseases.

Empirical models (EM) are considered superior for understanding the relationship between climate and the distribution of species. In an EM, the distribution of a species is defined by functions based on ecological response of that species; however ecological data limiting the distribution are not available for most species.

The aim of this study was to develop a consistent method to model potential future distribution of beech (*Fagus sylvatica* L.) near to the xeric limit with respect to the specific ecological and climatic problems of this region.

Most of the species distribution models do not differentiate between the "leading" and "trailing" edge, although the processes are fundamentally different (*Mátyás and Nagy, 2005*). Xeric limits of distribution are determined by climatic aridity, modified by local soil water regime conditions. These limits are more difficult to trace than thermal "upper" limits. This ecologically and climatically specific area has been chosen for the modelling which is largely neglected by European studies (*Mátyás, 2010*).

Beech is considered a climate sensitive species, which is uniquely vulnerable in the region, therefore well suited for modelling. Another advantage is, that compared to other tree species in Hungary it is in a relatively natural condition as it was seldom regenerated artificially and its reproductive material was not subject to commercial relocations (*Mátyás, 2010*).

The following scientific questions were addressed:

1. Which SDM can best describe the present distribution of beech in Hungary?
2. What is the relationship between weather conditions and vitality status of beech?
3. What are the projections for the potential future distribution of beech using SDMs and vitality condition using an EM?

6.2 Materials and methods

First the performance of eight different SDMs (Support vector machine (*SVM*); BioClim; Domain; Generalized linear model (*GLM*); Maximum likelihood classification (*MLC*); Artificial neural network using back-propagation algorithm (*BP-ANN*); Maximum entropy (*Maxent*); Classification Tree (*CTree*)) were evaluated using the ModEco platform (*Guo and Liu, 2010*).

96 different environmental predictor surface maps were used as input, all with a spatial resolution of 0.0083^o (approx. 1x1 km). Although the main environmental data used for the SDMs were climate data (monthly maximum, minimum, mean temperatures; monthly precipitation sums; and a set of 19 climate-derived variables), soil and geomorphological factors were also included as surrogates. Variables showing a correlation >0.80 were considered redundant. Between any two redundant variables, those related to climate extremes were preferred.

For current conditions, the WorldClim database (*Hijmans et al., 2005*) was used. For future simulation the A1B scenario of the "ClimateLimited-areaModelling" (CLM) regional climate model was applied.

Beech occurrence data for the habitat modelling were derived from the Hungarian Forest Inventory database.

The factor importance analysis of the models was carried out based on the Cohen's kappa values. This analysis enabled to rank the predictors.

Overall model performance of SDMs was assessed using cross-validation, the Area Under the Receiver Operator Curve (AUC); Receiver Operating Characteristic (ROC) matrix, and maximum Kappa values. For presence-only data, the above mentioned measures are not applicable therefore the true positive rate (TPR) vs. the factional prediction area (FPA) as a proxy for true positive rate vs. false positive rate and the area under TPR vs. FPA was used.

SDMs have two theoretical assumptions that may not hold in modelling the potential future distribution of beech near the xeric limit.

1. Importance of extreme weather: It is widely accepted in SDMs, that the resulting pattern of overall range limits may well reflect climatic means. This association of range margin and climatic mean may not hold when climatic extremes occur with an increasing frequency (future climate change), or when the fluctuation of weather overrides the tolerance limit of a species (Liebig minimum role). This later addition could be especially important for predicting the trailing edge of a tree species.
2. Equilibrium vs. non-equilibrium: SDMs assume that the modelled species is in equilibrium with its environment. Although this is a required assumption for projecting the model in space, a few critical considerations have been raised in the recent literature. The non-equilibrium consideration is a critical issue in modelling the distribution of invasive or retreating species.

To overcome the above mentioned problems an empirical model (EM) was set up. EMs concentrates in space and time on the specific momentum, when the modelled system is tipped out from its equilibrium state. As a result of the drought between 2000 and 2003 in Southwest of Hungary large volume of declining or already dead beech was logged. Forest regions affected by this beech dieback were chosen as study area for the EM. The meteorological database was set up for the period 1975-2006 using approx. 600 rain gauge stations and 31 temperature stations. Maps were created using the kriging algorithm. The effect of slope and aspect on air temperature was considered by global radiation using the solar radiation analyses tool of ArcGIS. This very attractive trait of the temperature maps allowed me to characterise beech stands even in non-zonal positions.

Sanitary logging information of beech as a proxy of vitality condition was coupled with meteorological data to obtain the vitality response of beech. The annual volume of beech sanitary logging was provided by State Forest Companies (Szombathelyi Erdőgazdaság Zrt., Zalaerdő Zrt.) for each subcompartment of the study area for the period 2000-2008.

The future vitality status of beech to different terms of this century was simulated using the response and the A1B scenario of the CLM regional climate model.

6.3 Results

Results will be discussed through answering the addressed scientific questions.

1. ***Which SDM can best describe the present distribution of beech in Hungary?***

Most of the SDM algorithms performed fair or good by describing the current distribution of beech.

Presence-only methods (*BioClim; Domain; one-class SVM*) showed marked variation in modelling success. Using the ROC score by the accuracy assessment Domain showed the best performance. Domain has predicted very precisely the current distribution of beech, almost all observation point were enclosed in the potential area.

Presence/absence classification methods (*GLM*; *MLC*; *BP-ANN*; *Maxent*; *CTree*) outperformed presence-only models. *CTree and BP-ANN methods performed significantly better than the other models because these models were able to capture non-linear responses and could handle interactions between the variables.*

The breakdown of the accuracy indicated that false negative rates (overprediction) were higher in Mecsek, Göcsej Hills, Lower Őrség, East-Zala loess region, Marcali ridge of hills and Western Zselic. False negatives typically reflect the inability of static models suggesting that beech at its trailing edge is not in equilibrium with the climate.

Except Domain all models predicted larger potential area than the current distribution. The systematic overprediction of the models could be explained mainly by the following factors:

- Human interaction and land use change has resulted a general reduction of the distribution.
- The lack of soil data: the occurrence of beech is often hindered by unfavourable water-air, physical and textural characteristics of the soil.
- Competition and other biotic interactions.
- Extreme events: predictions based on climatic means alone could overestimate ranges when climatic extremes occur with a skewed frequency.

While the presence-only methods performed fair by describing the current distribution of beech all the three methods were unsuited for predicting climate change impacts. Prediction with Domain and Bioclim was only possible when the number of the environmental predictors were strongly reduced.

MLC predicted complete extinction of beech for the whole country for the period 2011-2040. GLM overpredicted the distribution of beech in the near future while MAXENT predicted a considerable dieback even for the near future removing more than 91.6 % of the current beech stands. BP-ANN predicted almost no reduction in the potential area for the period 2011-2040 and a very slight (8.0%) for 2036-2065. A considerable shrinkage (56.8 %) of the potential area was predicted only to the end of this century which results that 45.2% of the current stands will be out of the potential area. Regionally the most serious decrease was predicted for the sub-Mediterranean region in the Southwest.

Among the environmental variables the maximum temperature of May (*Tmax_05*) and the *EQm* appeared repeatedly as the most influential predictor. In addition, maximum temperatures of summer and precipitation of late summer played a significant role in determining the presence of beech.

2. ***What is the relationship between weather conditions and vitality status of beech?***

In the EM first the response function was set up. Originally the predictor selection for the response function was planned to base on the factor importance analyses carried out only within the study area of the EM, but SDMs in these regions (close to xeric limits) clearly failed. Therefore the predictor selection for the response function was based on the factor importance analyses of the SDMs applied for the whole of the country. Based on that, EQ_m has been chosen as environmental predictor in the EM.

Coupling sanitary logging information with the above mentioned bioclimatic index showed an abrupt decline of the vitality condition with worsening climatic conditions. The relationship showed an abrupt change towards drier weather conditions, thus application of a continuous function was rejected. Instead, the range of distribution was divided into three categories (*EQm*<53 with no damage, 53<*EQm*<65 moderate damage and *EQm*>65 serious damage). Simulation results obtained from the EM showed considerable changes in vitality conditions only after 2025. Beech vitality condition is expected to decline significantly by 2050. Serious decline is expected regionally not only at the lower distribution range, but at optimal site conditions. Moderate damage is likely at almost all beech sites, except the mountainous regions approximately above 500-600 m. Beech might not be sustained by the end of the century in most of the country, except above 700-800 m mainly in the Northeast.

3. ***What are the projections for the potential future distribution of beech using SDMs and vitality condition using an EM?***

The BP-ANN and the EM model showed considerable regional differences, and as expected the EM predicted more severe dieback for the middle and the end of this century. There was almost no difference between the two model predictions for 2025. BP-ANN predicted no reduction in the potential area while the EM predicted serious damage on 0.7% and medium damage on 23.1% mainly close to the margins. The difference between the two approaches get visible only in 2050, where BP-ANN predicted only minor shrinkage in the potential area (15.0%), while the EM reported damage on 84.3% of the stands. By the end of this century the EM predicted stability problems on 99.9% of the beech stands, while the potential area according the BP-ANN reduced only to 43.2%.

Regionally the most serious decrease is predicted for the sub-Mediterranean region in the Southwest using BP-ANN, while the EM predicted a spatially more homogeneous and more pronounced vitality loss.

The results have explicitly confirmed the general assumption that beech forests in South-eastern Europe are particularly threatened by climate change. Potential impacts are highest for beech stands at lower elevations. The most endangered regions are South Transdanubia (Western and Eastern Zselic, Heves-Borsod Hills, Outer Somogy, Göcsej Hills and East-Zala loess region).

The results suggest that the range margins of beech in Hungary are formulated by short-term dry periods rather than by long-term climatic means, therefore the application of SDMs, based on the equilibrium assumption is restricted on the xeric limit. Moreover SDMs for predicting current distributions often ‘overfit’ the data and such loss of generality could make them less suitable to predict future distributions.

This is by no means a complete analysis, and important questions remain but results could advance our understanding of the strengths and weaknesses of methods and the differences between them. In conclusion, I believe that progress in using SDMs to predict the effect of climate change on species distributions can be made through a number of complementary approaches, including:

1. evaluating the ability of SDMs to provide accurate estimates of the effect of climate change by comparing them with empirical approaches, as was done in this study;
2. increasing understanding of the drivers of species distributions, and the extent to which these are directly related to individual climatic variables;
3. how responses to climate change are affected by genetic variability and
4. integrating SDM and empirical modelling approaches.

7 Utilization of the results

“Shift” in beech distribution and decline in vitality condition triggered by climate change is predicted to occur very fast. Forest management and conservation strategies will have to be modified in the light of rapid climate change. The results of this work may support the developing of such management and conservation strategies.

7.1 Utilization of the meteorological database

The meteorological and climate database of this work has been used several times for different purposes (*Móricz and Rasztovits, 2007*). The interpolated maps were used by Führer, who developed the “forest aridity index” FAI. *Führer et. al (2011)* characterized the girth-growth of trees (organic matter production) and the different climate categories in forestry practice by the forestry aridity index (FAI) for Hungarian conditions (FAI values for beech: <4.75; hornbeam—oak: 4.75—6.00; sessile oak and Turkey oak: 6.00—7.25; forest-steppe: >7.25).

Later *Berki et al. (2009)* used the same database for determining the lower tolerance limit and predicting the future distribution of beech (see Literature review).

This meteorological database was applied by *Mátyás et al. (2010)* to assess the macroclimatic adaptedness of beech. The aim was to analyse provenance tests of beech situated close to the South-eastern continental limits of the species, in order to develop a response model of adaptation and plasticity of populations on evolutionary-ecological basis, following sudden climatic changes as a result of transplanting.

The database was further utilized for evaluating the provenance and test sites of the international beech provenance network within the COST E52 scientific cooperation ("Evaluation of Beech Genetic Resources for Sustainable Forestry").

The climate database could de used to delineate beech seed zones and to formulate rules for the use of beech reproductive material.

7.2 Utilization of the modelled distribution/vitality conditions results

Although results of species distribution modelling could influence several disciplines, dialog among modellers and modellers and end-users are rare.

Wildlife response to spatial and temporal changes in forest habitat is under intense research. The future vitality condition maps were used by *Katona et al. (2012)* to assess the impact of climate change on the optimal food selection rule of red deer in Hungary. *Náhlik* used in the TÁMOP 4.2.2-08/1-2008-0020 (Forestry, agriculture and technologies of renewable energy generation and the effects of climate change) project the potential future distribution maps of beech to assess the potential effect of future climate change on game damage.

After the serious economical and ecological consequences of the beech decline in the early 2000’s, forest companies showed an increased interest on predicting the possible impacts of future climate change on beech. Within the FaKlim project (“*Beech dieback and climate change in the West-Pannonic region*”) a decision supporting system (DSS) is currently under construction which is fundamentally based on the results of this work. This is web-based assessment and reporting tool that substantively connects current climate change knowledge and forest planning information. The system aims to support mainly forest stakeholders and forest managers by identifying the most vulnerable forests (on subcompartment level) and by utilizing a database of climate change forecasts (the A1B scenario of the CLM regional climate model) and direct ecosystem impacts (future potential growth and dieback).

The preliminary results of the empirical model were included in a collaborative FP7 project proposal in 2011 (FORGER, Towards the Sustainable Management of Forest Genetic Resources in Europe) where the integration of stochastic, empirical and genetic models is aimed.

7.3 Potential utilizations

Modelled distribution/vitality conditions results could be further utilized in several disciplines as input.

The analysis clearly indicated the vulnerable beech regions in Hungary. This could be utilized by nature conservation for selection and maintenance of beech conservation areas.

The decline of vitality conditions of beech and the development of different pests and pathogens was observed during the beech dieback in Hungary. This connection (meteorological variables and the large amount of declining beech trees) offers another modelling option for forest protection.

Beech associations in Hungary offer suitable habitat for several protected plant species. Some of these plants are exclusively connected to the microclimatic conditions of beech forests. This co-occurrence offers the possibility to nature conservation to model and assess the potential future distribution of these protected plant species.

Beech dieback could influence solar energy fluxes with feedbacks to regional climate, alterations in hydrology, changes in groundwater recharge and local carbon pools. Models dealing with the above mentioned disciplines could also utilize the results.

Ecosystem service connected to the presence of beech forest could be also assessed using the results of this work.

I hope that my model comparisons will stimulate more research into further development of more successful methods (integration of stochastic and empirical models), and greater integration among modellers and end-users.

8 Conclusions

The aim of this study was to develop a consistent method to model the potential future distribution of beech (*Fagus sylvatica* L.) near to the xeric limit with respect to the specific ecological and climatic problems of this region. To achieve this eight different stochastic algorithms and an empirical model was compared and evaluated. A novel aspect of my work is the inclusion of a new modelling approach that has had little exposure in previous comparative studies.

Most of the species distribution models performed fair or good by describing the current distribution of beech, but machine learning methods like classification trees and artificial neural networks with backpropagation algorithm generally outperformed established ones.

Six out of the eight methods were unsuited for predicting climate change effects on the future distribution of beech. This confirms that a good model performance in predicting the current distribution does not guarantee success in predicting distribution under different climates. The relative failure of the five methods underlines that predictions for conservation and management issues should be based on multimodel assessments.

Even machine learning methods like artificial neural networks with backpropagation algorithm failed in regions of the xeric limit. The inability of static models suggests that the basic theoretical assumption of species distribution models may not hold at the trailing edge. This means that:

- beech in Hungary at its trailing edge (xeric limit) is not in equilibrium with the climate and
- range margins of beech in Hungary are formulated by short-term dry periods rather than by long-term climatic means.

The factor importance analysis of the species distribution models ranked the maximum temperature of May and the modified Ellenberg Quotient repeatedly as the most influential predictor. In addition, maximum temperatures of summer and precipitation of late summer played a significant role in determining the presence of beech. The ranking suggests that beech is distributed in Hungary mainly in relation to maximum temperatures during spring and secondly are related to precipitation.

In the empirical model - based on the results of the factor analysis - sanitary logging information was coupled with the modified Ellenberg Quotient to obtain the “response function” of beech. The “response function” showed an abrupt decline in the vitality with worsening climatic conditions. Based on “response function” it can be stated that four consecutive extreme dry years with the average modified Ellenberg Quotient value of 65 are enough for mass mortality in beech stands situated near to the xeric limit.

Prediction for 2025 obtained from the empirical model was in agreement with those of the artificial neural networks with backpropagation algorithm, but to the end of the century the empirical model predicted a more serious decline in all regions of Hungary. The result of the comparison suggests that predictions based on climate means are prone to overoptimism.

While results are encouraging, several caveats need consideration. In reality, species distributions may be limited by both biotic and abiotic factors such as species interactions and dispersal limitation, some of which are anthropogenic. Furthermore climate models also add a high level of uncertainty to the predictions.

This is by no means a complete analysis, and important questions remain but results could advance our understanding of the strengths and weaknesses of the evaluated methods and the differences between them. Finally, I would like to stress that modelling can never provide a complete substitute for detailed, ongoing collection of field data.

Collaborative efforts between modellers and users such as forest and conservation managers are rare. I hope that my model comparisons will stimulate more research into further development of more successful methods (integration of stochastic and empirical models), and greater integration among modellers and end-users.

9 Theses

1. All evaluated models (BioClim, Domain, One-Class SVM, Maximum Entropy, Maximum likelihood, Artificial Neural Networks with backpropagation algorithm, Classification Tree) performed “fair” by describing the potential current distribution of beech in Hungary, but only the Artificial Neural Networks with backpropagation algorithm and Classification Trees was suitable for future predictions.
2. The range margins of beech in Hungary are formulated by short-term dry periods rather than by long-term climatic means.
3. Beech in Hungary at its trailing edge (xeric limit) is not in equilibrium with the climate, therefore the application of species distribution models, based on the equilibrium assumption is restricted.
4. Beech is distributed in Hungary mainly in relation to maximum temperatures during spring (maximum temperature of May) and secondly is related to precipitation.
5. Four consecutive extreme dry years with the average modified Ellenberg Quotient (EQ_m) value of 65 are enough for mass mortality in beech stands situated near to the xeric limit.
6. Although the artificial neural networks with backpropagation algorithm and the empirical model showed temporal and spatial differences, both methods identified the same vulnerable areas:

Zselic	(Nyugat-Zselic, Kelet Zselic)
Outer Somogy	(Külső-Somogy)
Heves-Borsod Hills	(Heves-Borsodi-dombság)
Göcsej Hills	(Göcseji-dombság)
East-Zala loess region	(Kelet-Zalai-löszvidék)

10 Acknowledgements

I would like to thank my supervisor, *Prof. Dr Csaba Mátyás* for the patient guidance, encouragement and advice he has provided throughout my time as his student. I have been extremely lucky to have a supervisor like him. His careful editing contributed enormously to the production of this thesis.

In particular I would like to thank *Dr. Norbert Móricz, Dr. Imre Berki* for the suggestions made during my work. I also would like to thank all the members of the Institute of Environmental and Earth Sciences who helped me, especially *to Dr. Borbála Gálos, Dr. Péter Vig* and to *Attila Eredics*.

I am grateful to *Prof. Dr. Ferenc Lakatos* and to *Dr. Sándor Szalai* for the useful comments.

I would like to express my gratitude to *Dr. Tibor Szép* and *Zoltán Góber* for providing sanitary logging data for this exciting analysis.

I must express my gratitude to Judit, my wife, for her continued support and encouragement.

I’m deeply grateful to my mother, father and sisters who experienced all of the ups and downs of my research and supported me during the “hard times”.

11 References

AGROTOPO (2002): AGROTOPO database of RISSAC, HAS, Budapest.

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008): Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications, 1: 95-111.

Allen CD, Macalady A, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Gonzales P, Hogg T, Rigling A, Breshears DD, Fensham R, Zhang Z, Kitzberger T, Lim J-H, Castro J, Allard G, Running SW, Semerci A, Cobb N (2010): A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management, 259: 660-684.

Annan J, Hargreaves J (2007): Efficient estimation and ensemble generation in climate modelling. Philisophical Transactions of the Royal Society, 365 (1857): 2077-2088.

Araújo MB, Luoto M (2007): The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography, 16: 743-753.

Araújo MB, Pearson RG (2005): Equilibrium of species' distributions with climate. Ecography, 28: 693–695.

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005): Validation of species-climate impact models under climate change. Global Change Biology, 11: 1504-1513.

Araújo MB, Williams PH (2000): Selecting areas for species persistence using occurrence data. Biological Conservation 96: 331-45.

Attorre F, Francesconi F, Scarnati L, De Sanctis M, Alfò M, Bruno F (2008): Predicting the effect of climate change on tree species abundance and distribution at a regional scale iForest : Biogeosciences and Forestry, 1: 132-139.

Austin MP (1987): Models for the analysis of species' response to environmental gradients. Vegetatio, 69: 35-45.

Austin MP (2002): Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling, 157: 101-118.

Austin MP, Smith TM (1989): A new model for the continuum concept. Vegetatio, 83: 35-47.

Backes K, Leuschner Ch (2000): Leaf water relations of competitive *Fagus sylvatica* and *Quercus petraea* trees during 4 years differing in soil drought. Canadian Journal of Forest Research, 30: 335-346.

Badeau V, DLpouey J, Cluzeau C, Drapier J, Bas C (2005): Modélisation et cartographie de l’aire climatique potentielle des grandes essences forestières françaises". http://www.inra.fr/la_science_et_vous/dossiers_scientifiques/changement_climatique/evaluer_predire_les_impacts/rechauffement_climatique_et_foret [online 25 October 2011]

Bahn V, McGill BJ (2007): Can niche-based distribution models outperform spatial interpolation? Global Ecology and Biogeography, 16: 733–742.

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002): Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Global Change Biology, 8: 390–407.

Bartholy J, Pongrácz R (2007): Regional analysis of extreme temperature and precipitation indices. Global and Planetary Change, 57: 83–95.

Bartholy J, Pongrácz R, Gelybó Gy (2007): Regional climate change expected in Hungary for 2071-2100. Applied Ecology and Environmental Research, 5: 1-17.

Bergh J, Freeman M, Sigurdsson B, Kellomaki S, Laitinen K, Niinisto S, Peltola H, Linder S (2003): Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. Forest Ecology and Management, 183: 327-340.

Berki I, Rasztovits E, Móricz N, Mátyás Cs (2009): Determination of the drought tolerance limit of beech forests and forecasting their future distribution in Hungary. Cereal Research Communications, 37: 613-616.

