Impact of Species Parameter Uncertainty in Simulations of Tree Species Migration with a Spatially Linked Dynamic Model

Julia E.M.S. Nabel [a], Natalie Zurbriggen[a b], Heike Lischke[a]

[a] *Dynamic Macroecology, Landscape Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland (Julia.Nabel@wsl.ch, Natalie.Zurbriggen@wsl.ch, Heike.Lischke@wsl.ch)*

[b] *Forest Ecology, Institute of Terrestrial Ecosystems, Swiss Federal Institute of Technology ETH, Universitätstr. 22, 8092 Zurich, Switzerland*

Abstract: The simulation of tree species migration suffers from many sources of uncertainty. In our study we examined the influence of species parameter uncertainty on simulated tree species migration, using the spatially linked dynamic forest landscape model TreeMig. The impact of uncertainty becomes especially apparent under critical conditions arising from the interaction of species sensitivities to climate, species competition and spatial fragmentation. Therefore we examined the differences in migration success and speed in a realistic scenario including these critical conditions. The south-north migration of the submediterranean tree species *Ostrya carpinifolia* through the highly fragmented and climatically heterogeneous landscape of the Swiss Alps was simulated for 27 different species parameter sets covering the plausible range of species parameters for *O. carpinifolia*. To account for the additional uncertainty introduced by the stochastic representation of future climate variability, each species parameter set was simulated with multiple repetitions. We found that migration success and speed resulting from simulations with the different sets varied highly. The current situation of rapid climate change and high landscape fragmentation due to human land use could create critical conditions comparable to the simulated scenario for various species. We therefore recommend testing for species parameter sensitivities and – if indicated – to repeat simulations with different parameter sets when projecting future tree species distributions with explicit simulation of migration.

Keywords: Tree species migration; spatially linked dynamic model; species parameter uncertainty; TreeMig

1 INTRODUCTION

The capabilities of plants to track climate changes crucially influence future plant species distributions, because climate controls many key processes, such as establishment, growth and mortality. In particular the migration of tree species can lag behind rapid climate changes, amongst others due to their long generation times [FAO, 2010]. Despite the acknowledged importance of migration, many modelling studies projecting future plant distribution do not explicitly model migration [Thuiller et al., 2008]. One reason is the requirement for sufficiently accurate spatial and temporal representations of several processes and interactions involved, for example, maturation, seed dispersal and establishment in competitive situations driven by environmental influences. In contrast to other

model types, spatially linked dynamic models can fulfil this requirement, if they make a successful trade-off between accuracy and computational efficiency (time and memory). One such model is TreeMig [Lischke et al., 2006], the model used for the present study. TreeMig approaches the trade-off between accuracy and computational efficiency by employing a distribution-based representation of the local spatial forest heterogeneity and by applying empirically derived formulations of important processes and species parameters characterising species traits. Empirically derived species parameters, however, are associated with uncertainties. Bugmann [1994] has shown that such uncertainties have small influences on the overall species composition, but can impact single species abundances in simulations with the forest gap model ForClim, the predecessor model of TreeMig. The influence of species parameter uncertainties on tree species migration simulated with TreeMig has not been examined so far and is considered in the present study.

Additional sources of uncertainty include assumptions about model drivers. The bioclimatic drivers, used to represent climate in TreeMig, directly influence simulated tree species growth, establishment and mortality and therefore migration. Simulations of tree species migration requires long-term climate data, which is often not available. One approach to generate climatic influences, for time-spans exceeding measured data or predictions of climate models, is the sampling from distributions based on available data, as proposed in Bugmann [2001] and applied in TreeMig [Lischke et al., 2006]. The present study explored potential influences of species parameter uncertainty on tree species migration, taking into account this stochastic sampling from distributions. The impact of uncertainties presumably becomes most obvious where a species is not abundant, hence in critical situations, which for example can arise from the interaction of species limitations, presence of competitors and spatial fragmentation. Therefore we examined the differences in migration success and speed among different species parameter sets within the plausible parameter range of an example species under realistic and critical conditions. The simulation scenario was a south-north migration of the submediterranean tree species *Ostrya carpinifolia* in a transect through the Swiss Alps, a highly fragmented and climatically heterogeneous landscape.

