

Predicting distribution patterns and recent northward range shift of an invasive aquatic plant: *Elodea canadensis* in Europe

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Abstract

Climate data and distribution data for the Canadian waterweed *Elodea canadensis* Michx. from North America, whole Europe and Finland were used to investigate the ability of bioclimatic envelope models to predict the distribution range and recent northward range shift of the species in Europe. Four different main types of models were developed using the North American data, including either three ‘baseline’ climate variables (growing degrees days, temperature of the coldest month, water balance) or an extended set of seven climate variables, both averaged either over a 30 year time slice or a longer 90 year time slice. Ten different random selections of pseudo-absences were generated from the North American data, on the basis of which ten separate generalized additive models (GAMs) were developed for each main model type. All the 40 developed GAMs were applied first to North America and then transferred to whole Europe and Finland. All the models showed a statistically highly significant accuracy in the three study areas. Although the differences among the four main model types were only minor, the two extended model types showed on average statistically better performance than the two baseline models based on Bayesian information criterion (BIC) values, the amount of deviance explained by the models, resubstitution validation and four-fold cross-validation in North America. They also provided slightly more accurate predictions of climatically suitable area for *Elodea canadensis* in Finland both in 1961–1984 and 1985–2006. However, the projections from the individual extended models were more variable than projections from the baseline models. Thus model predictions based on a variety of predictor variables but only one selection of pseudo-

absences may be subject to biases, and outputs from multiple models should be investigated to better account for uncertainties in modelling. Overall, our results suggest that more attention should be paid to the careful selection of predictor variables and the use of multiple pseudo-absence sets in the ecological niche modelling in order to increase the reliability of the projections of the range shifts of invasive species.

Keywords

aquatic invasions, bioclimatic envelope model, Canadian waterweed, climate predictor, model performance, pseudo-absences, species distribution modelling, variable selection

Introduction

Invasive species are recognized as a major environmental problem which can have manifold ecological impacts (Mack et al. 2000, Weidema 2000, Peterson 2003a), cause high economical costs (Forman 2003, Pimentel 2005), change hydrological cycles, fire regimes and nutrient cycling, and cause significant environmental damage (Forman 2003). When successfully established into a new area, invasive species can displace populations of native species, threaten rare species and ultimately cause local extinctions attributable to predation, grazing and habitat alteration (Forman 2003, Rahel and Olden 2008), and more rarely competition (Davis 2003, Sax and Gaines 2008).

The spread of invasive species will probably be accelerated by the on-going and projected climate change (Dukes and Mooney 1999, Weber 2001, Hellmann et al. 2008). The magnitude of the projected global warming is particularly high in northern latitudes (ACIA 2005), including northern Europe, and thus the likelihood of climate change-induced range shifts of invasive species is pronounced in such areas (Rahel and Olden 2008). In southern and central Europe, warming climate has already boosted the spread of many invasive species, e.g. palms (Walther et al. 2007) and other exotic evergreen broad-leaved plant species (Walther et al. 2001), and thermophilic tropical and Capensis ornamental plants (Vesperinas et al. 2001). Similar evidence is accumulating from northern Europe (Weidema 2000, ACIA 2005), but more systematic analyses of the observed range shifts of invasive species in relation to recent climatic changes are largely lacking.

Identification of areas most at risk of becoming invaded by a given alien species and projections of the further spread of already naturalised species can provide valuable information for management planning (Weber 2001, Mau-Crimmins et al. 2006) and targeting control measures (Kriticos et al. 2003, Richardson and Thuiller 2007). One proactive approach to identify areas at risk is provided by ecological niche modelling (Weber 2001, Roura-Pascual et al. 2004, Ficetola et al. 2007). The main steps in ecological niche modelling include: (i) relating the known occurrences of the target species to the ecological characteristics of the study landscape, (ii) producing a model that defines the ecological dimensions of the species niche, and (iii) projecting the derived ecological niche model back onto the geographical space to identify regions with environmental conditions inside or outside the species' niche (Peterson and Vieglais 2001).