Bigler C, Braker OU, Bugmann H, Dobbertin M, Rigling A (2006): Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems, 9: 330–343.

Bohn U (1992): Zum internationalen Projekt einer Karte der natürlichen Vegetation Europas im Maßstab 1:2,5 Mio. Konzept, Inhalt Erarbeitung, kartographische Darstellung und Anwendungsmöglichkeiten. Natur und Landschaft, 67: 476-480.

Bonan GB (2008): Forests and climate change: Forcings, Feedbacks and the climate benefits of forests, Science, 320: 1444-1449.

Bony S, Colman R, Kattsov VM, Allan RP, Bretherton Cs, Dufresne JL, Hall A, Hallegatte S, Holland MM, Ingram W, Randall DA, Soden DJ, Tselioudis G, Webb MJ (2006): How well do we understand and evaluate climate change feedback processes? Journal of Climate, 19: 3445-3482.

Boone CK, Aukema BH, Bohlmann J, Carroll AL, Raffa KF (2011): Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. Canadian Journal of Forest Research, 41: 1174–1188.

Borhidi A (2003): Magyarország növénytársulásai [Forest associations of Hungary - in Hungarian]. Akadémiai Kiadó, Budapest, 610 pp.

Box EO (1981): Predicting physiognomic vegetation types with climate variables. Vegetatio, 45: 127–139.

Bréda N, Huc R, Granier A, Dreyer E (2006): Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science, 63: 625-644.

Brown JH, Stevens GC, Kaufman DM (1996): The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology, Evolution, and Systematics, 27: 597–623.

Budyko MI (1974): Climate and life. Academic Press, Orlando, FL, USA.

Bugmann H (2001). A review of forest gap models. Climatic Change, 51: 259–305.

Busby JR (1986): "A biogeoclimatic analysis of *Nothofagus cunninghamii* (hook.) oerst. In southeastern Australia", Australian Journal of Ecology, 11: 1-7.

Busby JR (1991): BIOCLIM – a bioclimate analysis and prediction system. In: Nature Conservation: Cost Effective Biological Surveys and Data Analysis (eds. Margules, CR, Austin MP). CSIRO, Melbourne, pp. 64–68.

Carpenter G, Gillison AN, Winter J (1993): Domain: a fexible modelling procedure for mapping potential distributions of plants and animals. Biodiversity Conservation, 2: 667-680.

Cech T, Perny LB (2000): Kiefernsterben in Tirol. Forstschutz-aktuell, 22: 12–15.

Cech T, Tomiczek C (1996): Zum Kiefernsterben in Niederoösterreich. Forstschutzaktuell, 17/18: 12–13.

Chapin III, Randerson FS, McGuire AD, Foley JA, Field CB (2008): Changing feedbacks in the climate-biosphere system. Frontiers in Ecology and the Environment, 6: 313–320.

Chow GC (1960): Tests of Equality between Sets of Coefficients in Two Linear Regressions.

Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon WT, Laprise R, Magana Rueda V, Mearns L, Menéndez CG, Räisänen J, Rinke A, Sarr A, Whetton P (2007): Regional climate projections. In: Solomon, S., et al. (eds.), Climate Change 2007: The Physical Science Basis. Contributions of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambride, United Kingdom/New York, NY.

Chuine I, Cambon G, Comtois P (2000): Scaling phenology from the local to the regional levels: advances from speciesspecific phenological models. Global Change Biology, 6: 1-11.

Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grunwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005): Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature, 437: 529-533.

Cochard H, Cruiziat P, Tyree MT (1992): Use positive pressures to establish vulnerability curves, Plant Physiology, 100: 205-209.

Cochard H, Lemoine D, Ameglio T, Granier A (2001): Mechanisms of xylem recovery from winter embolism in *Fagus sylvatica*. Tree Physiology, 21: 27-33.

Comps B, Mátyás Cs, Letouzey J, Geburek T (1998): Genetic variation in beech populations (*Fagus sylvatica* L.) along the alpine chain and in the Hungarian basin. Forest Genetics, 5(1): 1–9.

Crawford RMM (2000): Ecological hazards of oceanic environments. Tansley Review No. 114. New Phytologist, 147: 257-281.

Crawford RMM (2008): Plants at the margin. Ecological limits and climate change. Cambridge University Press. 494 pp.

Cressie NAC (1991): Statistics for Spatial Data, John Wiley and Sons, Inc., New York, 900 pp.

Csóka Gy (1997): Increased insect damage in Hungarian forests under drought impact. Biologia, Bratislava, 52(2): 1-4.

Csóka Gy, Koltay A, Hirka A, Janik G (2007): Az aszályosság hatása kocsánytalan tölgyeseink és bükköseink egészségi állapotára [Influence of drought on health of sessile oak and beech stand in Hungary - in Hungarian with English summary]. In: Mátyás, Cs. – Vig, P. (eds.): Erdő és Klíma V. NyugatMagyarországi Egyetem, Sopron, 229-240.

Czúcz B, Gálhidy L, Mátyás C (2011): Present and forecasted xeric climatic limits of beech and sessile oak distribution at low altitudes in Central Europe. Annals of Forest Science, 68 (1): 99-108.

De Martonne E (1942): Nouvelle carte mondiale de l'indice d'aridite. Annales de Geographie, 51: 242-250.

De'Ath G, Fabricius KE (2000): Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology, 81: 3178–92.

Degen B, Gregorius HR, Scholz F (1996): ECO-GENE, a model for simulation studies on the spatial and temporal dynamics of genetic structures of tree populations. Silvae Genetica, 45: 323–329.

Dingman SL, Seely-Reynolds DM, Reynolds RC (1988): Application of kriging to estimating mean annual precipitation in a region of orographic influences. Water Resources Bulletin, 24: 329-339.

Dobbertin M, Mayer P, Wohlgemuth T, Feldmeyer-Christe E, Graf U, Zimmermann NE, Rigling A (2005). The decline of *Pinus sylvestris* L. forests in the swiss Rhone Valley — a result of drought stress? Phyton-Annales Rei Botanicae, 45: 153–156.

Dobbertin M, Rigling A (2006): Pine mistletoe (*Viscum album* ssp. austriacum) contributes to Scots pine (*Pinus sylvestris*) mortality in the Rhone valley of Switzerland. Forest Pathology, 36: 309–322.

Dobbertin M, Wermelinger B, Bigler C, Buergi M, Carron M, Forster B, Gimmi U, Rigling A (2007): Linking increasing drought stress to Scots pine mortality and bark beetle infestations. The Scientific World Journal, 7: 231–239.

Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J,Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilso R (2007): Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography, 30: 609-628.

Drüszler Á, Csirmaz K, Vig P, Mika J (2009): A földhasználat változásainak hatása az éghajlatra és az időjárásra [Effect of land use change on climate and weather - in Hungarian]. Természet Világa, 140: 521-523.

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000): Building roots in a changing environment: implications for root longevity. New Phytologist, 147: 33-42.

Elith J, Burgman MA (2002): Predictions and their validation: rare plants in the Central Highlands, Victoria, Australia. In: Predicting Species Occurrences: Issues of Accuracy and Scale (eds Scott JM, Heglund PJ, Morrison ML, Raphael MG, Wall WA, Samson FB). Island Press, Covelo, CA, pp. 303–314.

Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick J, Lehmann A, Li J, Lohmann LG, Loiselle B, Manion G, Moritz C, Nakamura M, Nakazawa Y, McC. Overton J, Peterson AT, Phillips S, Richardson K, Scachetti-Pereira R, Schapire R, Soberon J, Williams S, Wisz M, Zimmerman N (2006): Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29: 129-151.

Ellenberg H (1988): Vegetation ecology of central Europe. 4th edition. Cambridge University Press, New York, NY. 731 pp.

Ellenberg H (1996): Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart.

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W (1992): Zeigerwerte der Pflanzen in Mitteleuropa. 3. edition. Goltze, Göttingen (Scripta Geobotanica 18)

Felicisimo AM, Frances E, Fernandez JM, Gondalez-Diez A, Varas J (2002): "Modeling the potential distribution of forests with a gis", Photogrammetric Engineering and Remote Sensing, 68: 455-462.

Ferrier S, Drielsma M, Manion G, Watson G (2002): Extended statistical approaches to modelling spatial pattern in biodiversity in north-east New South Wales. II. Community level modelling. Biodiversity and Conservation, 11: 2309–2338.

Ferrier S, Guisan A (2006): Spatial modelling of biodiversity at the community level. Journal of Applied Ecology, 43: 393-40.

Fielding AH, JF Bell (1997): A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation, 24: 38-49.

Fonseca MS, Whitfield PE, Kelly NM, Bell SS (2002): Statistical modeling of seagrass landscape pattern and associated ecological attributes in relation to hydrodynamic gradients, Ecological Applications, 12: 218-237.

Forman G (2003): An extensive empirical study of feature selection metrics for text classification. Journal of Machine Learning Resources, 3: 1289-1305.

Forster B, Meier F, Braendli UB (2008): Deutlicher Rückgang der Fichten im Mittelland. Vorratsabbau - auch durch Sturm und Kafer. Wald Holz, 89 (3): 52–54.

Fotelli MN, Rienks M, Rennenberg H, Geßler A (2004): Climate and forest management affect 15N-uptake, N balance and biomass of European beech seedlings. Trees - Structure and Function, 18: 157-166.

Franke J, Köstner B (2007): Effects of recent climate trends on the distribution of potential natural vegetation in Central Germany. International Journal of Biometeorology, 52: 139-147.

Frech A (2006): Walddynamik in Mischwäldern des Nationalparks Hainich. Untersuchung der Mechanismen und Prognose der Waldentwicklung. PhD thesis, University of Göttingen. http://webdoc.sub.gwdg.de/diss/2006/frech/frech.pdf [online 25 October 2011]

French Forest Health Department (Département Sante´ des Foréts), 1998–1999, 2003–2008 Annual Reports. Union Européenne, Aix en Provence, 236 pp.

Frescino TS, Edwards TC, Jr Moisen GG (2001): Modeling spatially explicit forest structural attributes using Generalized Additive Models. Journal of Vegetation Science, 12: 15–26.

Friedlingstein P, Cox P, Betts R, Bopp L, Von Bloh W, Brovkin V, Cadule P, Doney S, Eby M, Fung I, Bala G, John J, Jones C, Joos F, Kato T, Kawamiya M, Knorr W, Lindsay K, Matthews HD, Raddatz T, Rayner P, Reick C, Roeckner E, Schnitzler KG, Schnur R, Strassmann K, Weaver AJ, Yoshikawa C, Zeng N (2006): Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison. Journal of Climate, 19: 3337-3353.

Friedman JH (1991). Multivariate adaptive regression splines. Annals of Statistics, 19: 1–67.

Fu P, Rich PM (2000): The Solar Analyst 1.0 Manual. Helios Environmental Modelling Institute (HEMI), USA.

Führer E (1998): Oak decline in central Europe: A synopsis of hypotheses. Proceedings: population dynamics, impacts, and integrated management of forest defoliating insects. ML McManus and AM Liebhold (eds). USDA Forest Service General Technical Report NE., 247: 7-24.

Führer E, Horváth L, Jagodics A, Machon A, Szabados I (2011): Application of a new aridity index in Hungarian forestry practice. Időjárás, 115 (3): 205-216.

Führer E, Mátyás Cs, Csóka Gy, Lakatos F, Bordács S, Nagy L, Rasztovits E (2010): Current status of European beech (*Fagus sylvatica* L.) genetic resources in Hungary. Communicationes Instituti Forestalis Bohemicae, 25: 152-163.

Gálos B (2010): Analyses of forest-climate interactions, applying the regional climate model, REMO, PhD dissertation, NyME, Sopron.

Gálos B, Lorenz Ph, Jacob D (2007): Will dry events occur more often in Hungary in the future? Environmental Research Letters, 2 034006 (9 pp.)

Gan JB (2004): Risk and damage of southern pine beetle outbreaks under global climate change. Forest Ecology and Management, 191: 61–71.

Garen DG, Johnson GL, Hanson CL (1994): Mean areal precipitation for daily hydrologic modeling in mountainous regions. Water Resources Bulletin, 30(3): 483-491.

Gärtner S, Reif A, Xystrakis F, Sayer U, Bendagha N, Matzarakis A (2008): The drought tolerance limit of *Fagus sylvatica* forests on limestone in southwestern Germany. Journal of Vegetation Science, 19: 757-768.

Geßler A, Schrempp S, Matzarakis A, Mayer H, Rennenberg H, Adams MA (2001): Radiation modifies the effect of water availability on the carbon isotope composition of beech (*Fagus sylvatica*). New Phytologist, 150: 653-664.

Góber Z (2005): A Zalaerdő Rt. kezelésében lévő területeken 2004-ben végbement erdőpusztulás értékelése [Forest mortality in 2004 in Zalaerdő State Forest Company - in Hungarian] Erdészeti Lapok CXL.: 156-159.

Gömöry D (2009): Geographic patterns in the reactions of beech provenances to transfer. Report for COST E52 meeting, Thessaloniki, Greece (manuscript) 8 pp.

Granier A, Biron P, Lemoine D (2000): Water balance, transpiration and canopy conductance in two beech stands. Agricultural and Forest Meteorology, 100: 291-308.

Grinnell J (1917): Field tests of theories concerning distributional control. The American Naturalist, 51 (602): 115–12.

Guisan A, Edwards T, Hasti T (2002): Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling, 157: 89-100.

Guisan A, Theurillat JP, Kienast F (1998): Predicting the potential distribution of plant species in an Alpine environment. Journal of Vegetation Science, 9: 65–74.

Guisan A, Thuiller W (2005): Predicting species distribution: offering more than simple habitat models. Ecology Letters, 8: 993–1009.

Guisan A, Zimmermann NE (2000): Predictive habitat distribution models in ecology. Ecolocical Modeling, 135: 147-186.

Guo Q, Kelly M, Graham C (2005): Support vector machines for predicting distribution of Sudden Oak Death in California. Ecological Modeling, 182: 75-90.

Guo Q, Liu Y (2010): ModEco: An integrated software package for ecological niche modelling. Ecography, 33: 637-642.

Halász G (ed.) (2006): Magyarország erdészeti tájai [Forest regions of Hungary - in Hungarian]. Állami Erdészeti Szolgálat, Budapest. 154 pp.

Hampe A, Petit R (2005): Conserving biodiversity under climate change: the rear end matters. Ecological Letters, 8: 461-467.

Hannah L, Midgley GF, Hughes G, Bomhard B (2005): The view from the Cape: extinction risk, protected areas, and climate change. Bioscience, 55: 231–242.

Hannah L, Midgley GF, Millar D (2002): Climate change-integrated conservation strategies. Global Ecology and Biogeography, 11: 485-495.

Hastie TJ, Tibshirani R (1990): Generalized additive models. Chapman and Hall, London, UK.

Hay LE, Wilby RL, Leavesley GH (2000): A comparison of delta change and downscaled GCM scenarios for three mountainous basins in the United States, Journal of the American Water Resources Association, 36: 387-398.

Hegerl GC, Zwiers FW, Braconnot P, Gillett NP, Luo C, Marengo JA, Nicholls N, Penner JE, Stott PA (2007): Understanding and attributing climate change. InClimate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller), pp. 663–745. Cambridge, UK: Cambridge University Press.

Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006): Methods and uncertainties in bioclimatic envelope modeling under climate change. Progress in Physical Geography, 30: 751–777.

Heikkinen RK, Luoto M, Virkkala R, Pearson RG, Korber JH (2007): Biotic interactions improve prediction of boreal bird distributions at macro-scales. Global Ecology and Biogeography, 16: 754-763.

Hevesi JA, Istok JD, Flint AL (1992): Precipitation estimation in mountainous terrain using multivariate geostatistics. Part I: Structural analysis. Journal of Applied Meteorology and Climatology, 31: 661-676.

Hickler T, Smith B, Sykes MT, Davis M, Sugita S, Walker K (2004): Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA. Ecology, 85: 519–530.

Higgins SI, Richardson DM (1999): Predicting plant migration rate in a changing World: the role of longdistance dispersal. The American Naturalist, 153: 464–475.

Hijmans RJ (2003): The effect of climate change on global potato production, American Journal of Potato Research, 80:271-280

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005): Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25: 1965/1978.

Hijmans RJ, Cruz M, Rojas E, Guarino L (2001): DIVA-GIS, version 1.4. A geographic information system for the management and analysis of genetic resources data. Manual. International Potato Center and International Plant Genetic Resources Institute, Lima, Peru.

Hijmans RJ, Graham CH (2006): The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology, 12: 2272–2281.

Hirzel AH, Hausser J, Chessel D, Perrin N (2002): Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology, 83 (7): 2027–2036.

Hogg EH, Brandt JP, Michaellian M (2008): Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 38: 1373-1384.

Horner GJ, Baker PJ, MacNally R, Cunningham SC, Thomson JR, Hamilton F (2009): Mortality of developing floodplain forests subjected to a drying climate and water extraction. Global Change Biology, 15: 2176–2186.

Horvat I, Glavac V, Ellenberg H (1974): Vegetation Südosteuropas. Fischer, Stuttgart. 768 pp.

Huntley B, Bartlein PJ, Prentice IC (1989): Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. Journal of Biogeography, 16: 551–560.

Huntley B, Berry PM, Cramer W, McDonald AP (1995): Modelling present and potential future ranges of some European higher plants using climate response surfaces. Journal of Biogeography, 22: 967-1001.

Hutchinson MF (1957): Cold Spring Harbour Symposia on Quantative. Biology, 22: 415–427.

Huxman TE, Wilcox BP, Breshears DD, Scott R, Snyder K, Small EA, Hultine K, Pockman W, Jackson RB (2005): Woody plant encroachment and the water cycle: an ecohydrological framework. Ecology, 86: 308–319.

Igmandy Z (1987): Die Welkeepidemie von *Quercus petraea* (Matt.) Lieb. in Ungarn (1978 bis 1986). Österreichische Forstzeitung, 98: 48-50.

IPCC (2007): Summary for Policymakers. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H. L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Isaaks EH, Srivastava RM (1989): An Introduction to Applied Geostatistics, Oxford University Press, New York, 561 pp.

Iversen J (1973): The Development of Denmark’s Nature since the Last Glacial. Danmarks Geologiske Undersøgelse, V. Række, Nr. 7-C, 1–126.

Jahn G (1991): Temperate deciduous forests of Europe. Ecosystems of the world 7. Temperate deciduous forests (ed. by Röhrig E, Ulrich B), Elsevier London, pp. 377–502.

Jeltsch F, Moloney KA, Schurr FM, Ko¨chy M, Schwager M (2008): The state of plant population modelling in light of environmental change. Perspectives in Plant Ecology, Evolution and Systematics, 9: 171–190.

Jones C, Lowe J, Liddicoat S, Betts R (2009): Committed terrestrial ecosystem changes due to climate change. Nature GeoScience, 2: 484–487.

Jump AS, Hunt JM, Penuelas J (2006): Rapid climate change related growth decline at the southern edge of *Fagus sylvatica*. Global Change Biology, 12: 1-12.

Jump AS, Mátyás C, Penuelas J (2009): The altitude-for-latitude disparity in the range retractions of woody species. Trends in Ecology and Evolution, 24: 694–701.

Kauhanen H, Wallenius T, Kuuluvainen T, Aakala T, Mikkola K (2008): Extensive mortality of spruce forests in Arkhangelsk Region: satellite image analysis. International Conference ‘‘Adaptation of Forests and Forest Management to Changing Climate with Emphasis on Forest Health: A Review of Science, Policies, and Practices’’, Umea, Sweden, FAO/IUFRO, 25–28 August 2008.

Kearney M, Porter WP (2004): Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. Ecology, 85: 3119-3131.

Kelly NM (2002): Monitoring sudden oak death in california using high-resolution imagery. In: pp. 799-810. USDA-Forest Service.

Klos RJ, Wang GG, Bauerle WL, Rieck JR (2009): Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. Ecological Applications, 19: 699–708.

Knutti R, Allen MR, Friedlingstein P, Gregory JM, Hegerl GC, Meehl GA, Meinshausen M, Murphy M, Plattner GK, Raper SCB, Stocker TF, Stott PA, Teng H, Wigley TML (2008): A review of uncertainties in global temperature projections over the twenty-first century. Journal of Climate, 21: 2651–2663.

Kolozs L. (ed.) (2009): Erdővédelmi Mérő- és Megfigyelő Rendszer 1998-2008 [Forest Measuring and Monitoring System 1988-2008 - in Hungarian]. pp. 33-36. MGSZH, Központi Erdészeti Igazgatóság, Budapest. ISBN 978-963-06-8245-9.

Köppen W (1918): Klassifikation der Klimate nach Temperatur, Niederschlag und Jahresablauf (Classification of climates according to temperature, precipitation and seasonal cycle). Petermanns Geographische Mitteilungen, 64: 193-203, 243-248.

Körner C, Sarris D, Christodoulakis D (2005): Long-term increase in climatic dryness in the East-Mediterranean as evidenced for the island of Samos. Regional Environmental Change Journal 5: 27–36.

Kotroczó Zs, Krakomperger Zs, Koncz G, Papp M, Bowden RD, Tóth JA (2007): A Síkfőkúti cseres-tölgyes fafaj összetételének és struktúrájának hosszútávú változása [Long-term structural and species change in the Síkfőkút project – in Hungarian). Természetvédelmi Közlemények, 13: 93-100.

Kramer K, Buiteveld J, Forstreuter M, T Geburek, S Leonardi, P Menozzi, F Povillone, MJ Schelhaas, E Teissier du Cros, GG Vendramin, van der Werf DC (2008): Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech. Ecological Modelling, 216: 333–353.

Kramer K, Degen B, Buschbom J, Hickler T, Thuiller W, Sykes M, De Winter W (2010): Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change – Range, abundance, genetic diversity and adaptive response. Forest Ecology and Management, 259: 2213–2222.

Krisztián K, Szemethy L, Kiss M, Rasztovits E, Bleier N, Székely J, Nyeste M, Kovács V, Terhes A, Fodor Á, Olajos T (2012): Climate adaptation to ungulate browsing impact in the Hungarian even-aged forests, Biodiversity and Conservation, under review.

Kursar TA, Engelbrecht BMJ, Burke A, Tyree MT, El Omaru B, Giraldo JP (2009): Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. Functional Ecology, 23: 93-102.