2 METHODS

2.1 Model

The applied TreeMig version is described in Lischke et al. [2006] with amendments described in Rickebusch et al. [2007]. TreeMig is a grid-based, spatially linked dynamic forest landscape model with a spatial resolution of 1km^2 and yearly time steps. It is designed for use at regional to subcontinental extent. The local dynamics are calculated on height-structured distributions which can be regarded as aggregations of single patches with individual trees [Lischke et al., 1998]. This aggregation covers the small scale stochasticity representing local processes in gap models, such as establishment and mortality. It was introduced to replace multiple single patch repetitions with a deterministic representation and thereby to counterbalance the increase in computational complexity accompanying the spatial linkage and the increased spatial extent compared to single site simulations in forest gap models. However, the model still has a high computational complexity and the approximate computation time for each 1km^2 cell and each year amounts to 0.001 seconds on a 2.8GHz CPU of an AMD Opteron cluster.

The driving variables of the model are three bioclimate variables per year and cell: degree-day sum (sum of daily mean temperatures above 5.5 °C), minimum winter temperature (average temperature of the coldest winter month) and an index describing the severity of drought events. These variables can be derived from monthly mean temperatures, monthly precipitation sums and constant site data (slope, aspect and water
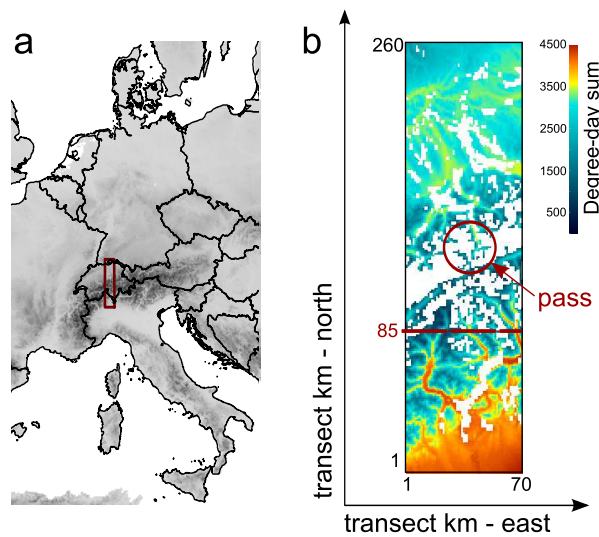
Figure 1. The 260km x 70km simulation transect (1km^2 cells). Panel a shows the location in central Europe. In panel b the mean degree-day sum (sum of daily mean temperatures above 5.5 °C) of the distributions used for bioclimatic influences after 2100 is depicted. White areas represent non-stockable cells, i.e. cells where trees can not grow. The circle marks the pass through the Swiss Alps and the dashed line at km 85 the starting point for the migration of *Ostrya carpinifolia* in the year 1800.

storage capacity) with the model ForClim-E [Bugmann and Cramer, 1998]. In addition to the bioclimate variables, a zero-one mask is required, which indicates for each cell if it is stockable, i.e. if something can grow in this cell. Cells with a stockability of zero can, for example, represent big water bodies, solid rock surfaces or different kinds of human land use. The mask is constant over time and is the main representation of fragmentation.

2.2 Simulation setup

The simulated scenario was a south-north migration of the submediterranean tree species *Ostrya carpinifolia* in a 260km x 70km transect (see Figure 1). Most of the cells in the area of the Swiss Alps, in the centre of the transect, are bare rock surfaces, regarded as not stockable for trees in TreeMig. Therefore the only possibility to cross the Swiss Alps in the simulations is through one pass with several bottlenecks (see Figure 1, panel b). *O. carpinifolia* is currently limited to the southern side of the Swiss Alps, according to the Swiss National Forest Inventory (NFI) [2004/06] and to the European Forest Data Center [2000]. In addition to *O. carpinifolia*, 21 other species (*Abies alba, Larix decidua, Picea abies, Pinus cembra, P. sylvestris, Taxus baccata, Acer platanoides, A. pseudoplatanus, Alnus incana, Betula pendula, Carpinus betulus, Castanea sativa, Fagus sylvatica, Fraxinus excelsior, Populus tremula, Quercus petraea, Q. pubescens, Sorbus aucuparia, Tilia cordata, T. platyphyllos, Ulmus scabra*) were included as competitors in the simulations. All species besides *Quercus pubescens*, which was added because of its importance at dry sites, are in the list of the 30 species identified as most abundant in Switzerland in the first Swiss NFI [Brändli, 1998].