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L (2008): Mountain pine beetle and forest carbon feedback to climate change. Nature, 452: 987-990.

Lahti T, Lampinen R (1999): From dot maps to bitmaps—Atlas Florae Europaeae -goes digital. Acta Botanica Fennica, 5–9.

Lakatos F (1997): Feromonos szúcsapdák alkalmazhatósága az erdészeti gyakorlatban. [Applicability of pheromon baited traps in the forest practice – in Hungarian] Növényvédelem. 33 (4): 165-172.

Lakatos F (2006): Fenyőállományokban végrehajtott egészségügyi termelések szerepe védett és/vagy veszélyztetett fában és kéregben költő bogárfajok esetén (Coleoptera) [The effect of sanitary cuttings in coniferous stands on bark and xylem breeding beetles (Coleoptera) - in Hungarian with English summary]. Természetvédelmi Közlemények, 12:123-131.

Lakatos F, Molnár M (2009): Mass mortality of beech on Southwest Hungary. Acta Silvatica et Lignaria Hungarica, 5: 75-82.

Landmann G, Dreyer E (Eds.) (2006): Impacts of drought and heat on forest. Synthesis of available knowledge, with emphasis on the 2003 event in Europe. Annals of Forest Science, 3 (6): 567–652.

Latimer AM, Wu SS, Gelfand AE, Silander JA (2006): Building statistical models to analyze species distributions, Ecological Applications, 16: 33-50.

Lebourgeois F, Bréda N, Ulrich E, Granier A (2005): Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). Trees-Structure and Function, 19: 385-401.

Lehmann A, Overton JM, Leathwick JR (2002): GRASP: generalized regression analysis and spatial prediction. Ecological Modeling, 157: 189–207.

Lemoine D, Jacquemin S, Granier A (2002): Beech (*Fagus sylvatica* L.) branches show acclimation of xylem anatomy and hydraulic properties to increased light after thinning. Annals of Forest Science, 59: 761-766.

Leskó K (1995): Az ormánsági kocsányos tölgyesek és a mecseki bükkösök egészségi állapota Az erdők egészségi állapotának változása. [Healt condition of oak and beech forest in Mecsek and Ormánság, The change of the health condition of forest – in Hungarian]. MTA Erdészeti Bizottság, Budapest, pp. 181-187.

Leuschner Ch, Voss S, Foetzki A, Clases Y (2006): Variation in leaf area index and stand leaf mass of European beech across gradients of soil acidity and precipitation. Plant Ecology, 186: 247-258.

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolstrom M, Lexer MJ, Marchetti M (2010): Climate change impacts adaptive capacity and vulnerability of European forest ecosystems. Forest Ecology Management, 259 (4): 698-709.

Livingston SA, Todd CS, Krohn WB, Owen RB (1990): Habitat models for nesting bald eagles in maine, Journal of Widlife Management, 54: 644-665.

Lloret F, Siscart D, Dalmases C (2004): Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). Global Change Biology, 10: 2092–2099.

Magri D, Vendramin GG, Comps B, Dupanloup I, Geburek T, Gömöry D, Latalowa M, Litt T, Paule L, Roure JM, Tantau I, vander Knaap WO, Petit RJ, deBeaulieu JL (2006): A new scenario for the Quaternary history of European beech populations: paleobotanical evidence and genetic consequences. New Phytologist, 171: 199–221.

Majer A (1968): Magyarország erőtársulásai [Forest associations of Hungary - in Hungarian]. Budapest, Akadémiai Kiadó: 515 pp.

Majer A (1980): A Bakony tiszafása [The yew forest of the Bakony - in Hungarian]. Budapest, Akadémiai Kiadó: 373 pp.

Malanson GP, Westman WE, Yan YL (1992): Realized versus fundamental niche functions in a model of chaparral response to climatic change. Ecological Modelling, 64: 261-277.

Manel S, Dias JM, Ormerod S (1999): Comparing discriminant analysis, neural networks and logistic regression for predicting species distribution: a case study with a Himalayan river bird. Ecological Modelling, 120: 337–47.

Manion PD (1991): Tree Disease Concepts, 2nd ed. Prentice-Hall Inc., Upper Saddle River, NJ, 416 pp.

Martínez-Meyer E, Peterson AT (2006): Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. Journal of Biogeography, 33: 1779–1789.

Martinez-Vilalta J, Pinol J (2002): Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. Forest Ecology and Management, 161: 247–256.

Mastrorillo S, Lek S, Dauba F, Belaud A (1997): The use of artificial neural networks to predict the presence of smallbodied fish in a river. Freshwater Biology, 38: 237–246.

Mátyás Cs (2006): Migratory, genetic and phenetic response potential of forest tree populations facing climate change. Acta Silvatica et Ligniaria Hungarica, 2: 33-46.

Mátyás Cs (2007): What do field trials tell about the future use of forest reproductive material? In: Koskela J, Buck A, Teissier du Cros E (eds.): Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, pp. 53-69.

Mátyás Cs (2009): Ecological challenges of climate change in Europe's continental, drought-threatened Southeast. In: P Y Groisman, S V Ivanov Regional aspects of climate-terrestrial-hydrologic interactions in non-boreal Eastern Europe. Berlin: Springer-Verlag, 2009. pp. 35-46.

Mátyás Cs (2010): Forecasts needed for retreating forests (Opinion). Nature, 464:(1271).

Mátyás Cs, Berki I, Borovics A, Csóka Gy, Eredics A, Führer E, Gálos B, Jáger L, Lakatos F, Móricz N, Palócz-Andresen M, Rasztovits E, Tóth J A, Vig P (2009): Country report Hungary, COST ECHOES July 2009, COST FP0703 action – ECHOES: Expected Climate Change and Options for European Silviculture.

Mátyás Cs, Nagy L (2005): Genetic potential of plastic response to climate change.. In: M. Konnert (editor): Tagungsberichte, Forum Genetik und Wald 2004, Bavarian Centre for Forest Reproductive Material, Teisendorf, pp. 55–69.

Mátyás Cs, Nagy L, Ujvári-Jármay É (2008): Genetic background of response of trees to aridification at the xeric forest limit and consequences for bioclimatic modelling. In: Strelcova K, Mátyás Cs, Kleidon A (eds.) Bioclimatology and natural hazards. Springer Verlag, Berlin pp. 179-196.

Mátyás CS, Vendramin GG, Fady B (2009): Forests at the limit: evolutionary-genetic consequences of environmental changes at the receding (xeric) edge of distribution. Annals of Forest Science, 66: 800–80.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Yepez EA (2008): Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb? New Phytologist, 178, 719–739

McDowell NG (2011): Mechanisms linking drought, hydraulics, carbon metabolism, and mortality. Plant Physiology, 155: 1051–1059.

McGregor JL (1997): Regional climate modelling. Meteorology and Atmospheric Physics, 63: 105-117.

Meehl GA, Stocker TF (2007): Global climate projections. In Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller), Cambridge, UK: Cambridge University Press. pp. 747–845.

Meier ES, Thomas C Edwards Jr, Felix Kienast, Matthias Dobbertin, Niklaus E Zimmermann (2010): Co-occurrence patterns of trees along macroclimatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. Journal of Biogeography, 38: 371-382.

Mészáros I, Veres Sz, Kanalas P, Oláh V, Szőllősi E, Sárvári É, Lévai É, Lakatos G (2007): Leaf growth and photosynthetic performance of two co-existing oak species in contrasting growing seasons. Acta Silvatica et Ligniaria Hungarica, 3: 7-20.

Midgley GF, Hannah L, Millar D, Thuiller W, Booth A (2003): Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic region. Biological Conservation, 112: 87–97.

Mika J (1988): A globális felmelegedés regionális sajátosságai a Kárpát-medencében. [Regional characteristic of the global warming in the Carpathian-Basin – in Hungarian] Időjárás, 95: 265-278.

Mika J (2007): Új eredmények és összevetések a klímaváltozás hazai sajátosságairól [New results and comparsions of climate change science – in Hungarian with English summary]. In: Mátyás Cs., Vig P. (szerk.) Erdő és klima V., Sopron, pp. 13-29.

Minerbi S (1993): Wie gesund sind unsere Wälder? 10. Bericht über den Zustand der Wälder in Südtirol. Agrar- und Forstbericht, Autonome Provinz Bozen, Assessorate für Land-und Forstwirtschaft, 40 pp.

Mladenoff DJ, Sickley TA, Haight RG, Wydeven AP (1995): A regional landscape analysis and prediction of favorable grey wolf habitat in the northern great lakes region, Conservation Biology, 9: 279-294.

Moisen GG, Frescino TS (2002): Comparing five modelling techniques for predicting forest characteristics. Ecological Modelling, 157: 209–225.

Molnár M, Brück-Dyckhoff C, Petercord R, Lakatos F (2010): A zöld karcsúdíszbogár (*Agrilus viridis* L.) szerepe a bükkösök pusztulásában [The role of Agrilus viridis in the mass mortality of beech – in Hungarian]. Növényvédelem, 46 (11): 522-528.

Móricz N (2010): Water Balance Study of a Groundwater-dependent Oak Forest. Acta Sylvatica and Lignaria Hungarica, 6: 49-66.

Móricz N, Rasztovits E (2007): Éves csapadék és hőmérséklet térképek erdészeti ökológiai és genetikai kutatásokhoz. [Annual precipitation and temperature maps for ecological and enetic research - in Hungarian with English summary]. In: Mátyás Cs, Vig P (eds.): Erdő és klíma V., Sopron, pp. 145-153.

Munoz MES, Giovanni RD, Siqueira MF, Sutton T, Brewer P, Pereira RS, Canhos DAL, Canhos VP (2009): OpenModeller: a generic approach to species' potential distribution modelling. Geoinformatica, doi: 10.1007/s10707-009-0090-7.

Nakićenović, N, Swart R (eds.) (2000): Special Report on Emissions Scenarios. A Special Report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 599 pp.

Oberhuber W (2001): The role of climate in the mortality of Scots pine (*Pinus sylvestris* L.) exposed to soil dryness. Dendrochronologia, 19: 45–55.

Ogaya R, Penuelas J (2007): Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought. Plant Ecology, 189: 291–299.

Pálfai I, Boga T, L-Sebesvári J (1999): Adatok a magyarországi aszályokról 1931-1998 [Droughts in Hungary 1931-1998 – in Hungarian]. Éghajlati és Agrometeorológia tanulmányok 7. OMSZ, Budapest pp. 67-91.

Pearson RG, Dawson TE (2003): Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? Global Ecology and Biogeography, 12: 361-371.

Pearson RG, Dawson TE, Berry PM, Harrison PA (2002): SPECIES: a spatial evaluation of climate impact on the envelope of species. Ecological Modelling, 154: 289-300.

Péczely Gy (1979): Éghajlattan. [Climatology – in Hungarian]. Nemzeti Tankönyvkiadó, Budapest.

Penuelas J, Lloret F, Montoya R (2001): Severe drought effects on Mediterranean woody flora in Spain. Forest Science, 47: 214–218.

Penuelas J, Ogaya R, Boada M, Jump AS (2007): Migration invasion and decline changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography, 30: 829-837.

Petercord R (2008): Zukünftige gefährdung der Rotbuche durch rinden- und holzbrütende Käfer in Baden-Württemberg. Mitteilungen der Deutsche Gesellschaft für Allgemeine und Angewandte Entomologie, 16: 247-250.

Peters R (1997): Beech forests. Kluwer Academic, Dordrecht.

Peterson AT, Cohoon KP (1999): Sensitivity of distributional prediction algorithms to geographic data completeness. Ecological Modelling, 117: 159–64.

Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberon J, Buddemeier RH, Stockwell DRB (2002): Future projections for Mexican faunas under global climatic change scenarios. Nature, 416: 626–629.

Phillips S (2006): Maxent software for species habitat modelling. URL: http://www.cs.princeton.edu/~schapire/maxent/ [online 25 October 2011]

Phillips SJ, Anderson R, Schapire RE (2006): Maximum entropy modelling of species geographic distributions. Ecological Modelling, 190: 231-259.

Piso K (1886): A Máramaros megyében 1885. évben előfordult káros rovarokról [Forest pests in Máramaros County in 1885 - in Hungarian]. Erdészeti Lapok, 25 (11): 795-798.

Possingham HP, Davies I (1995): Alex: a model for the viability analysis of spatially structured populations. Biological Conservation, 73: 143–150.

Pott R (2000): Palaeoclimate and vegetation - long-term vegetation dynamics in central Europe with particular reference to beech. Phytocoenologia, 30 (3-4): 285-333.

Pratt RB, Jacobsen AL, Mohla R, Ewers FW, Davis SD (2008): Linkage between water stress tolerance and life history type in seedlings of nine chaparral species (*Rhamnaceae*). Journal of Ecology, 96: 1252-1265.

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992): A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography, 19: 117-134.

Pulliam HR (2000): On the relationship between niche and distribution. Ecology Letters, 3: 349–361.

Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008): Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience, 58: 501-517.

Raftoyannis Y, Spanos I, Radoglou K (2008): The decline of Greek fir (*Abies cephalonica* Loudon): Relationships with root condition. Plant Biosystems, 142: 386–390.

Räisänen J (2007): How reliable are climate models? Tellus Series A: Dynamic Meteorology and Oceanography, 59: 2–29.

Randall DA, Richard A and coauthors (2007): Climate models and their evaluation. In Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller), pp. 589–662. Cambridge, UK: Cambridge University Press.

Raxworthy CJ, Martinez-Meyer E, Horning N, Nussbaum RA, Schneider GE, Ortega-Huerta MA, Peterson AT (2003): Predicting distributions of known and unknown reptile species in Madagascar. Nature, 426: 837–841.

Rennenberg H, Seiler W, Matyssek R, Gessler A, Kreuzwieser J (2004): Die Buche (*Fagus sylvatica* L.) - ein Waldbaum ohne Zukunft im südlichen Mitteleuropa? Allgemeine Forst- und Jagdzeitung, 175: 210-224.

Rice K, Matzner S, Byer W, Brown J. (2004): Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. Oecologia, 139: 190-198.

Rich PM, Breshears DD, White AB (2008): Phenology of mixed woody-herbaceous ecosystems following extreme events: net and differential responses. Ecology, 89: 342–352.

Richards JA, Jia X (1999): Remote Sensing Digital Image Analysis. An Introduction, Third edition. Springer. Berlin. Germany.

Rickebusch S, Lischke H, Bugmann H, Guisan A, Zimmermann NE (2007): Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data. Forest Ecology and Management, 246: 251-263.

Rigling A, Cherubini P (1999): Wieso sterben die Waldföhren im Telwald bei Visp? Schweizerische Zeitschrift für Forstwesen, 150: 113–131.

Rigling A, Dobbertin M, Bürgi M, Feldmeier-Christe E, Gimmi U, Ginzler C, Graf U, Mayer P, Zweifel R, Wohlgemuth T (2006): Baumartenwechsel in den Walliser Waldföhrenwäldern. In: Wohlgemuth, T. (Red.), Wald und Klimawandel. Forum für Wissen, 71 pp.

Rissler LJ, Hijmans RJ, Graham CH, Moritz C, Wake DB (2006): Phylogeographic lineages and species comparisons in conservation analyses: A case study of california herpetofauna. American Naturalist, 167: 655-666.

Rivas-Martínez S (1990): Bioclimatic belts of West Europe (relations between bioclimate and plant ecosystems). Proc. Eur. School Climate Nat. Hazards Course (Arles, 1990). 225-246. Strasbourg.

Rosenzweig C, Parry ML (1994): Potential impact of climate change on world food supply. Nature, 367: 133-138.

Rouault G, Candau JN, Lieutier F, Nageleisen LM, Martin JC, Warzee N (2006): Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Annals of Forest Science, 63: 613–624.

Sala A, Piper F, Hoch G (2010): Physiological mechanisms of drought-induced tree mortality are far from being resolved. New Phytologist, 186: 274-281.

Sanderson BM, Knutti R, Aina T, Christensen C, Faull N, Frame DJ, Ingram WJ, Piani C, Stainforth DA, Stone DA, Allen MR (2008): Constraints on model response to greenhouse gas forcing and the role of subgrid-scale processes. Journal of Climate, 21 (11).

Sarris D, Christodoulakis D, Körner C (2007): Recent decline in precipitation and tree growth in the eastern Mediterranean. Global Change Biology, 13 (6): 1187–1200.

Schipka F, Heimann J, Leuschner C (2005): Regional variation in canopy transpiration of Central European beech forests. Oecologia, 143: 260-270.

Segurado P, Araújo MB (2004): An evaluation of methods for modelling species distributions. Journal of Biogeography, 31: 1555-1568.

Shaw JD, Steed BE, DeBlander L (2005): Forest inventory and analysis (FIA) annual inventory answers the question: what is happening to pinyon–juniper woodlands? Journal of Forestry, 103: 80–285.

Shtrakhov (2008): Forest health and protection in Russia. In: Oral Presentation At: International Conference ''Adaptation of Forests and Forest Management to Changing Climate with Emphasis on Forest Health: A Review of Science, Policies, and Practices'', Umea, Sweden, FAO/IUFRO, 25–28 August 2008

Siwecki R, Ufnalksi K (1998): Review of oak stand decline with special reference to the role of drought in Poland. European Journal of Forest Pathology, 28: 99–112.

Smith B, Prentice IC, Sykes MT (2001): Representation of vegetation dynamics in modelling of European ecosystems: comparison of two contrasting approaches. Global Ecology and Biogeography, 10: 621–637.

Solberg S (2004): Summer drought: a driver for crown condition and mortality of Norway spruce in Norway. Forest Pathology, 34: 93–107.

Stainforth DA, Allen MR, Tredger ER, Smith LA (2007): Confidence, uncertainty and decision-support relevance in climate predictions. Philosophical Transactions of the Royal Society Academy, 365: 2145–2161.

Sterl A, Severijns C, Dijkstra H, Hazeleger W, Jan van Oldenborgh G, van den Broeke M, Burgers G, van den Hurk B, van Leeuwen PJ, van Velthoven P (2008): When can we expect extremely high surface temperatures? Geophysical Research Letters, 35: L14703

Stockwell D, Peters D (1999): The GARP modelling system: problems and solutions to automated spatial prediction. International Journal of Geographical Information Science, 13: 143–158.

Svenning, JC, Skov F (2004): Limited filling of the potential range in European tree species. Ecological Letters, 7, 565–573.

Swets J (1988) Measuring the accuracy of diagnostic systems. Science 240, 1285- 1293.

Sykes MT, Prentice IC, Cramer W (1996): A bioclimatic model for the potential distributions of North European tree species under present and future climates. Journal of Biogeography, 23(2):203–233.

Szalai S, Konkolyné BZ, Lakatos M, Szentimrey T (2005): Magyarország éghajlatának néhány jellemzője 1901-től napjainkig. [Climate characteristic of Hungary from 1901 till today – in Hungarian] OMSZ, 12 pp.

Szinell Cs, Bussay A, Szentimrey T (1998): Drought tendencies in Hungary. International Journal of Climatology, 18: 1479-1491.

Tax DMJ, Duin RPW (2002): Uniform object generation for optimizing one-class classifiers. Journal of Machine Learning Research, 2: 155-173.

Tebaldi C, Hayhoe K, Arblaster JM, Meehl GA (2006): Going to the extremes: an intercomparison of model-simulated historical and future changes in extreme events. Climatic Change, 79: 185–211.

Tebaldi C, Knutti R (2007): The use of the multi-model ensemble in probabilistic climate projections. Philosophical Transactions of the Royal Society A, 365: 2053-2075.

Thabeet A, Vennetier M, Gadbin-Henry C, Denelle N, Roux M, Caraglio Y, Vila B (2009): Response of Pinus sylvestris L. to recent climate change in the French Mediterranean region. Trees, Structure and Functions, 23 (4): 843–853.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Ferreira de Siquiera M, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarseveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004): Extinction risk from climate change. Nature, 427: 145–148.

Thornthwaite WC (1948): An approach toward a rational classification of climate. Geographical Review, 38 (1): 55-103.

Thuiller W (2003): BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. Global Change Biology, 9: 1353–1362.

Thuiller W (2004): Patterns and uncertainties of species' range shifts under climate change. Global Change Biology, 10: 2020–2027.

Thuiller W, Araújo MB, Pearson RG, Whittaker RJ, Brotons L, Lavorel S (2004): Biodiversity conservation - uncertainty in predictions of extinction risk. Nature, 430: 36.

Thuiller W, B. Lafourcade, R. Engler, Araújo MB (2009): BIOMOD - A platform for ensemble forecasting of species distributions. Ecography, 32: 369-373.

Thuiller W, Lavorel S, Sykes MT, Araújo MB (2006): Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Diversity and Distribution, 12: 49–60.

Thuiller W, Münkemüller T (2010): Habitat suitability modeling. In: Moeller AP, Fielde, W, Berthold P (eds.), Effects of climate change on birds. Oxford, University Press.

Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M (2005): Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology, 11: 2234-2250.

Thuiller W, Vaydera J, Pino J, Sabaté S, Lavorel S, Gracia C (2003): Large-scale environmental correlates of forest tree distributions in Catalonia (NE Spain). Global Ecology and Biogeography, 12: 313-325.

Tinner W, Lotter AF (2006): Holocene expansions of Fagus silvatica and Abies alba in Central Europe: where are we after eight decades of debate? Quaternary Science Reviews, 25: 526–549.

Tóth JA, Lajtha K, Kotroczó Zs, Krakomperger Zs, Caldwel B, Bowden RD, Papp M (2007): The effect of climate change on soil organic matter decomposition. Acta Silvatica et Ligniaria Hungarica, 3: 75-85.

Tsoar A, Allouche O, Steinitz O, Rotem D, Kadmon R (2007): A comparative evaluation of presence-only methods for modelling species distribution. Diversity and Distribution, 13: 397-405.

Tsopelas P, Angelopoulos A, Economou A, Soulioti N (2004): Mistletoe (*Viscum album*) in the fir forest of Mount Parnis, Greece. Forest Ecology and Management, 202: 59–65.

Tuhkanen S (1980): Climatic parameters and indices in plant geography. Acta Phytogeographica Suecica, 67:1–110.

van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fulé PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT (2009): Widespread increase of tree mortality rates in the western United States. Science, 323: 521–524.

Vapnik V (1995): The Nature of Statistical Learning Theory. Springer-Verlag. New York. USA.

Vennetier M, Cecillon L, Guénon R, Schaffhauser A, Vergnoux A, Boichard JL, Bottéro JY, Brun JJ, Carrara M, Cassagne N, Chandioux O, Clays-Josserand A, Commeaux C, Curt T, Czarnes S, De Danieli S, Degrange V, Di Rocco R, Domeizel M, Doumenq P, Doussan C, Estéve R, Faivre N, Favier G, Gaudu JC, Gros R, Guiliano M, Guillaumaud N, Hoepffner M, Juvy B, Le Roux X, Lebarriller S, Malleret L, Martin W, Mas C, Masion A, Massiani C, Mermin E, Mille G, Morge D, Pignot V, Poly F, Renard D, Ripert C, Ruy S, Tardif P, Tatoni T, Théraulaz F, Vassalo L, Asia L, (2008). Etude de l’impact d’incendies de forét répéte s sur la biodiversité et sur les sols: recherche d’indicateurs. Rapport final. Cemagref, Ministére de l’Agriculture et de la péche, Union Européenne, Aix en Provence, 236 pp.

Vennetier M, Vila B, Liang EY, Guibal F, Thabeet A, Gadbin-Henry C (2007): Impact of climate change on pine forest productivity and on the shift of a bioclimatic limit in a Mediterranean area. Options Méditerrane´ennes, Série A, n8 75, CIHEAM/IAMB, Bari, Italy, pp. 189–197.

Vertui F, Tagliaferro F (1998): Scots pine (*Pinus sylvestris* L.) die-back by unknown causes in the Aosta Valley, Italy. Chemosphere, 36: 1061–1065.

Walter H, Lieth H (1964): Klimadiagramm-Weltatlas. Verlag Gustav Fischer, Jena.

Wermelinger, B, Rigling, A, Schneider, M, Dobbertin, M (2008) Assessing the role of bark- and wood-boring insects in the decline of Scots pine (*Pinus sylvestris*) in the Swiss Rhone valley. Ecological Entomology. 33: 239–249.

Williams PH, Hannah L, Andelman S, Midgley GF, Arau´jo MB, Hughes GO, Manne L, Martinez-Meyer E, Pearson RG (2005): Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. Conservation Biology, 19: 1063–1074.

With KA (2002): The landscape ecology of invasive spread. Conservation Biology, 16: 1192–1203.

Wood S (2006): Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC.

Woodward FI (1992): Predicting plant responses to global environmental change. New Phytologist, 122, 239–251.

Woodward FI, Rochefort I (1991): Sensitivity analysis of vegetation diversity to environmental change. Global Ecology and Biogeography Letters, 1: 7-23.

Wühlisch G Von, Krusche D, Muhs HJ (1995): Variation in temperature sum requirement for flushing of beech provenances. Silvae Genetica, 44: 343-346.

Xin Y, Guoan T, Chenchao X, Fengdong D (2007): Terrain revised model for air temperature in mountainous area based on DEM’s, a case study in Yaoxian county. Journal of Geographical Sciences, 17(4): 399-408.

Zeileis A, Leisch F, Hornik K, Kleiber C (2002): Strucchange, an *R* Package for Testing for Structural Change in Linear Regression Models. Journal of Statistical Software, 7(2): 1-38.

Zimmermann NE, Yoccoz NG, Edwards TC, Meier ES, Thuiller W (2009): Climatic extremes improve predictions of spatial patterns of tree species. Proceedings of the National Academy of Sciences of the United States of America, USA 106: 19723-19728.

12 Web references

http://r-forge.r-project.org/projects/biomod/	[online 25 February 2011]
http://cran.r-project.org/web/packages/dismo/dismo.pdf	[online 25 February 2011]
http://srtm.csi.cgiar.org	[online 25 February 2011]
http://www.cru.uea.ac.uk	[online 25 February 2011]
http://cera-www.dkrz.de/CERA/jblob/	[online 25 February 2011]
http://www.arcscripts.esri.com	[online 25 February 2011]
http://www.unil.ch/biomapper	[online 25 February 2011]
http://www.diva-gis.org	[online 25 February 2011]
http://www.cifor.cgiar.org/docs/_ref/	[online 25 February 2011]
http://www.cscf.ch/grasp	[online 25 February 2011]
http://openmodeller.sourceforge.net/	[online 25 February 2011]
http://gis.ucmerced.edu/ModEco/	[online 25 February 2011]

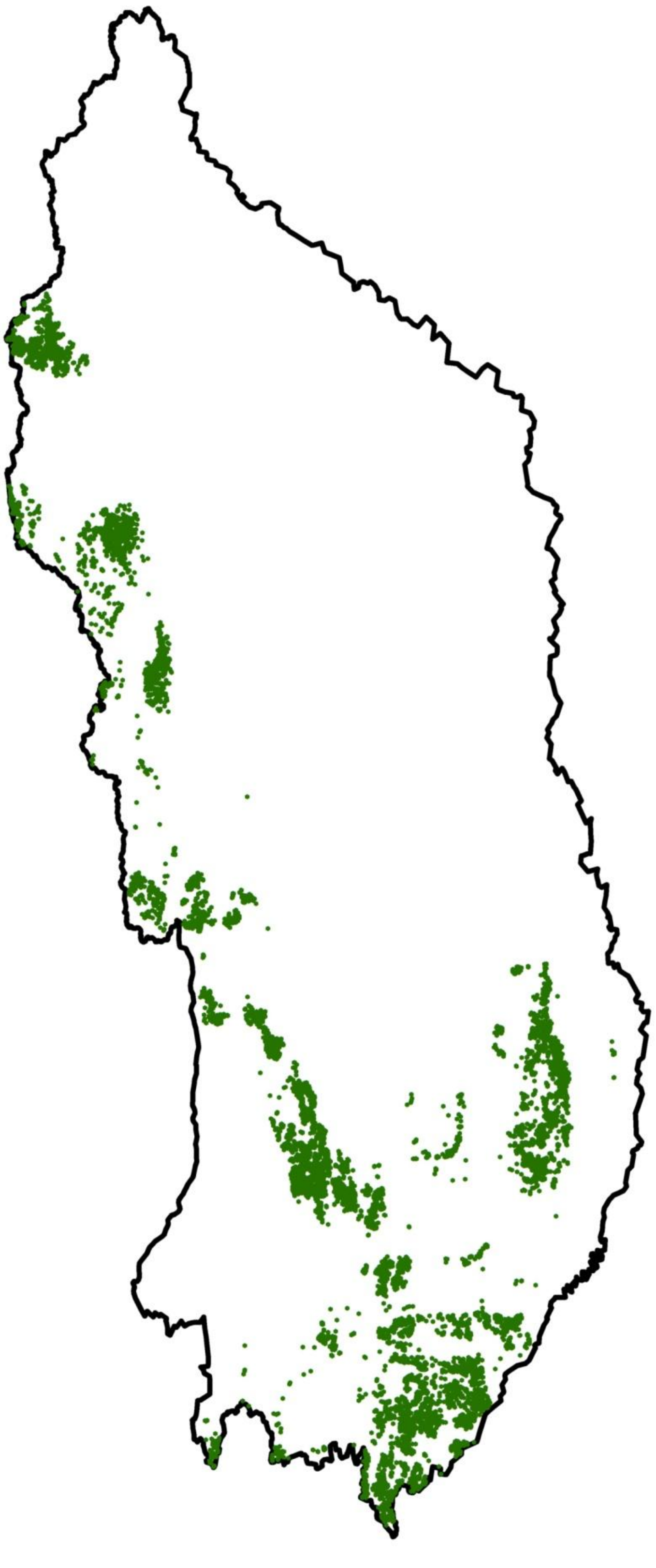
13 List of tables

14 List of figures

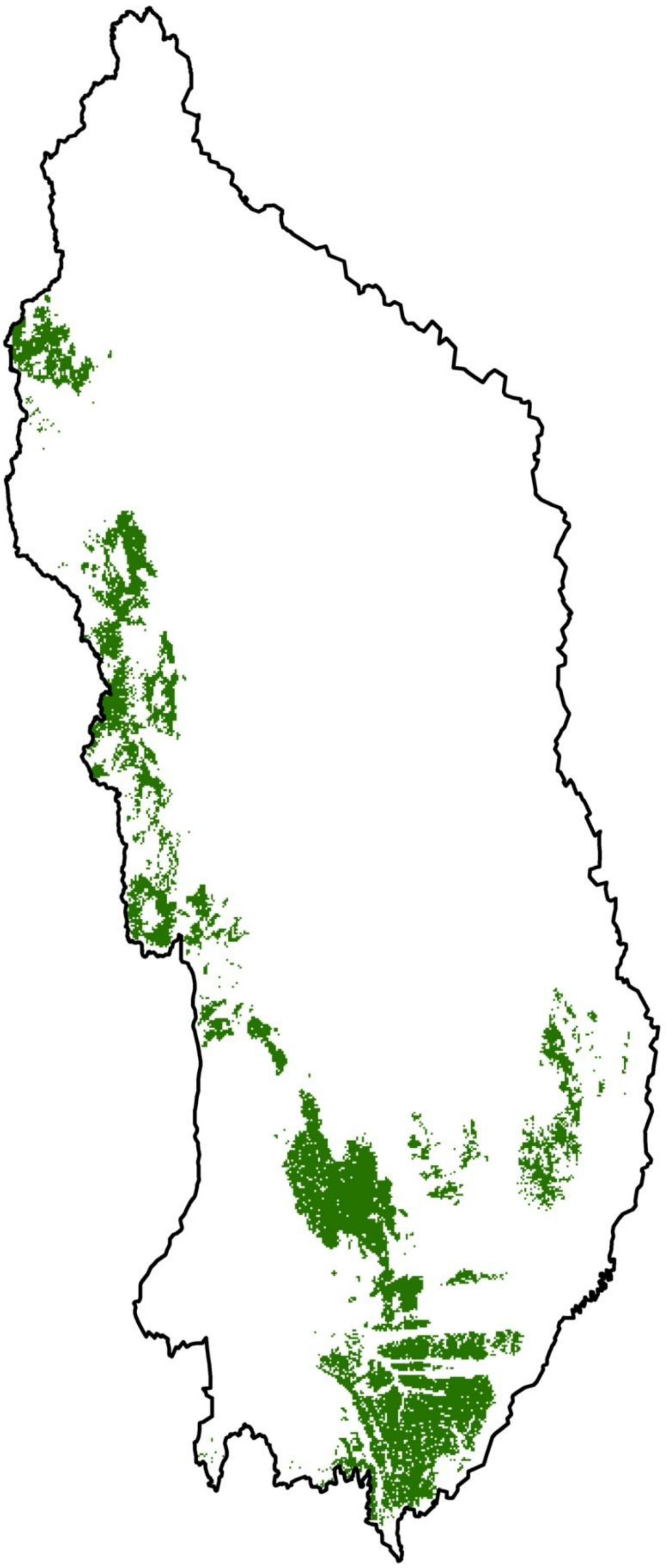
15 Annex

List of enclosures

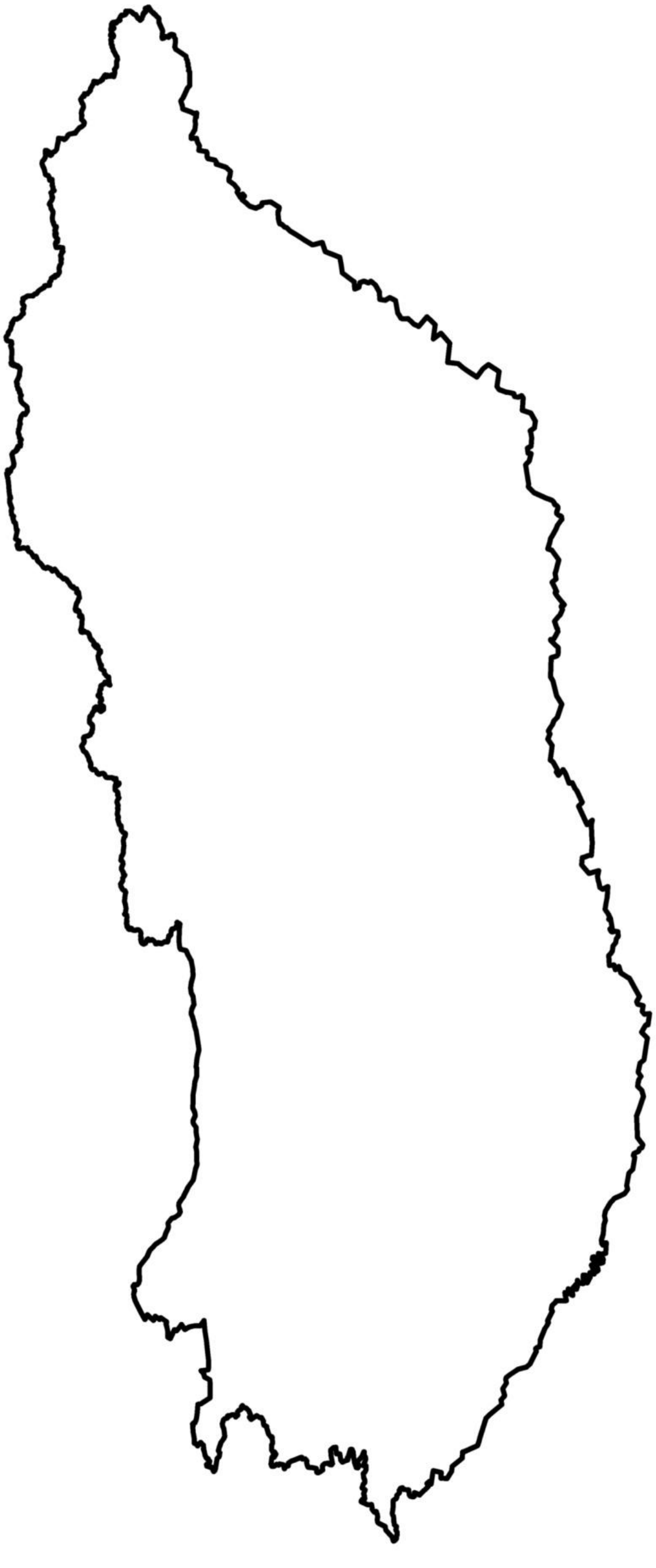
1. Current distribution of beech in Hungary



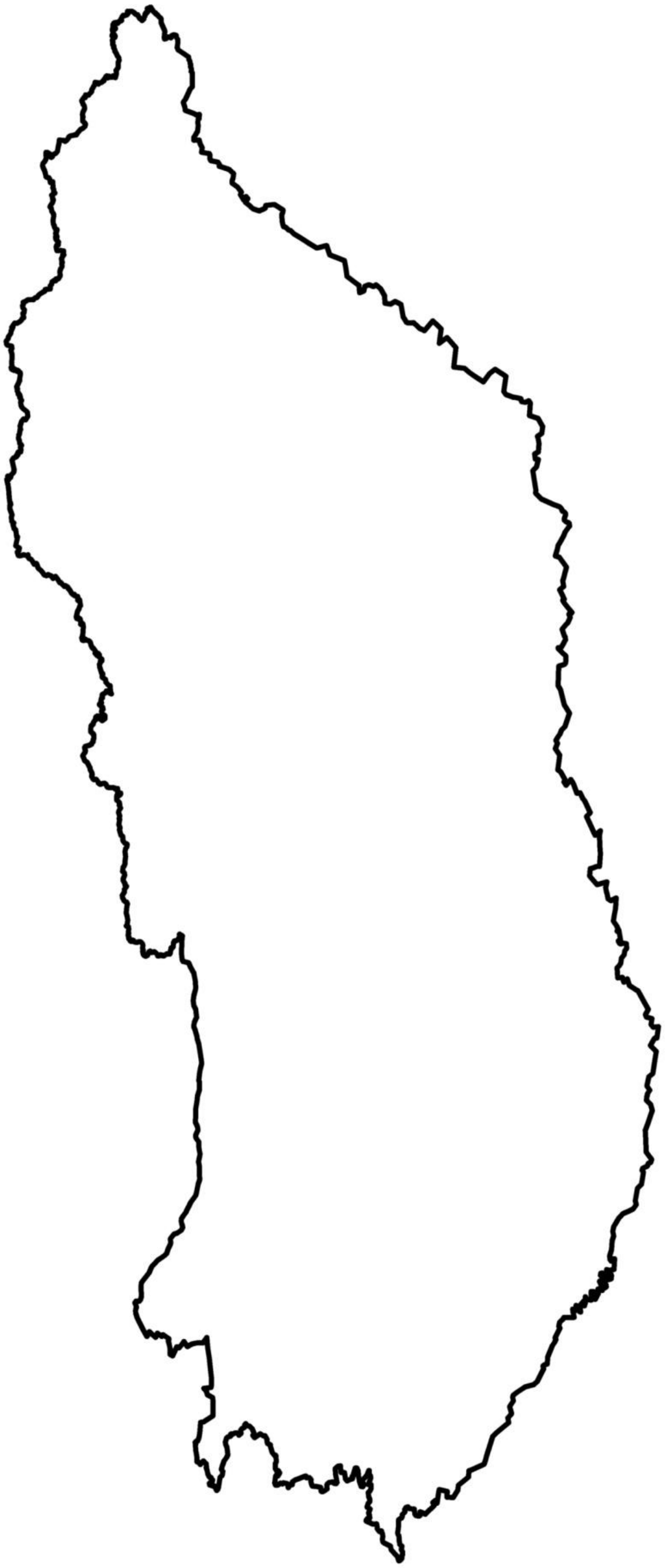
2. Potential current distribution of beech in Hungay using the BioClim model



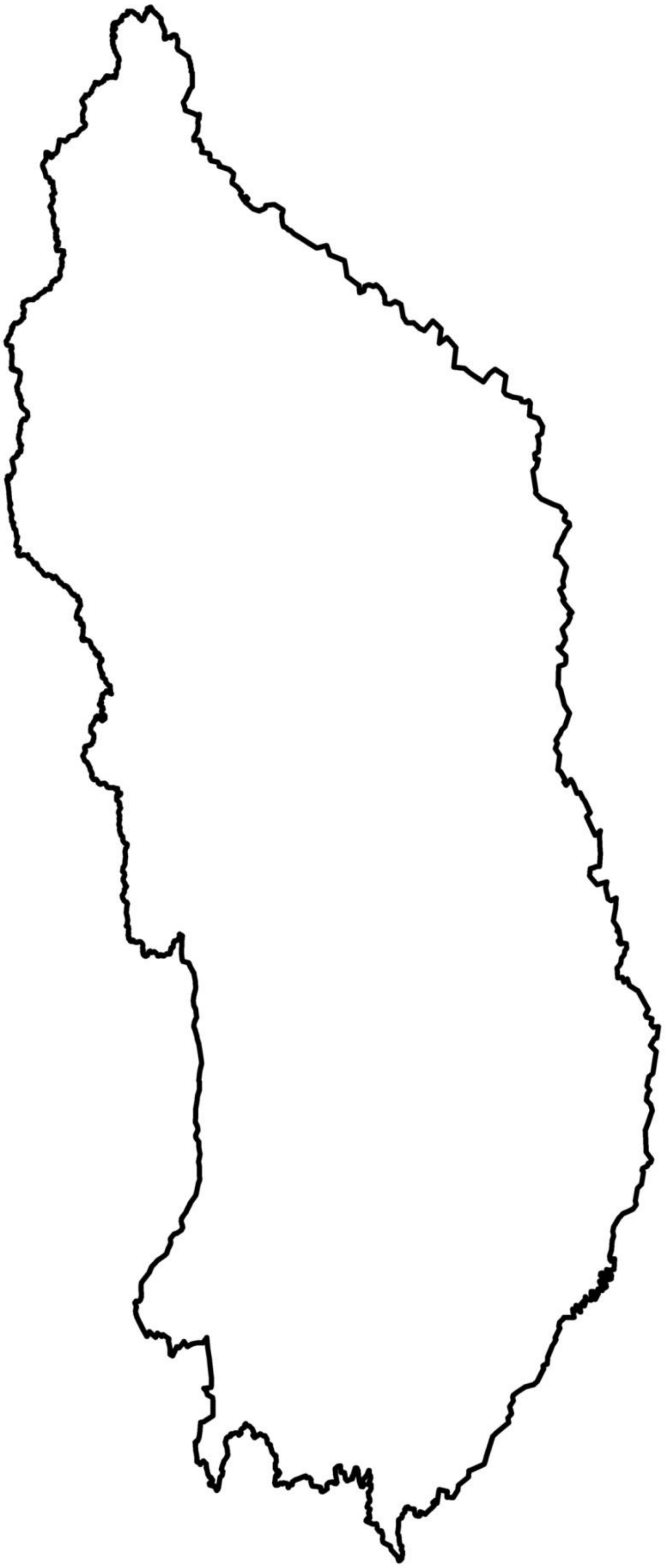
3. Potential future distribution of beech for 2011-2040 in Hungay using the BioClim model