The TreeMig simulations were computed for 1600 years (1400-3000). The bioclimate variables were derived from past climate (1901-2000: CRU data [Mitchell et al., 2003]) and from SRESA1B [Nakicenovic, N. et al., 2000] projections calculated with the regional climate model CLM (2001-2100) [Lautenschlager et al., 2009]. Both data sets were first

Table 1. Species parameters influencing fertility and competitiveness of *O. carpinifolia*. Listed are original, most optimistic and most pessimistic values – for max. height, max. age, min. height required for maturity, max. number of seeds, indices for sapling and adult shade tolerance, max. height growth rate, low nitrogen tolerance index and browsing susceptibility index.

Parameter	Max. h. [m]	Max. age [a]	Min. maturity h. [m]	Max. seeds	Sapl. shade tol.	Adult shade tol.	Max. growth [cm/a]	N tol. index	Browse sus. index
Original	16	150	3.4	91259	5	3	134	2	3
Optimistic	23[a]	200[b]	1.94	131185	3	1	161	1	2
Pessimistic	9	100[c]	4.9	51333	7	5	107	3	3
Uncertainty	± 7	± 50	$\pm 1.5^{e}$	$\pm 39926^{e}$	$\pm 2^{d}$	$\pm 2^{d}$	$\pm 30\,\%^{d}$	$\pm 1^{d}$	$\pm 1^{d}$

[a] Noack [1979] and Korkut and Guller [2008]; [b] Franz [2002]; [c] Hecker [1998]; [d] Bugmann [1994].
[e] Parameters estimated according to the uncertainty for species height (43.75 %).

downscaled to 30" using WorldClim data [Hijmans et al., 2005] and then projected with FIMEX-0.28 [Klein, 2012] to an Albers equal area projection of 1km^2 resolution using a bilinear interpolation.

The first 400 years (1400-1800) of the simulation were used as an initial spin-up phase with a general availability of propagules instead of simulating seed production and dispersal (cf. [Lischke et al., 2006]). In congruence with its approximate current distribution, *O. carpinifolia* was restricted to the the lower 85km of the transect (Figure 1, panel b) until the end of the spin-up phase. The bioclimate was stochastically drawn from distributions based on the years 1901-1931. After the 400 spin-up years, seed production and dispersal were enabled and the restriction of *O. carpinifolia* was removed. The bioclimate was drawn for another 100 years (1801-1900) from the 1901-1931 distributions. The subsequent 200 years represent the near past and the future up to 2100 for which yearly bioclimate values were available. After 2100 the bioclimate was stochastically drawn for another 900 years (2101-3000) from distributions based on the years 2071-2100.

2.3 Species parameters and species parameter plausibility ranges

The original parameter values for *Ostrya carpinifolia*, as well as the uncertainty in these parameters, are listed in Table 1 (parameters influencing fertility and competitiveness of *O. carpinifolia*) and Table 2 (parameters influencing the sensitivity to bioclimate). Most of the original values were taken from the Mediterranean mountain forest gap model GRE-FOS [Fyllas and Troumbis, 2009], which was possible, because GREFOS and TreeMig are both descendants of the forest gap model ForClim [Bugmann, 1994; Bugmann and Cramer, 1998] and therefore share important similarities in the calculations of local dynamics. Two parameters had to be transformed according to known relationships with regard to differences between ForClim and TreeMig (indices for sapling and adult shade tolerance). Another two parameters were scaled according to empirical relationships observed in other TreeMig species (max. number of seeds; max. growth rate). The remaining unknown parameter values (min. maturity height; low nitrogen tolerance index; browsing susceptibility index) and the probability kernel used for seed dispersal in TreeMig (see [Lischke et al., 2006] for more details) were taken from *Carpinus betulus*, which was already parametrised in TreeMig and – like *O. carpinifolia* – belongs to the *Coryloideae* subfamily.

Table 2. Species parameters influencing the sensitivity of *O. carpinifolia* to the bioclimatic drivers. Listed are original, most optimistic and most pessimistic values.