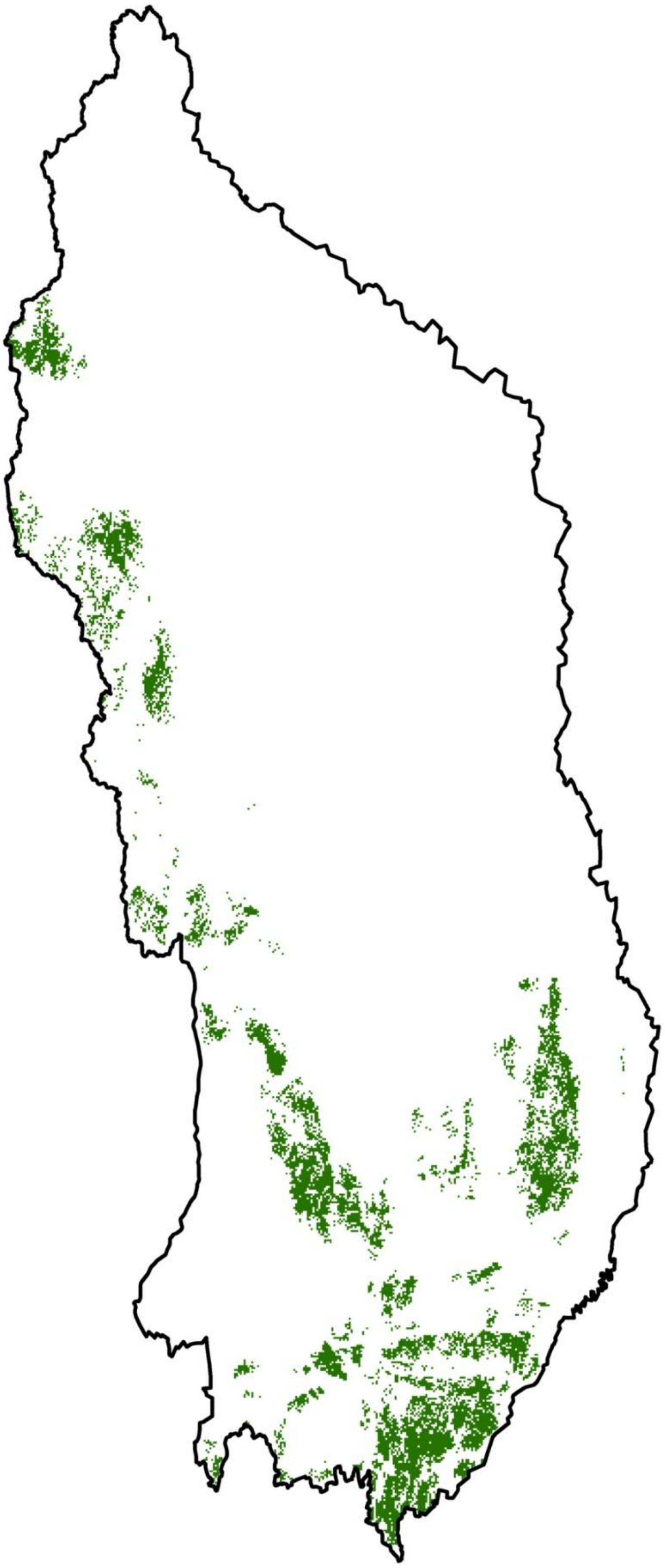
4. Potential future distribution of beech for 2036-2065 in Hungay using the BioClim model



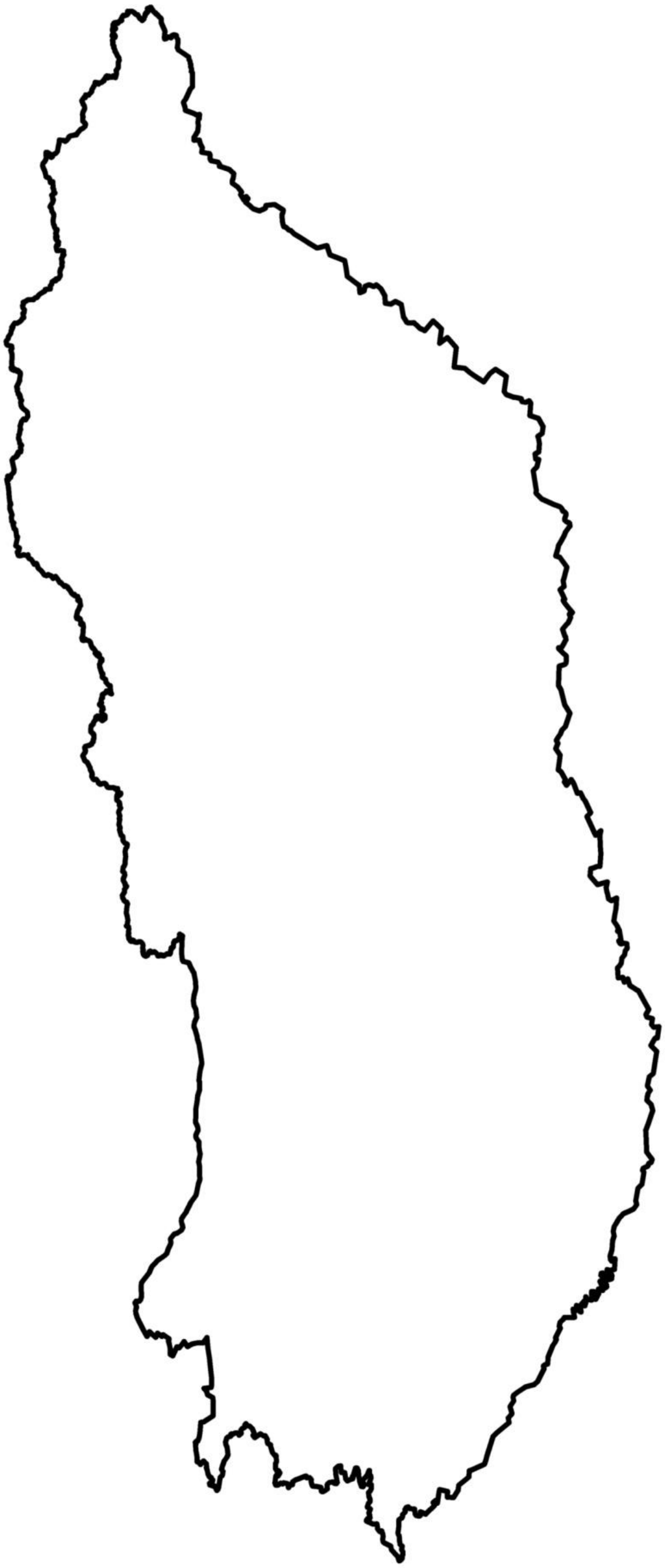
5. Potential future distribution of beech for 2066-2095 in Hungay using the BioClim model



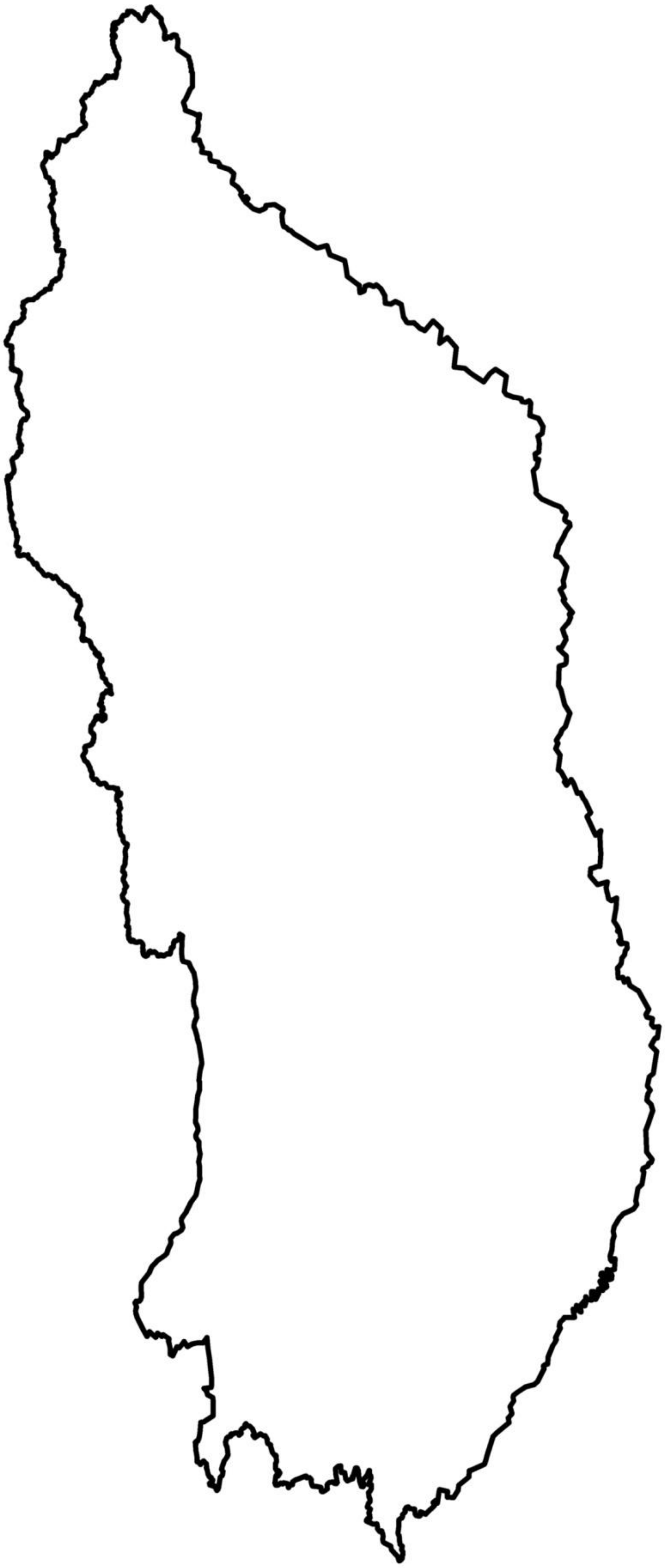
6. Potential current distribution of beech in Hungay using the Domain model



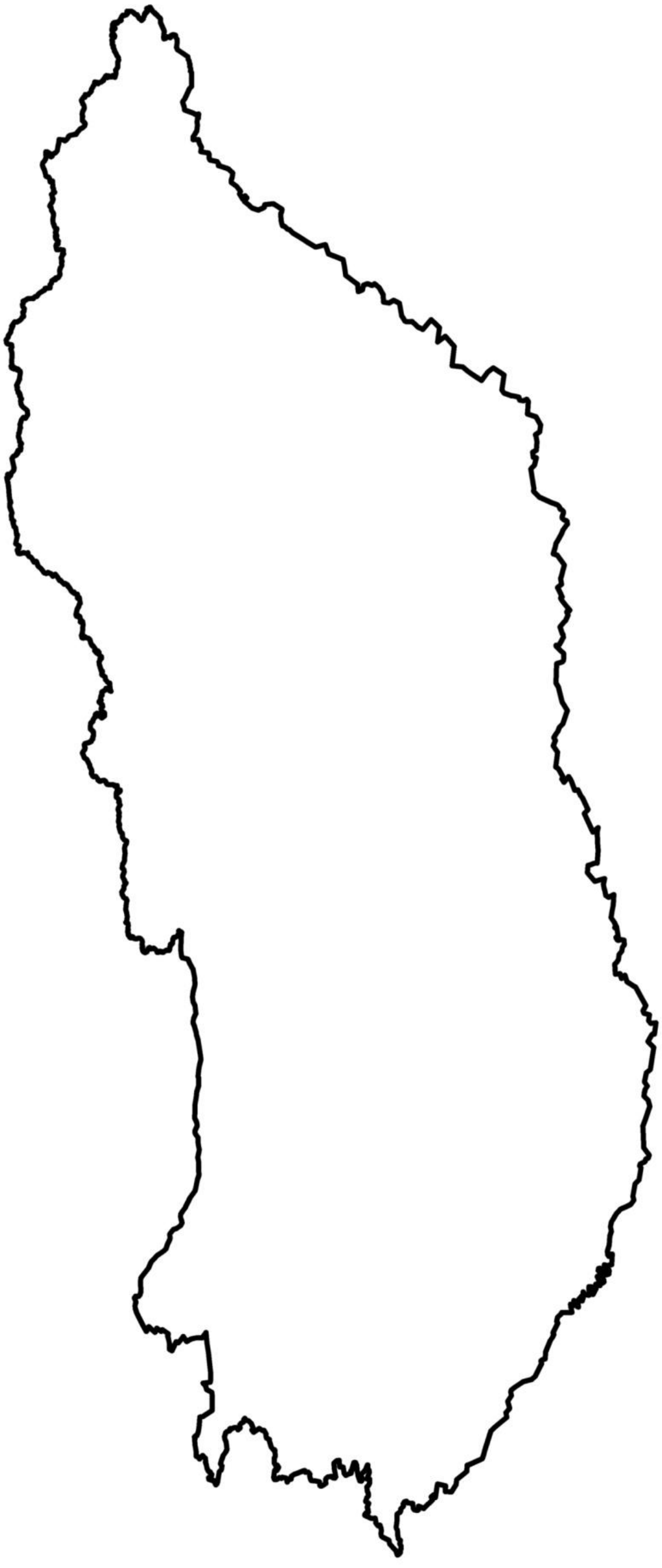
7. Potential future distribution of beech for 2011-2040 in Hungay using the Domain model



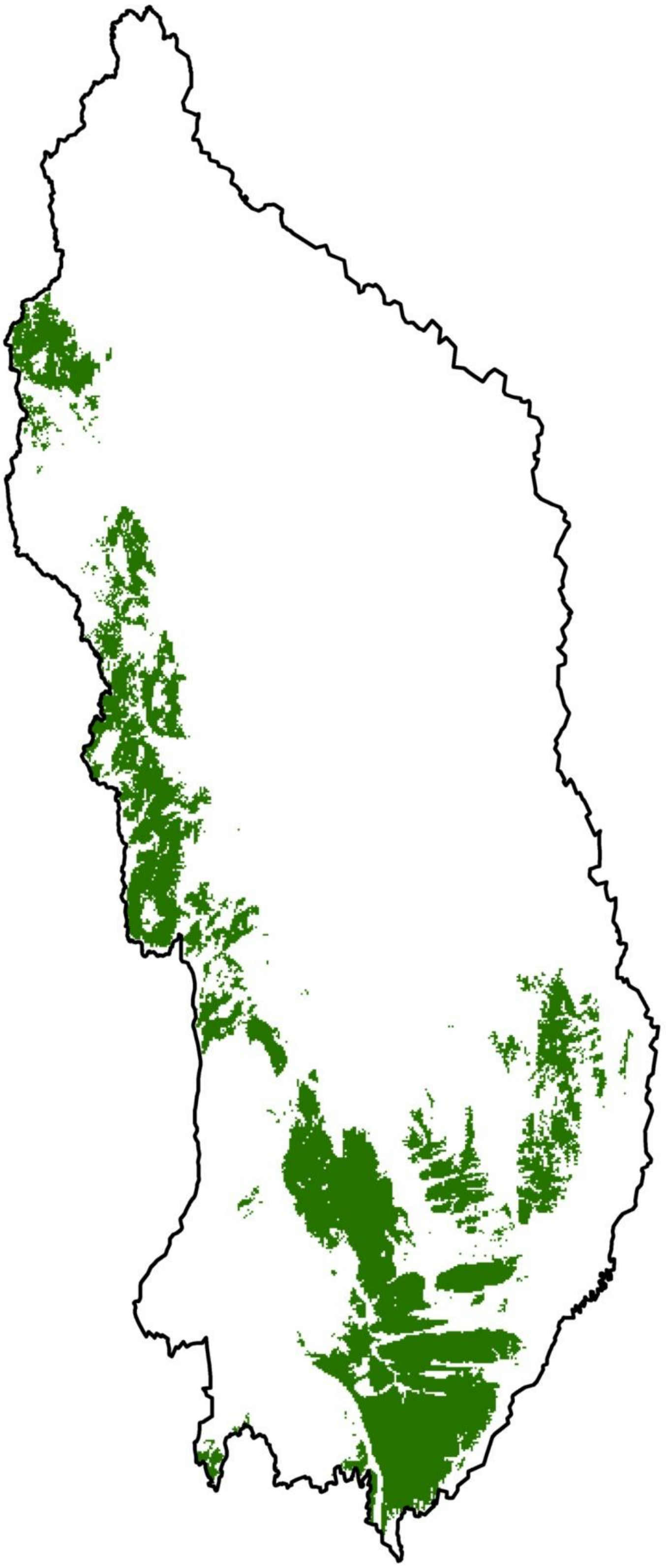
8. Potential future distribution of beech for 2036-2065 in Hungay using the Domain model



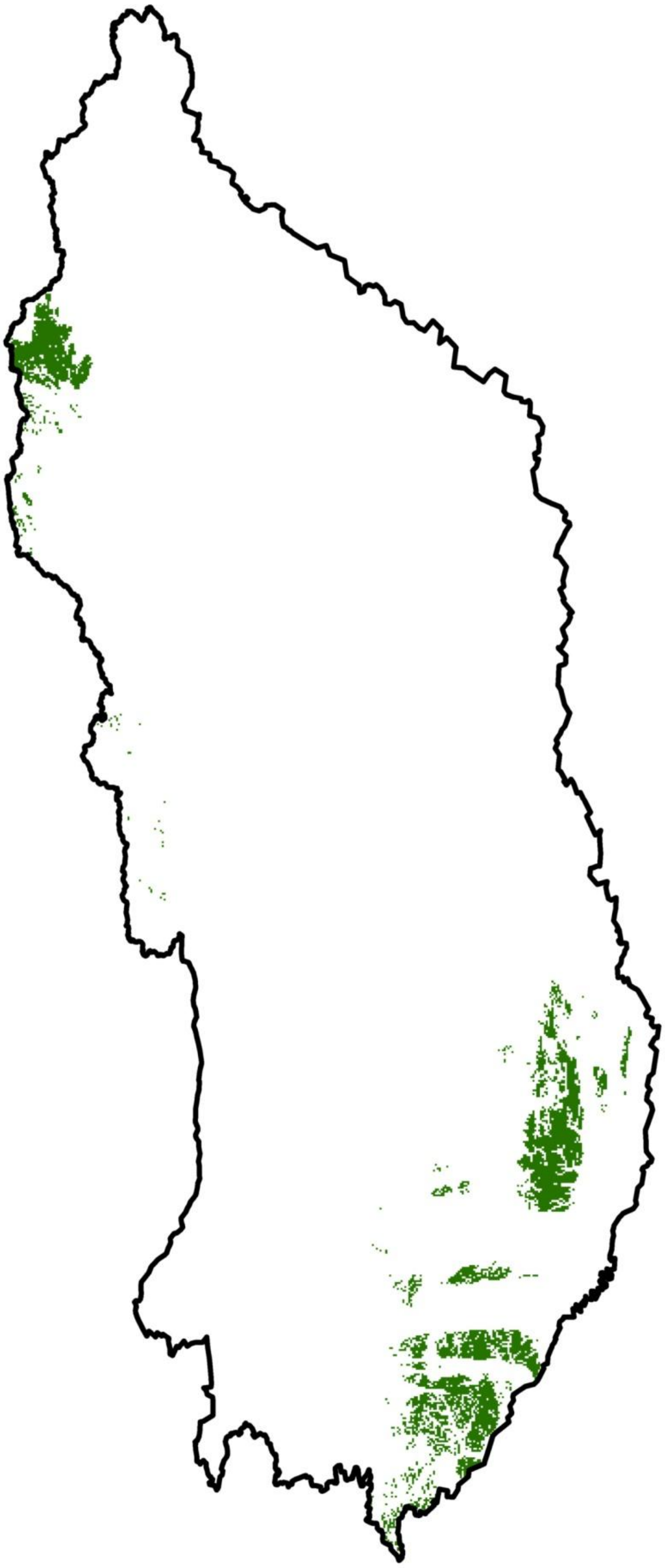
9. Potential future distribution of beech for 2066-2095 in Hungay using the Domain model



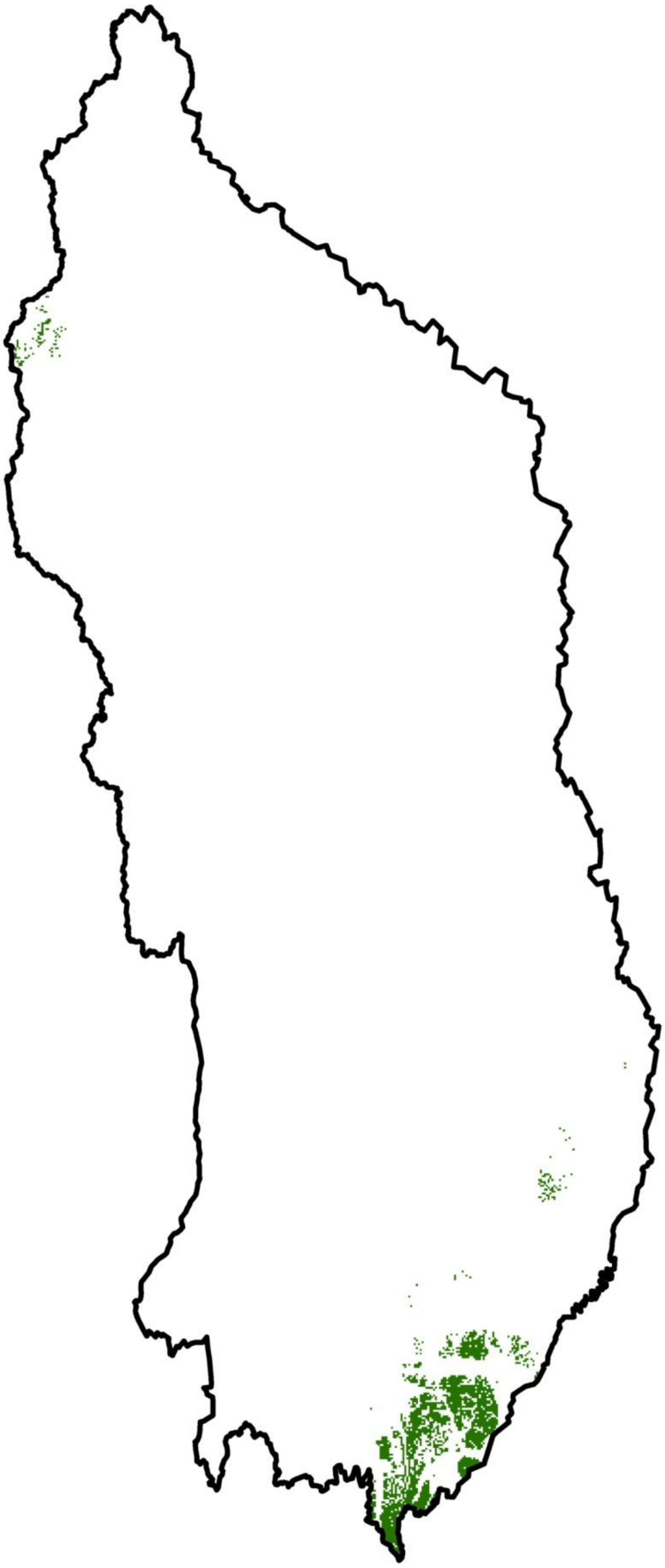
10. Potential current distribution of beech in Hungay using the one-class SVM model



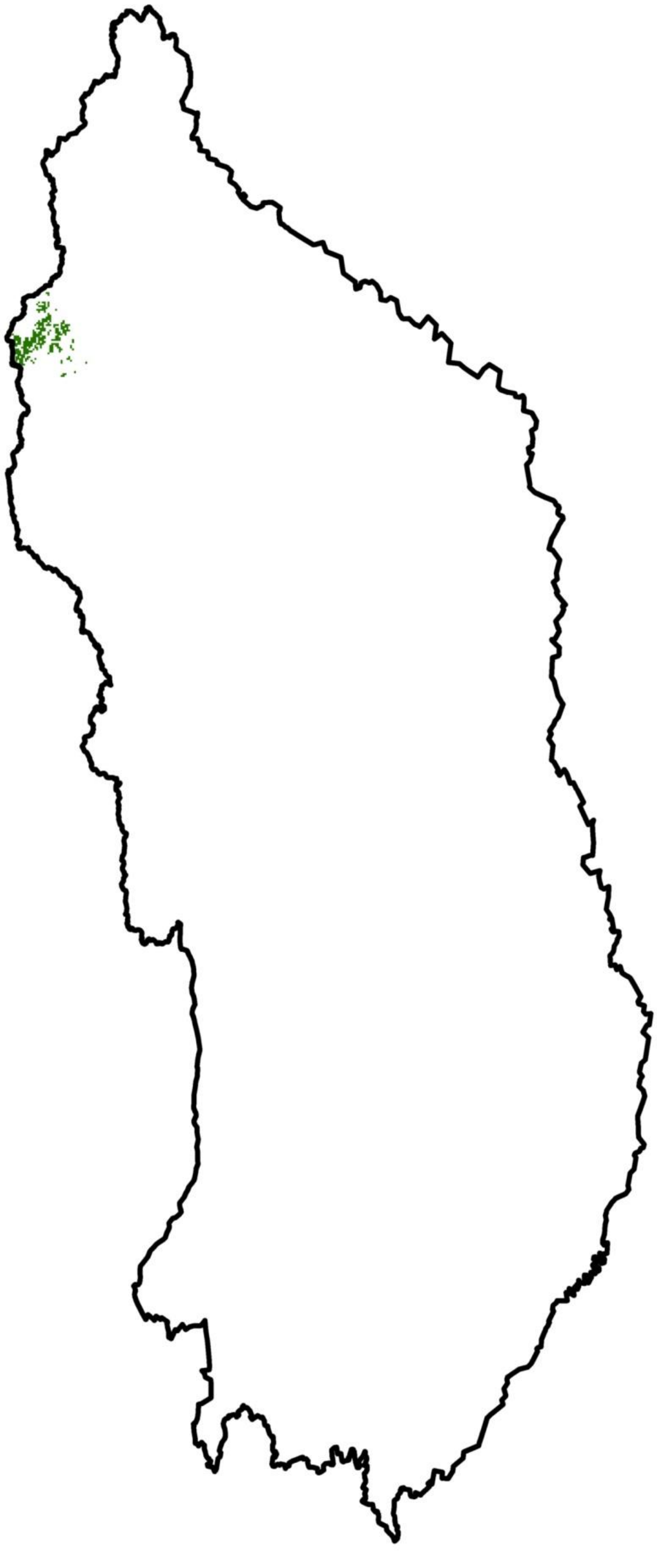
11. Potential future distribution of beech for 2011-2040 using the one-class SVM model



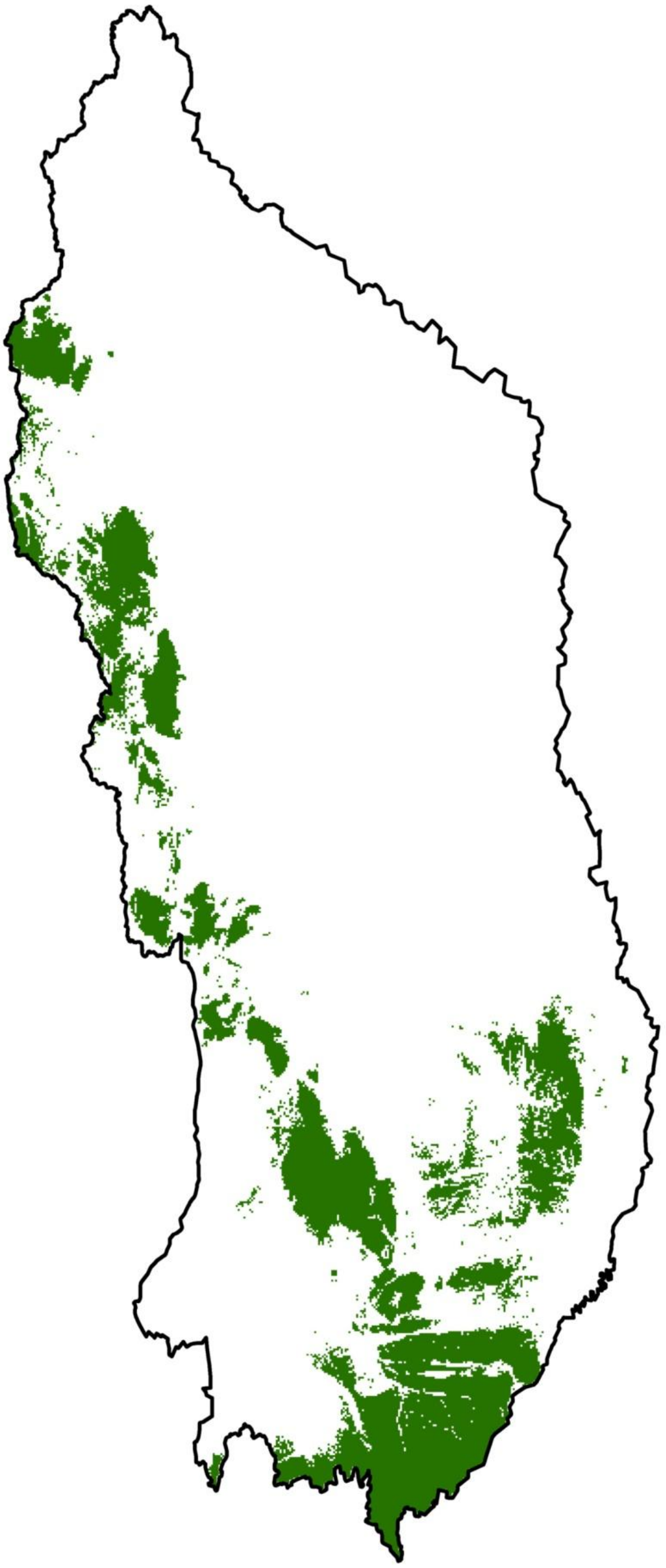
12. Potential future distribution of beech for 2036-2065 using the one-class SVM model



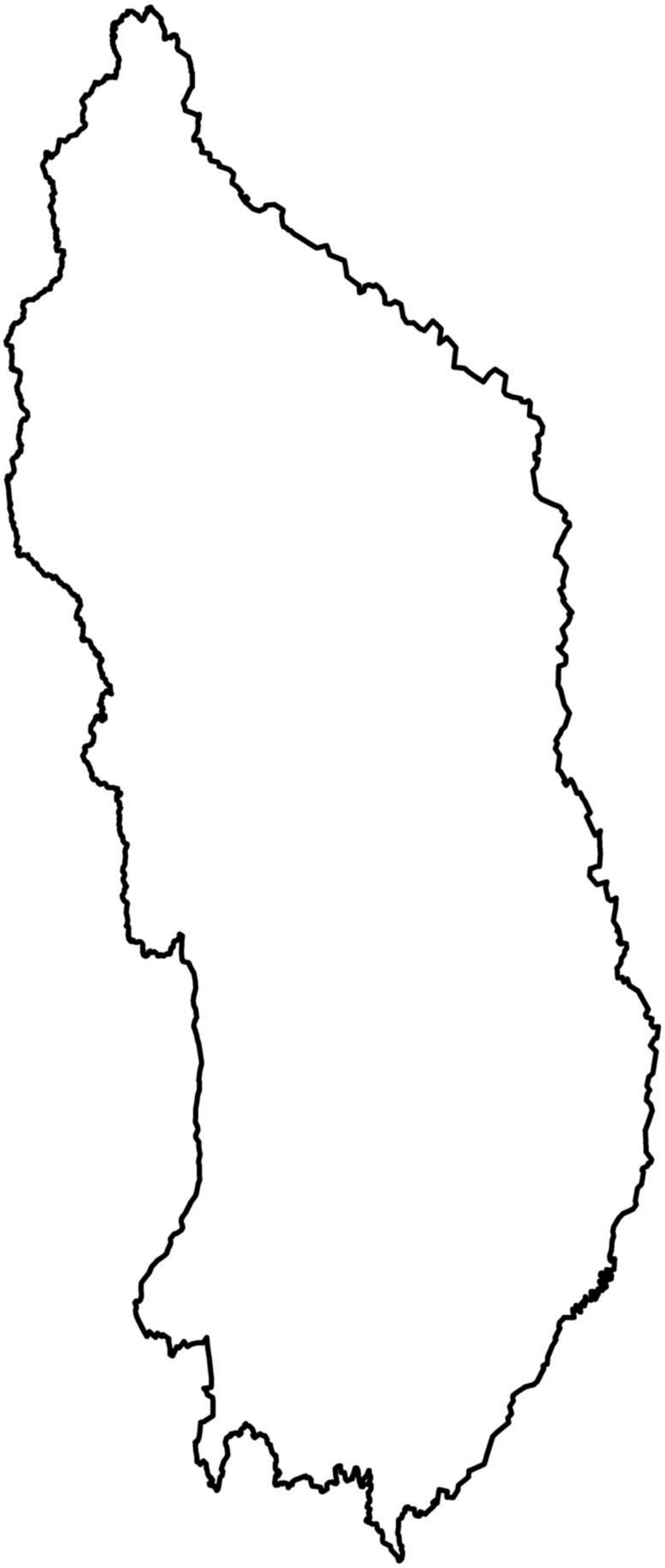
13. Potential future distribution of beech for 2066-2095 using the one-class SVM model



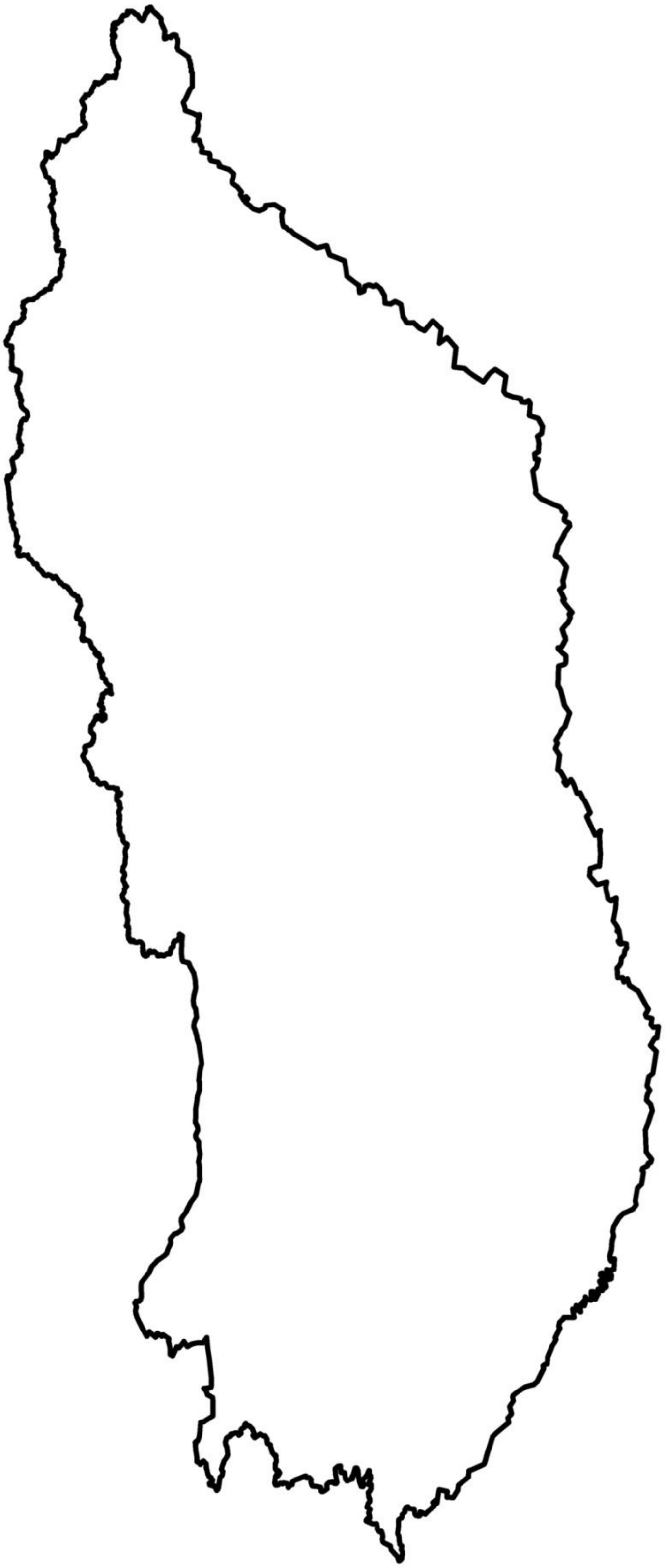
14. Potential current distribution of beech in Hungay using the MLC model



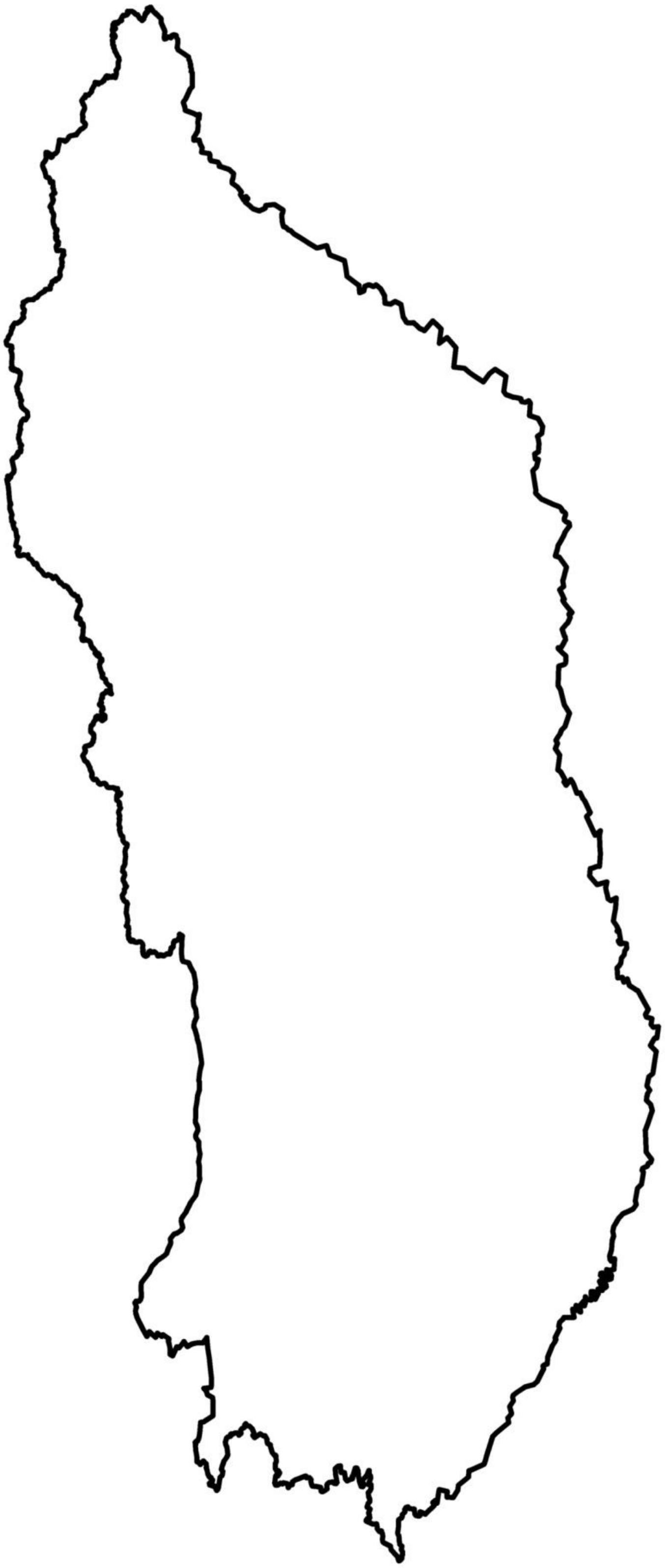
15. Potential future distribution of beech for 2011-2040 in Hungay using the MLC model



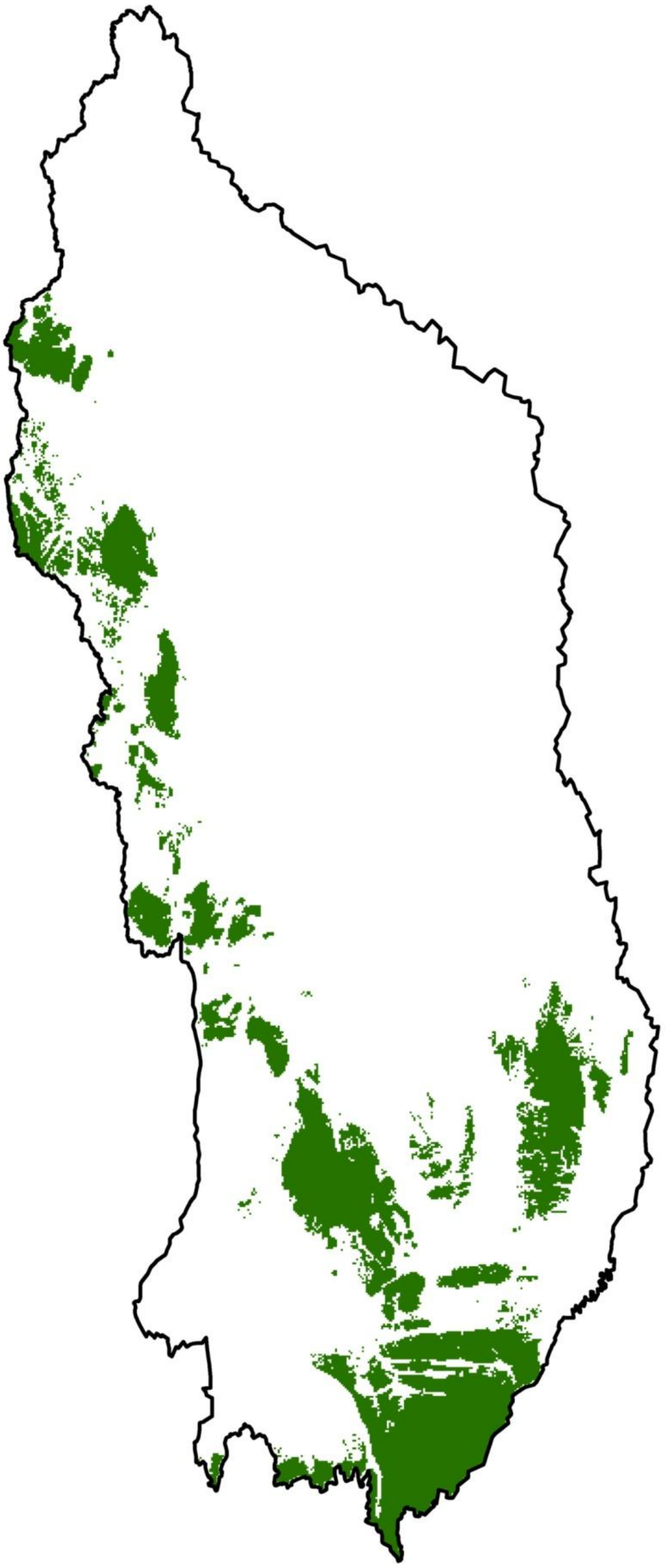
16. Potential future distribution of beech for 2036-2065 in Hungay using the MLC model



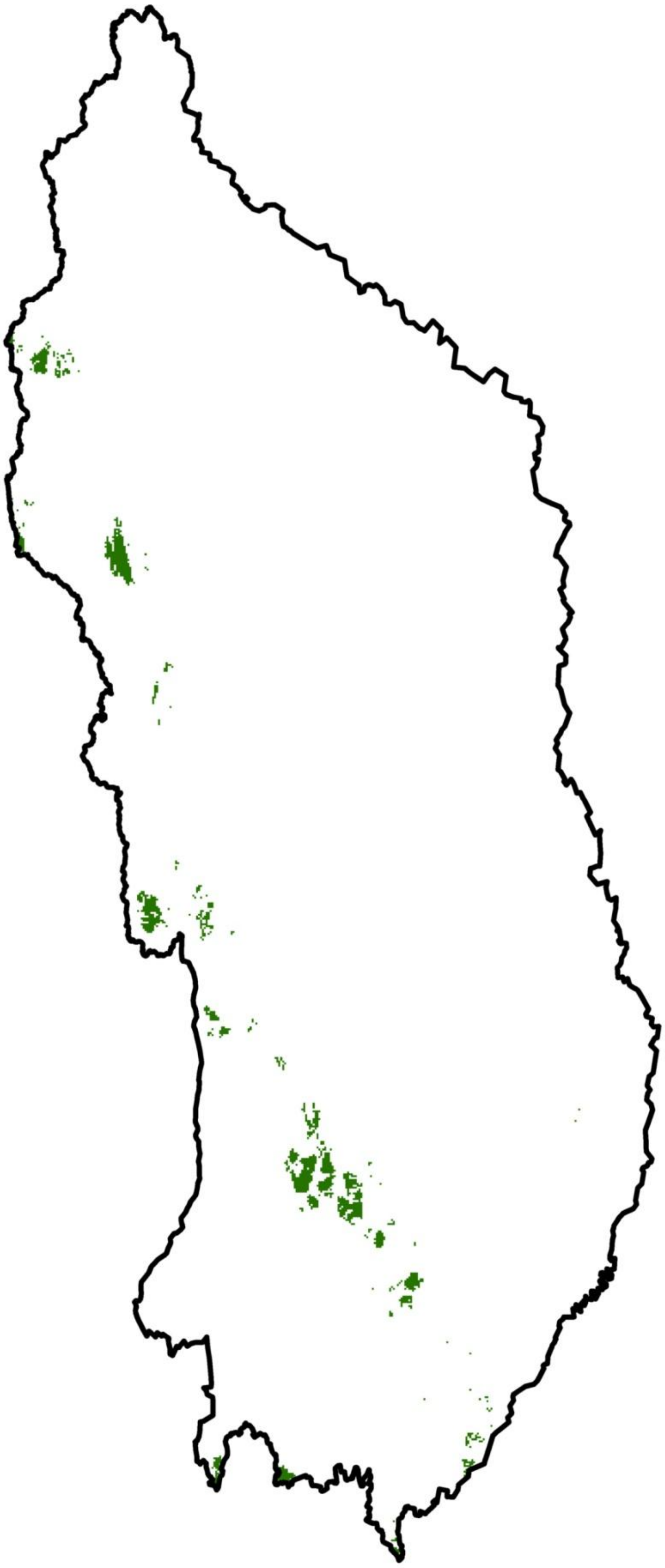
17. Potential future distribution of beech for 2066-2095 in Hungay using the MLC model