Parameter	Min. Degree-day sum	Min. wintertemp. [$^\circ$C]	Drought index
Original	1200	-10	0.33
Optimistic	960	-12	0.43
Pessimistic	1440	-8	0.23
Uncertainty	$\pm 20\,\%^{a}$	$\pm 2\,^\circ\mathrm{C}^{a}$	$\pm 0.1^{a}$

^{a} All parameter plausibility ranges originate from Bugmann [1994].

2.4 Simulations

The number of possible simulations was constrained due to the computational complexity of TreeMig. One single run of the simulation setup (1600 years and 260 x 70 cells) took approximately 21'840 seconds, i.e. around 6 hours, of computation time on a 2.8GHz CPU of an AMD Opteron cluster. Moreover, it was necessary to make multiple runs with different pseudo-random number (prn) streams, to account for the stochastic representation of future climatic influences. Each of the different species parameter sets was thus simulated 20 times with varying prn streams.

Since *O. carpinifolia* is known to be limited to warm temperatures and is suspected of being able to grow under conditions which are too dry for *Fagus sylvatica* (e.g. [Brändli, 1998; Noack, 1979]), the uncertainties in the bioclimate sensitivities listed in Table 2 are of special interest and were therefore in the focus when selecting species parameters for the simulations. However, the min. winter temperature sensitivity is only used as a threshold in TreeMig to determine if establishment is possible at all. Therefore, it was possible to exclude its uncertainties based on the fact that the most pessimistic value for *O. carpinifolia* (-8 $^\circ$C) was already significantly lower than the mean min. winter temperature (-4 $^\circ$C$\pm$ -2 $^\circ$C) found in the distributions used to draw future bioclimatic influences.

We simulated 27 species parameter sets, resulting from all combinations of the most optimistic, the original and the most pessimistic parameters for (1) the minimum required degree-day sum, (2) the drought tolerance index and (3) all other parameters (Table 1).

3 RESULTS

Table 3 shows the results for several measures calculated from the 20 repetitions for each of the 27 simulated species parameter sets. Migration success – defined as successfully crossing the two main stagnation points[1] at km 117 and km 137 (see Figure 2 dashed lines for a visualisation) – thereby depended most on the temperature sensitivity. A complete inhibition of migration within the simulated timespan only occurred for the three most pessimistic parameter sets, with either all parameters at the pessimistic end of the plausibility range, or with drought or temperature having its original value (for the most pessimistic runs see Figure 2, panel a). The variability between the 20 repetitions – measured as the standard deviation of the year in which the first stagnation point at km 117 was passed – is very low for all scenarios, except for the ones with pessimistic values for the temperature sensitivity. In contrast to the differing influences on migration success, all parameter changes for temperature and drought sensitivity, as well as for the group of all other parameters comparably affected migration speed of the furthest run. Parameter changes from optimistic to original or from original to pessimistic values led to a slowdown of 3 – 22 m/a (see Table 3 '(3) avg. speed of the furthest run' and Figure 2).

---

[1]Since the Alps lie diagonally in the transect (see Figure 1), the two stagnation points are not the actual bottlenecks of the pass but the furthest reachable dead ends east of the bottlenecks.

Table 3. Measures calculated from the 20 repetitions of each of the 27 simulated species parameter sets. The main columns show the measures: (1) mean year in which the first stagnation point at km 117 (Figure 2) was passed in the 20 runs, together with the standard deviation (in years) and, if not all runs passed km 117, the number of runs which did so; (2) the number of runs which passed the second stagnation point at km 137 and (3) the average speed of the run with the furthest migration distance.

T	D	(1) Mean year passed km 117 ± std (#of runs if not all passed)			(2) # passed km 137			(3) Avg. speed furthest run [m/a]		
		Other paras. (Table 1)			Other paras.			Other paras.		
		+	o	-	+	o	-	+	o	-
+	+	2072±0	2083±9	2123±9	20	20	20	109	90	68
+	o	2072±0	2083±12	2134±12	20	20	20	101	83	61
+	-	2072±0	2085±15	2165±15	20	20	20	90	73	51
o	+	2089±0	2120±10	2201±10	20	20	20	101	83	61
o	o	2089±0	2124±9	2234±9	20	20	20	94	76	54
o	-	2089±0	2147±19	2348±19	20	20	0	82	62	–
-	+	2442±237(19)	2522±262(17)	2621±235(11)	8	5	2	83	61	49
-	o	2443±237(19)	2604±219(17)	2720±208(12)	8	3	0	78	58	–
-	-	2528±250(19)	2627±205(17)	2806±107(6)	6	2	0	61	51	–

(T) temperature and (D) drought sensitivity (Table 2); '+' optimistic, 'o' original and '-' pessimistic values.

4 DISCUSSION

Migration speeds resulting from simulations with different parameter sets (50 − 110 m/a) were in the expected ranges [Svenning and Skov, 2007]. However, we found that species migration can be highly sensitive to species parametrisation, which is in agreement with the findings of Bugmann [1994] for single species abundances. Migration outside of the pass situation was not influenced to the same degree (see Figure 2) as inside the pass, despite the similar temperature influence on the cells in the near neighbourhood of the pass (see Figure 1, panel b). This simulation result indicates that the high fragmentation and the 'pass situation' are the main triggers for changes in the migration success. In the bottleneck situation of the pass, the temperature sensitivity appeared to be particularly important for the migration success, which agrees with the fact that temperature is the limiting factor for submediterranean species in the Swiss Alps. Although the selected scenario is a specific critical situation, the current global conditions of rapid climate change and high fragmentation of the landscape due to human land use could create comparably critical situations for various other species.
The variance in the results for repetitions of the same scenario indicates that the stochasticity in the climate driver can have an important impact. This impact might even be higher if spatial autocorrelation in the climatic influences was taken into account which is not the case in the current approach, where sampling from independent distributions is applied for each cell. This will be subject of future studies.

5 CONCLUSIONS AND RECOMMENDATIONS

The present study illustrates the necessity of sensitivity and uncertainty analyses in spatially linked dynamic modelling of tree species migration. The results emphasise that simulations with different parameter sets and multiple repetitions can be essential in estimating migration speed and migration success when simulating single species migration. The study also underlines the key role of the trade-off between computational efficiency and model specificity, and shows the need for further investigations into reducing computational costs in order to facilitate comprehensive simulation studies.
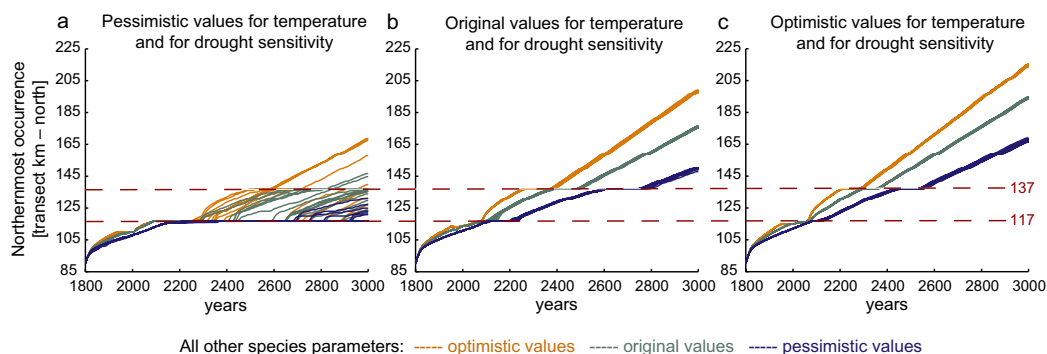
Figure 2. Northernmost occurrence (transect km - north – smoothed over 20 year periods) for the years 1800-3000, starting at km 85, to which *Ostrya carpinifolia* was restricted until 1800. Depicted are the results of simulations with different species parameter sets used for *O. carpinifolia*. The panels show the results for three out of nine combinations of parameter values for temperature and drought sensitivities: both pessimistic (panel a), both original (panel b) and both optimistic (panel c). The different colours represent scenarios of parameter values for all other parameters (see Table 1). In each panel, series of lines with the same colour depict the results of 20 repetitions with the according parameter set. The dashed horizontal lines mark the two main stagnation points at km 117 and km 137.