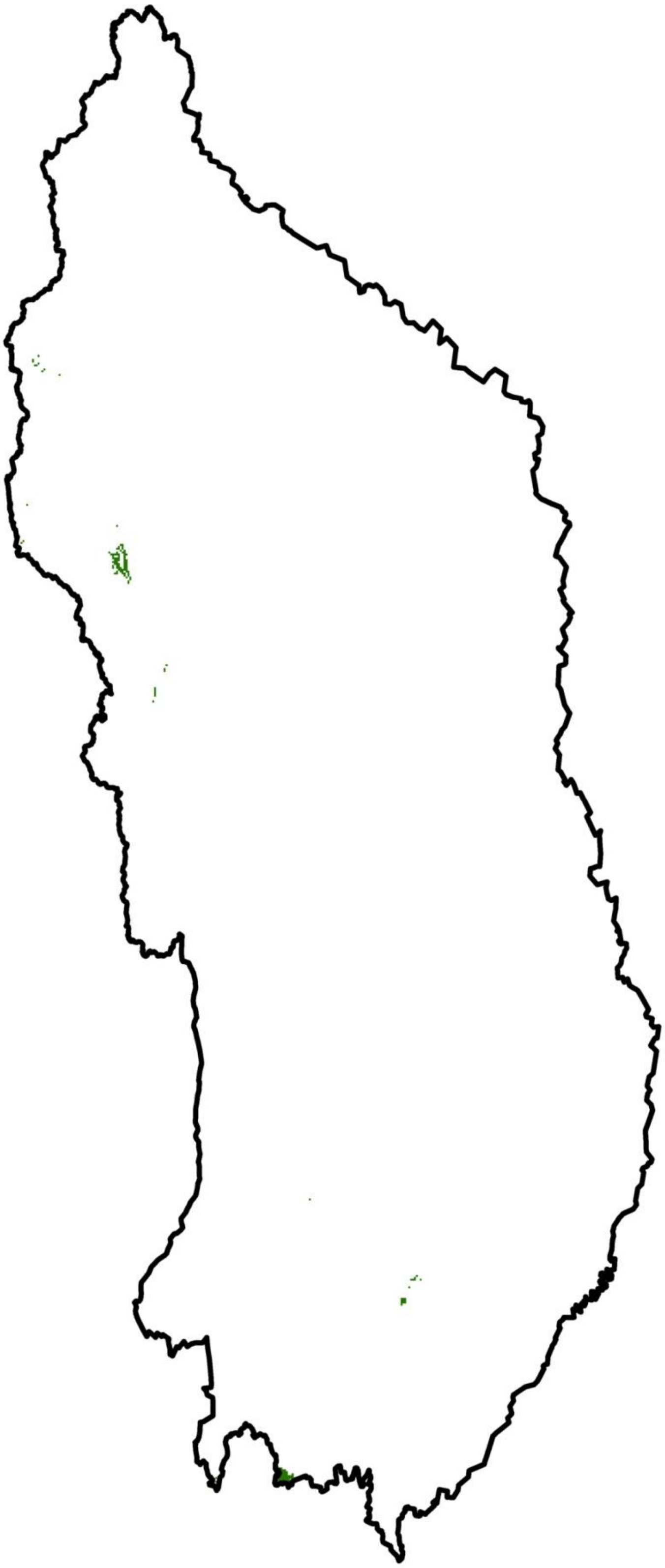
18. Potential current distribution of beech in Hungay using the MAXENT model



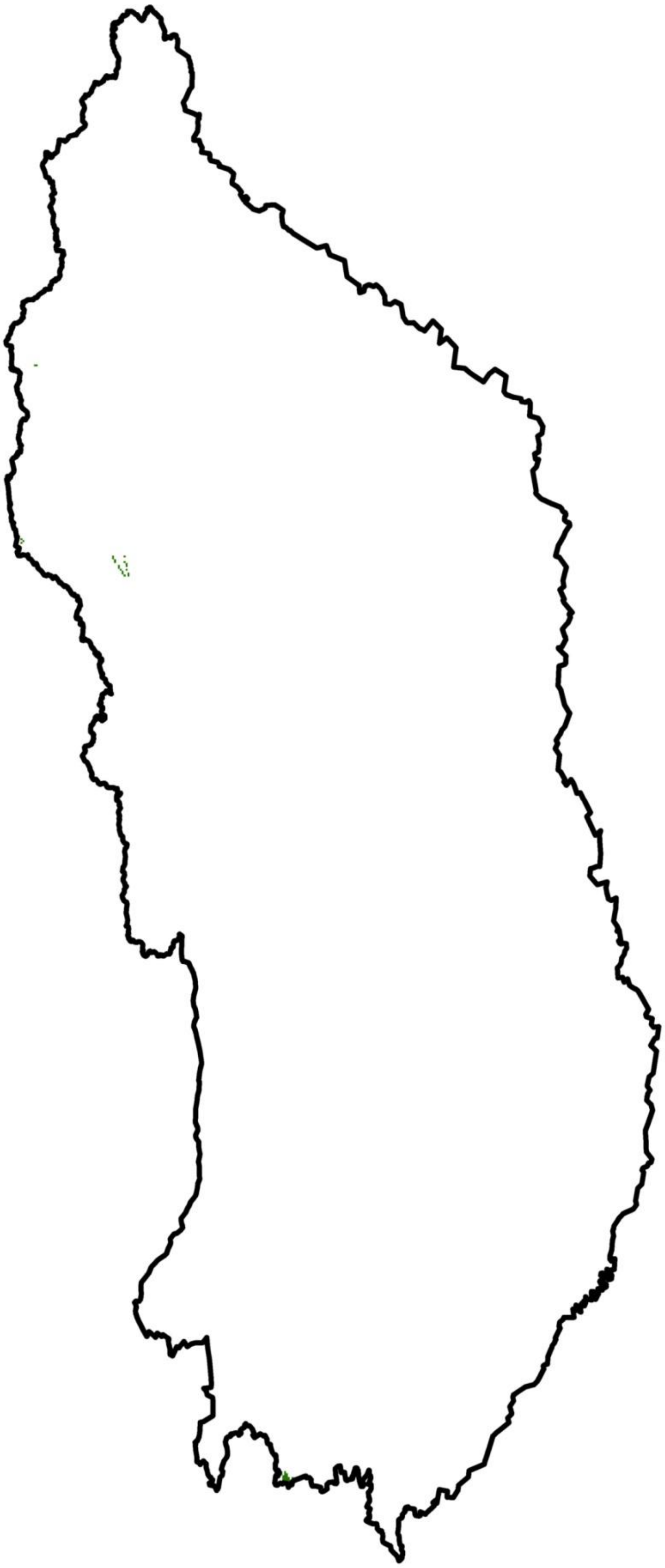
19. Potential future distribution of beech for 2011-2040 in Hungay using the MAXENT model



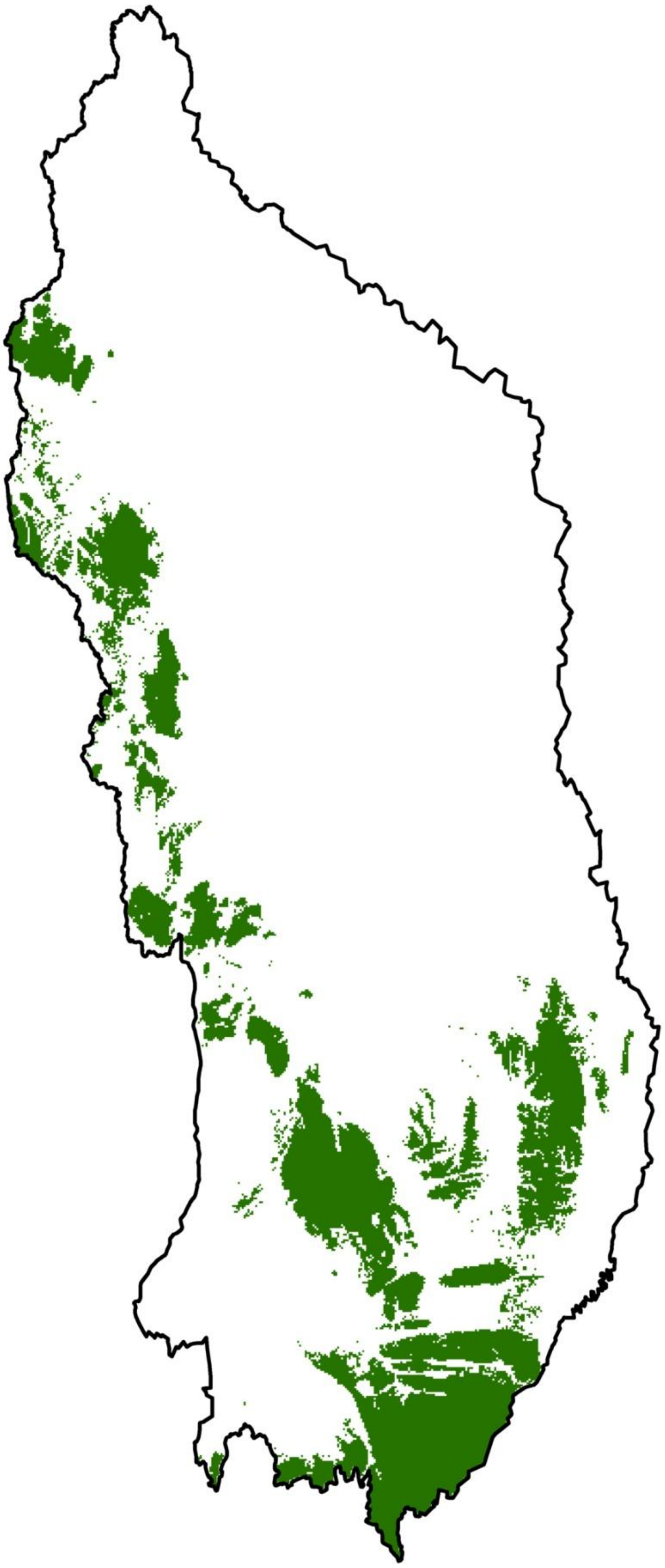
20. Potential future distribution of beech for 2036-2065 in Hungay using the MAXENT model



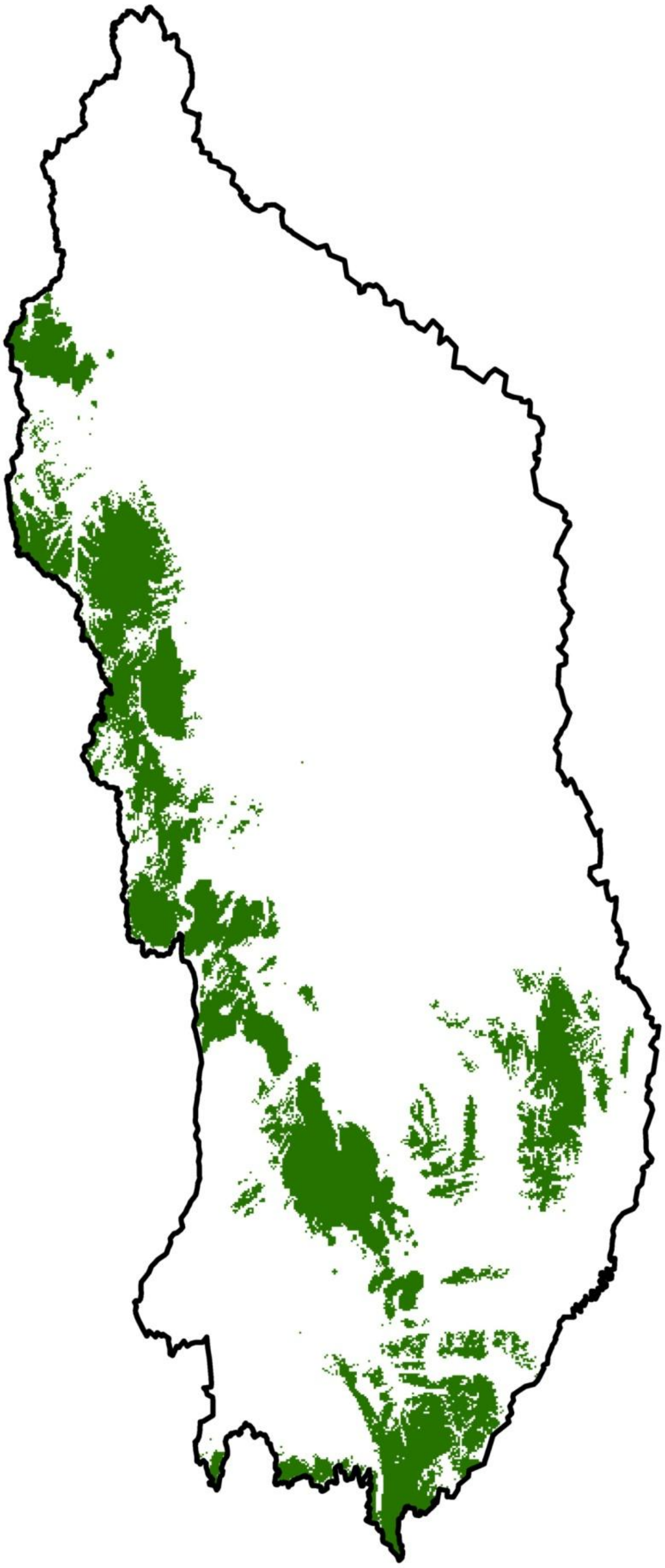
21. Potential future distribution of beech for 2066-2095 in Hungay using the MAXENT model



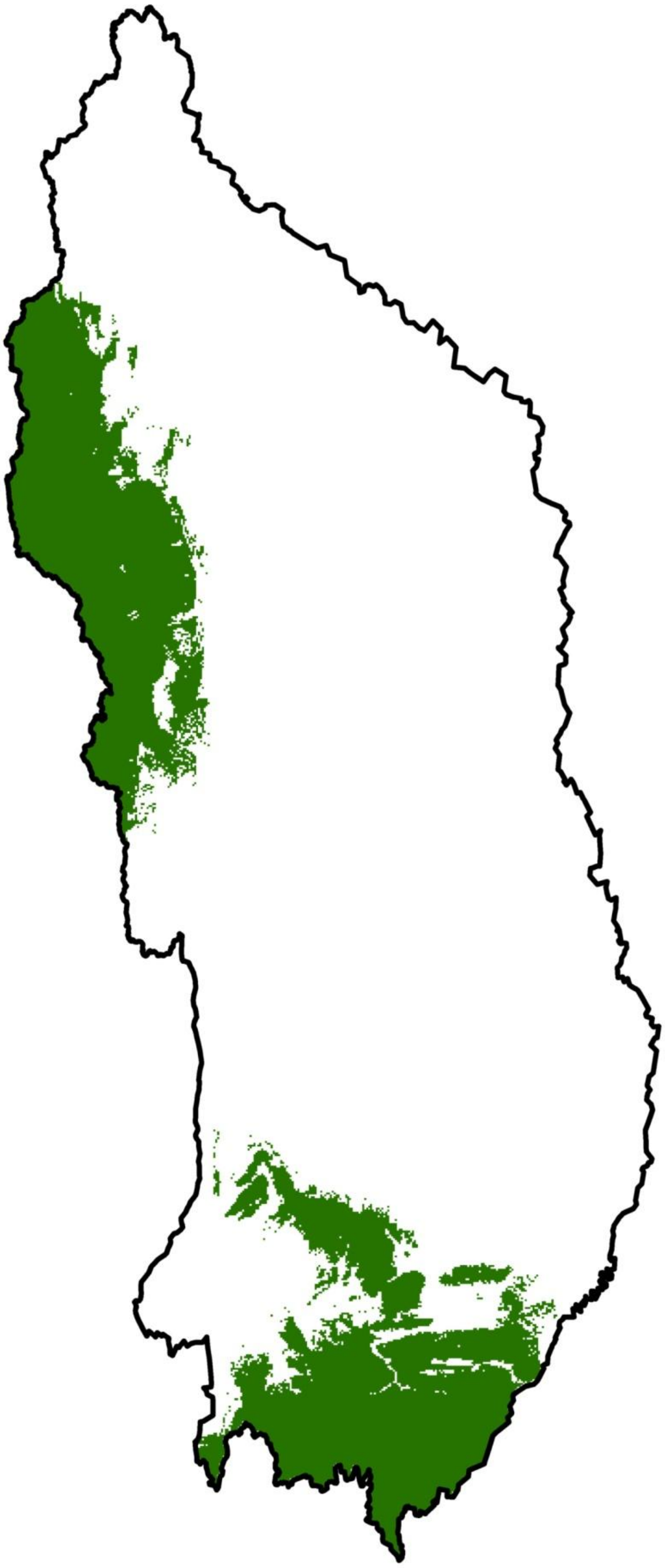
22. Potential current distribution of beech in Hungay using the GLM model



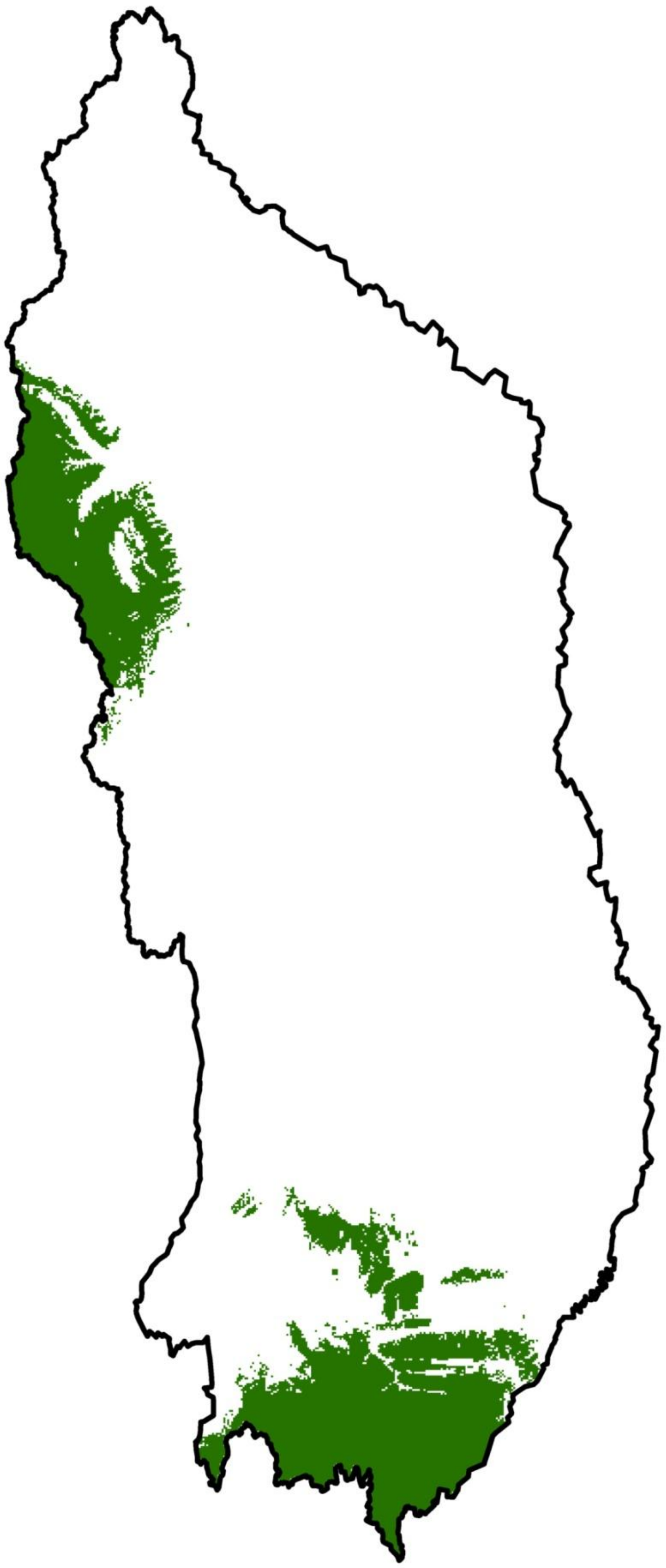
23. Potential future distribution of beech for 2011-2040 in Hungay using the GLM model