REFERENCES

Brändli, U.-B. Die häufigsten Waldbäume der Schweiz. Ergebnisse aus dem Landesforstinventar 1983-85: Verbreitung, Standort und Häufigkeit von 30 Baumarten. Berichte der Eidgenöss. Forschungsanstalt für Wald, Schnee und Landschaft, 1998.

Bugmann, H. A Review of Forest Gap Models. *Climatic Change*, 51:259–305, 2001.

Bugmann, H. and W. Cramer. Improving the behaviour of forest gap models along drought gradients. *Forest Ecology and Management*, 103:247–263, 1998.

Bugmann, H. *On the Ecology of Mountainous Forests in a Changing Climate: A Simulation Study*. PhD thesis, Swiss Federal Institute of Technology Zurich, 1994.

European Forest Data Center. Distribution of *Ostrya Carpinifolia*. Accessed from `http://efdac.jrc.ec.europa.eu/index.php/climate`, on 28.01.2012, 2000.

FAO. Global forest resources assessment 2010. Food and Agriculture Organization of the United Nations (FAO), Rome, `http://www.fao.org/docrep/013/i1757e/i1757e.pdf`. Latest access date: 20.12.11, 2010.

Franz, W. R. Die Hopfenbuche (Ostrya carpinifolia Scop.) in Österreich und Nordslowenien. Carinthia II. Naturwissenschaftliche Beiträge zur Heimatkunde Kärntens, Klagenfurt, 58. Sonderheft: 256 S., 2002.

Fyllas, N. M. and A. Y. Troumbis. Simulating vegetation shifts in north-eastern Mediterranean mountain forests under climatic change scenarios. *Global Ecology and Biogeography*, 18:64–77, 2009.

Hecker, U. Handbuch Bäume und Sträucher. Einbändige Neuausgabe der BLV Intensivführer Laubgehölze und Nadelgehölze - 2., durchges. Aufl. - München; Wien; Zürich: BLV, ISBN 3-405-14738-7, 1998.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25:1965–1978, 2005.

Klein, H. FIMEX-0.28. `https://wiki.met.no/fimex/start`. Last access date: 09.01.12, 2012.

Korkut, S. and B. Guller. Physical and mechanical properties of European Hophornbeam (Ostrya carpinifolia Scop.) wood. *Bioresource Technology*, 99:4780–4785, 2008.

Lautenschlager, M., K. Keuler, C. Wunram, E. Keup-Thiel, M. Schubert, A. Will, B. Rockel, and U. Boehm. Climate Simulation with CLM, Scenario A1B run no.1, Data Stream 3: European region MPI-M/MaD. World Data Center for Climate. `http://dx.doi.org/10.1594/WDCC/CLM_A1B_1_D3`, 2009.

Lischke, H., T. J. Löffler, and A. Fischlin. Aggregation of Individual Trees and Patches in Forest Succession Models: Capturing Variability with Height Structured, Random, Spatial Distributions. *Theoretical Population Biology*, 54:213–226, 1998.

Lischke, H., N. E. Zimmermann, J. Bolliger, S. Rickebusch, and T. J. Löffler. TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling*, 199:409–420, 2006.

Mitchell, T., T. Carter, P. Jones, M. , Hulme, and M. New. A comprehensive set of climate scenarios for Europe and the globe. Tyndall centre Working paper 55, 2003.

Nakicenovic, N. et al. *IPCC Special Report on Emissions Scenarios*. Cambridge University Press, 2000.

Noack, H. Das Portrait. Ostrya carpinifolia Scop. (Hopfenbuche). Mitteilungen der Deutschen Dendrologischen Gesellschaft, Nr 71, 257-259, 1979.

Rickebusch, S., H. Lischke, H. Bugmann, A. Guisan, and N. E. Zimmermann. Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data. *For. Ecol. Manage.*, 246:251–263, 2007.

Svenning, J.-C. and F. Skov. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters*, 10:453–460, 2007.

Swiss National Forest Inventory (NFI). Occurrence of *Ostrya Carpinifolia* in the different biogeographical regions of Switzerland according to the NFI3 grid. Accessed from `http://www.lfi.ch/resultate/regionen-en.php`, on 28.01.2012, 2004/06.

Thuiller, W., C. Albert, M. B. Arajo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, 9:137–152, 2008.