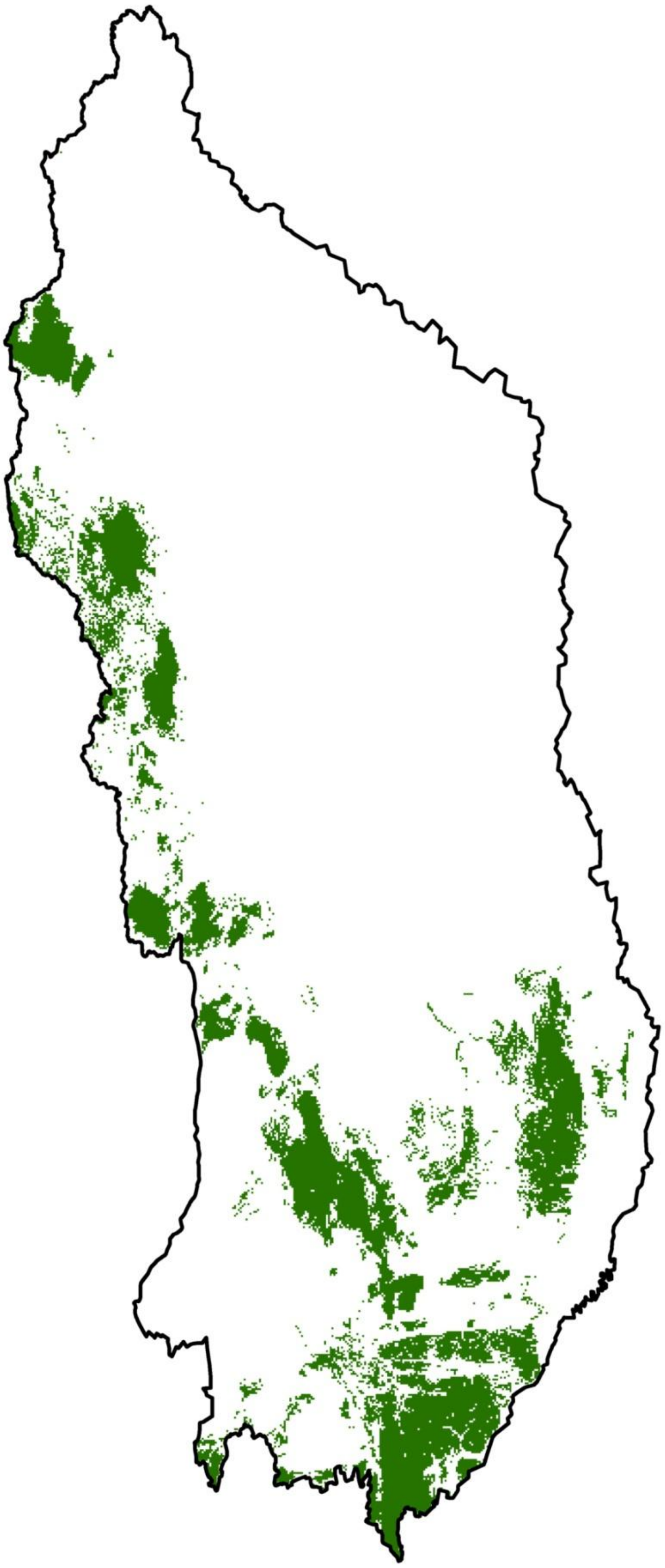
24. Potential future distribution of beech for 2036-2065 in Hungay using the GLM model



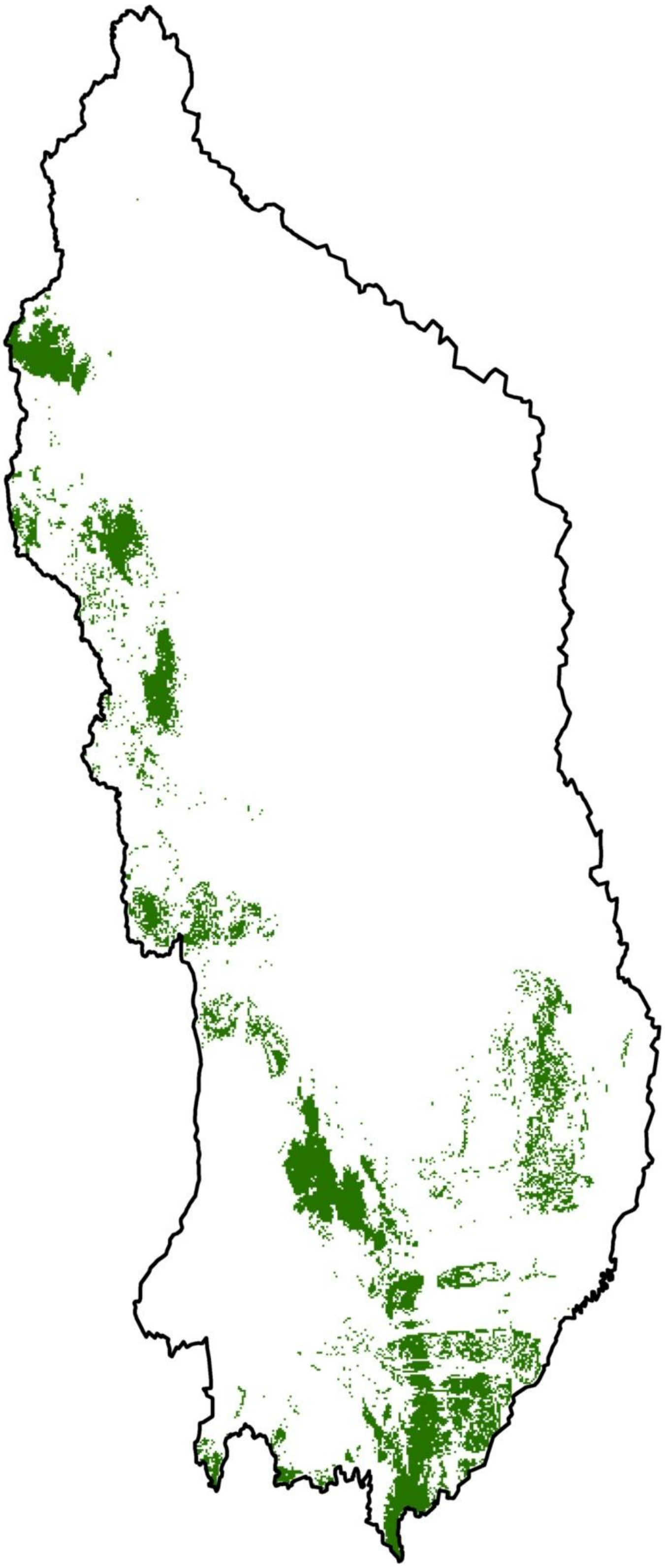
25. Potential future distribution of beech for 2066-2095 in Hungay using the GLM model



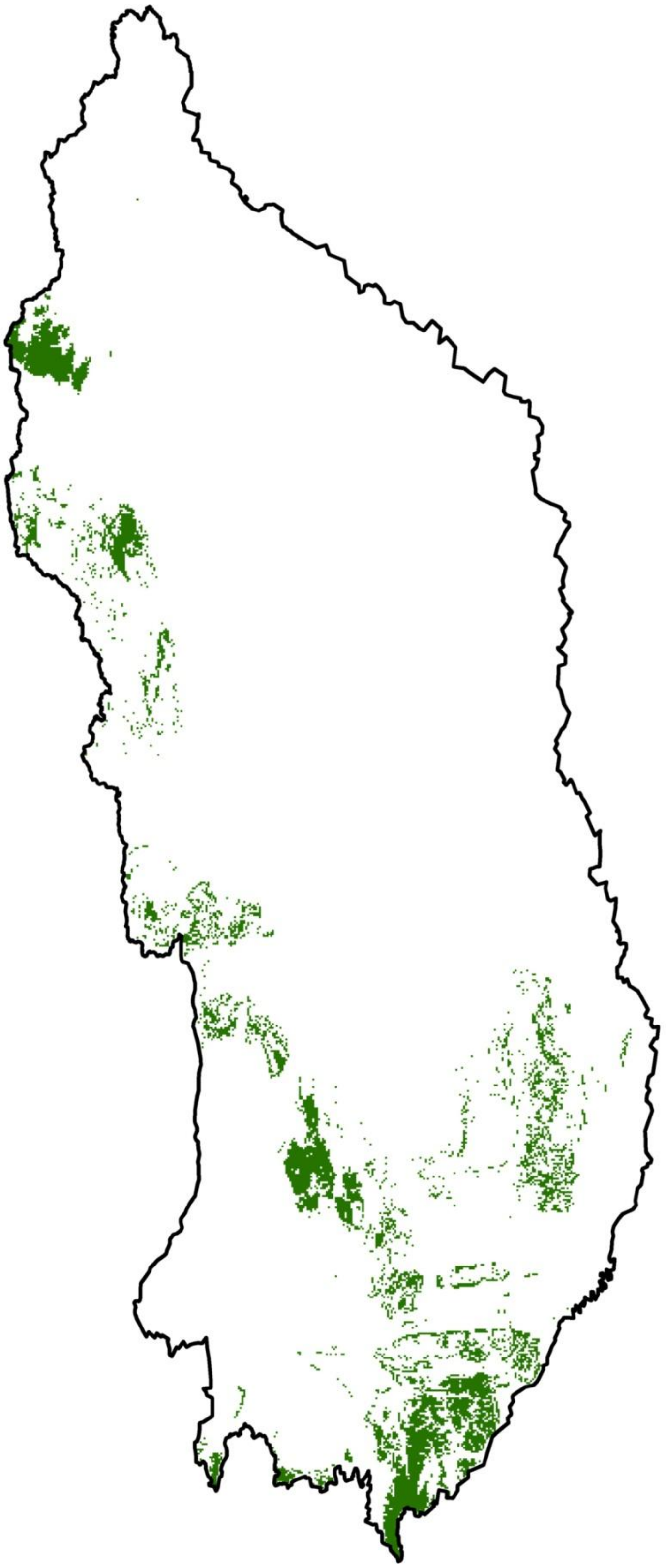
26. Potential current distribution of beech in Hungay using the CTree model



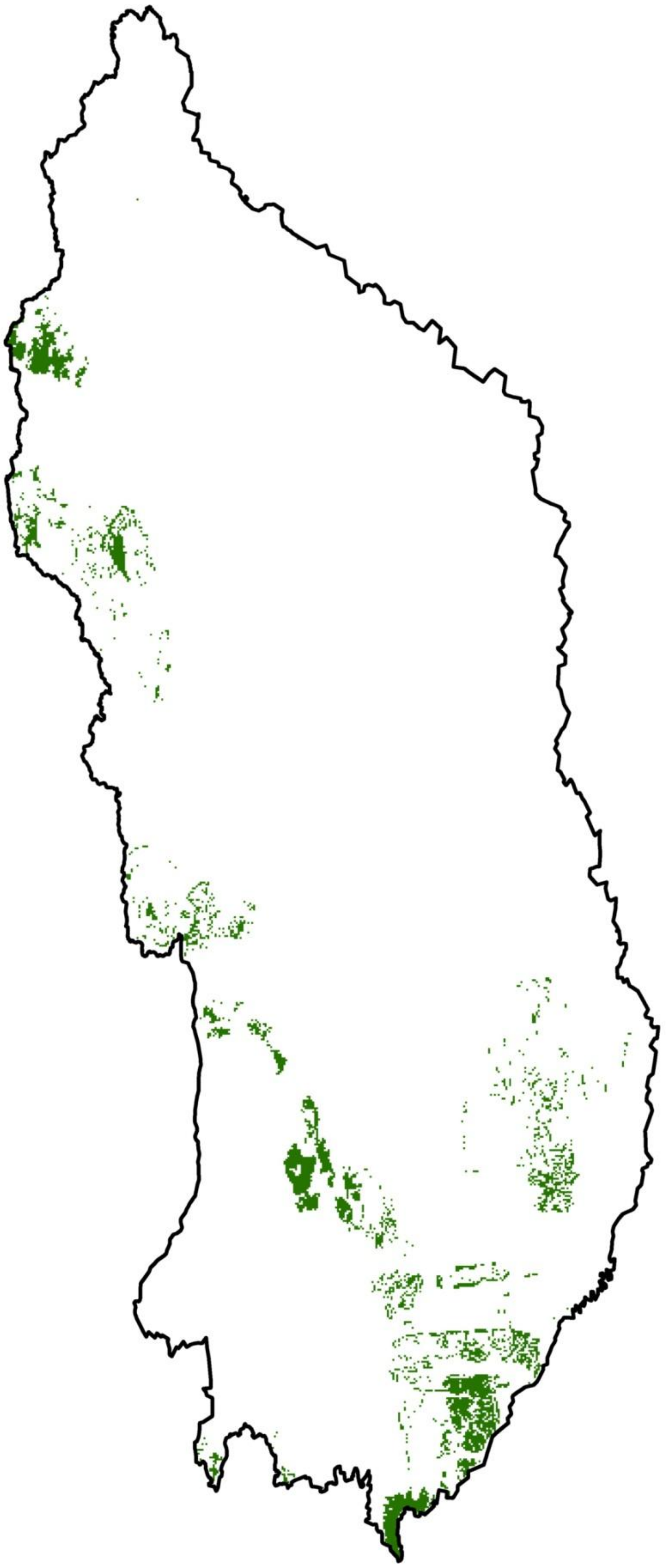
27. Potential future distribution of beech for 2011-2040 in Hungay using the CTree model



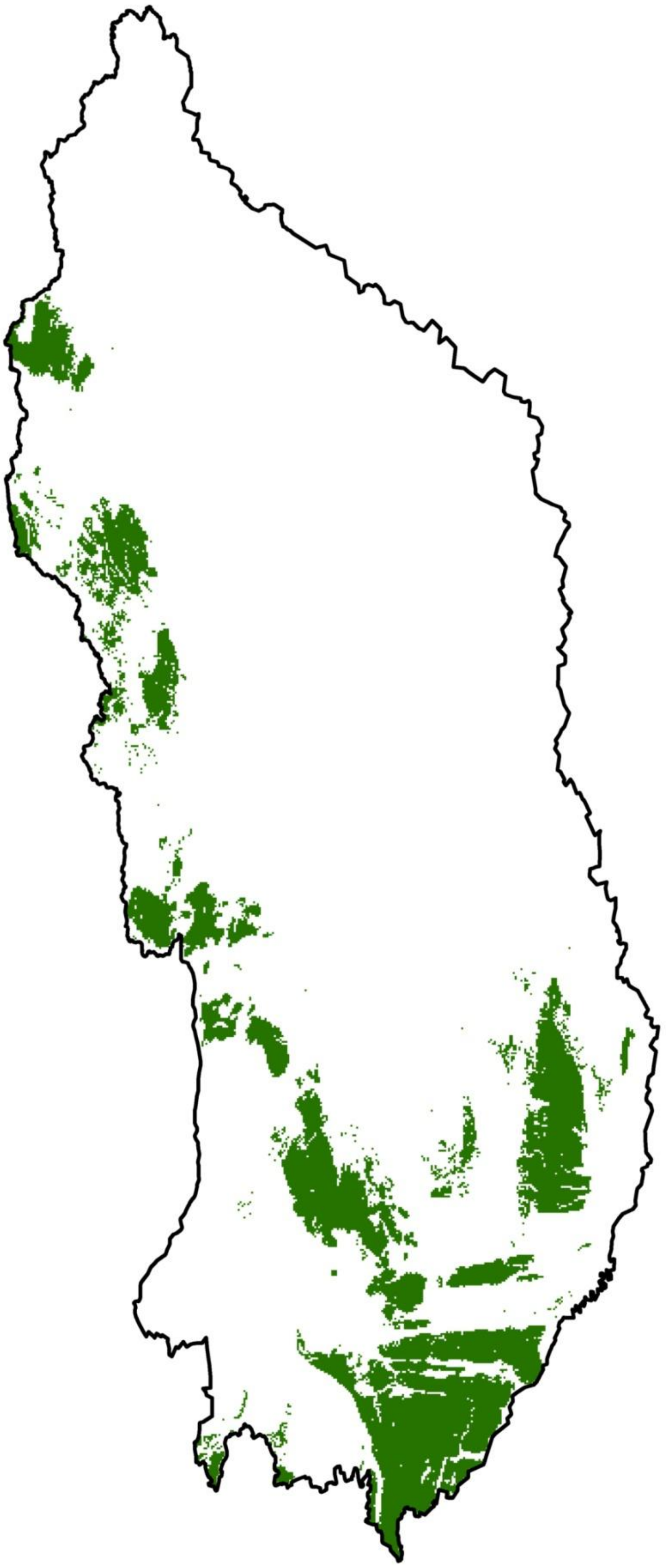
28. Potential future distribution of beech for 2036-2065 in Hungay using the CTree model



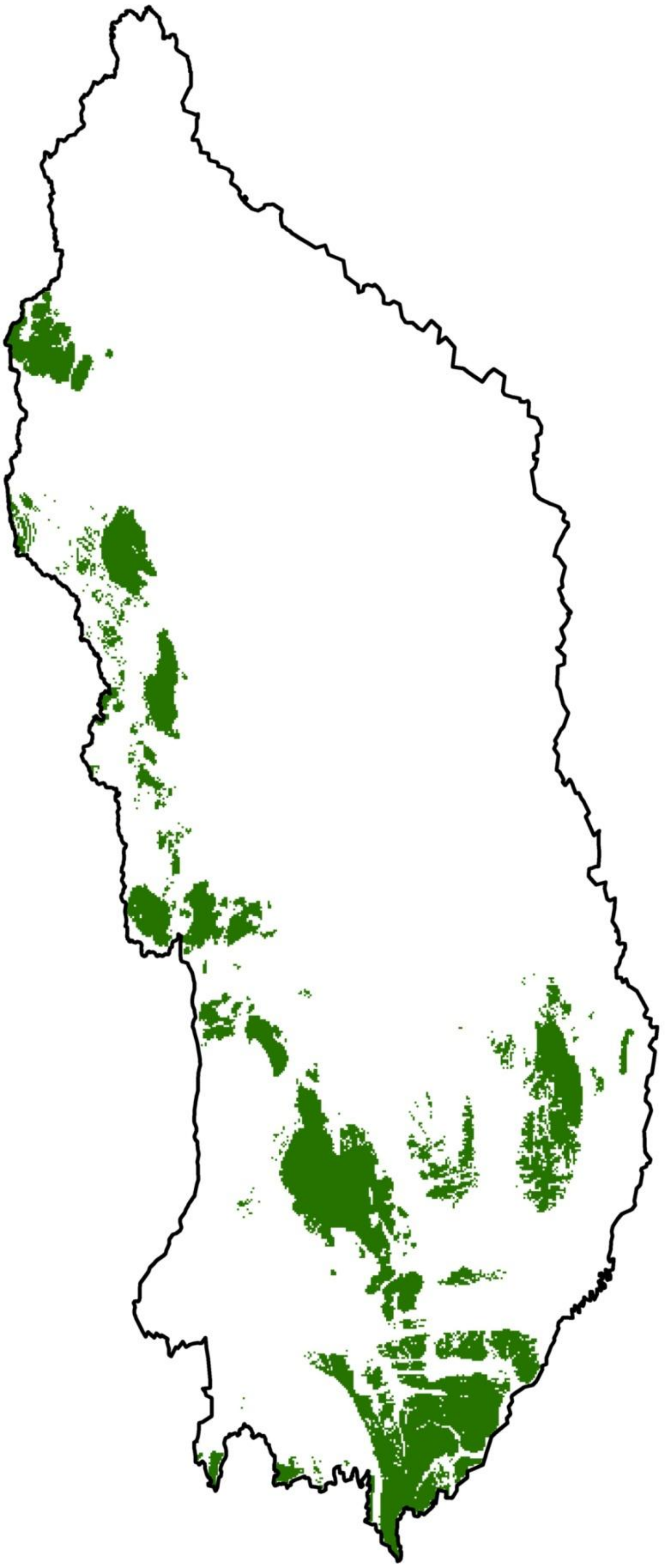
29. Potential future distribution of beech for 2066-2095 in Hungay using the CTree model



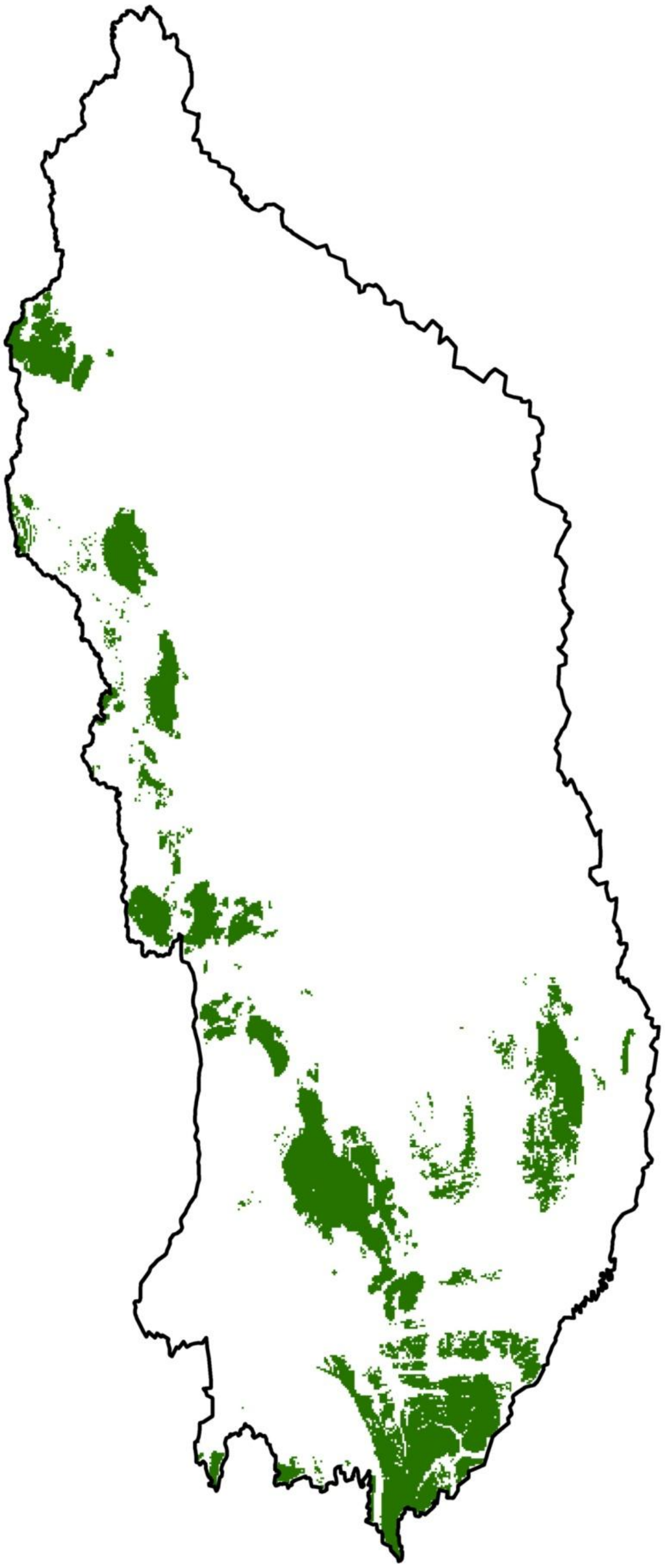
30. Potential current distribution of beech in Hungay using the BP-ANN model



31. Potential future distribution of beech for 2011-2040 in Hungay using the BP-ANN model



32. Potential future distribution of beech for 2036-2065 in Hungay using the BP-ANN model



33. Potential future distribution of beech for 2066-2095 in Hungay using the BP-ANN model