Ecological niche models can utilize many different environmental predictors such as climate, topography, soil classes and land cover (Peterson et al. 2003, Iguchi et al. 2004, Mau-Crimmins et al. 2006). However, at broad macroecological scales climate variables are often the only predictors available over large areas, and climate also largely determines species distributions (Thuiller et al. 2004, Luoto et al. 2007). Under such circumstances ecological niche modelling becomes materially the same as bioclimatic envelope modelling (Pearson and Dawson 2003, Guisan and Thuiller 2005). Indeed, increasing numbers of broad-scale applications of ecological niche models developed for invasive species have been based on climate variables (e.g. Beerling et al. 1995, Baker et al. 2000, Broennimann et al. 2007). This study also focuses on broad-scale species - climate models and the 'first-filter' identification of the areas potentially at risk of being invaded (Weber 2001, Welk 2004).

However, certain factors may decrease the usefulness of bioclimatic envelope models in modelling invasive species (Pearson and Dawson 2003, Thuiller 2004, Luoto et al. 2005, 2007, Heikkinen et al. 2006a, 2007). In this study we address three potential limitations. First, the selection of climate parameters may significantly affect the performance of the species - climate models (Beaumont et al. 2005, 2007, Heikkinen et al. 2006b, Loiselle et al. 2008, Peterson and Nakazawa 2008). Increasing attention should thus be paid to careful selection of climatic variables in order to model and assess potential future species distributions as accurately as possible (Heikkinen et al. 2006b, Beaumont et al. 2007, Peterson and Nakazawa 2008). Second, bioclimatic modelling studies often show a mismatch between the time slice over which the climate data is averaged and the time slice when species records have been collected, but it is insufficiently understood whether this affects model performance. Such mismatches are common in studies employing plant atlas data bases (such as Atlas Florae Europaeae; Jalas and Suominen 1988; <http://www.fmnh.helsinki.fi/english/botany/afe/>), which often include agglomerative records from several decades or even centuries (e.g. Beerling et al. 1995, Huntley et al. 1995, Sykes et al. 1996). Third, certain modelling methods require both presence and absence data. Many recent studies have adopted a strategy of selecting a set of pseudo-absences from the overall set of assumed absence data points to be used in the model calibration (e.g. McPherson et al. 2004, Guisan et al. 2007). The pseudo-absence approach may be a particularly attractive option when the modelling is based on atlases, museum data and databases. Such data sources often do not provide detailed enough information about the recording effort in the sites where species has not been detected, and consequently, false absences can be included in the models which decreases the reliability of their predictions (Chefaoui and Lobo 2008). However, models based on only one set of pseudo-absences may be vulnerable to sporadic biases in the selection process (Engler et al. 2004). Developing multiple models based on different sets of pseudo-absences is thus preferable (Thomaes et al. 2008). However, it is poorly known whether increasing the number of predictor variables used in the modelling increases the variability among projections from the models based on different pseudo-absence data sets.

Modelling studies with freshwater invasive species, especially invasive aquatic plant species, are more sparse than studies using terrestrial species (Dominguez-Dominguez

et al. 2006; but see Peterson et al. 2003), although invaders can have dramatic effects on freshwater communities (Kozhova and Izhboldina 1993, Simon and Townsend 2003). In this study we investigate the potentiality of bioclimatic envelope models to provide useful predictions for an invasive aquatic plant species, the Canadian waterweed *Elodea canadensis* Michx., in Europe, and to predict recent changes in its distribution range in northern Europe, in Finland, with respect to the climate. We specifically investigate the importance of the selection of climatic predictors and the delimitation of time slice over which climate data is averaged for the model performance. Modelling of terrestrial plant species has often focused on similar types of key variables, such as the mean temperature of the coldest month, growing degree day sum above a 5°C threshold, and the ratio of actual to potential evaporation (Huntley et al. 1995, Sykes et al. 1996). We study here how useful these three ‘baseline’ climate variables are in modelling the distribution of *Elodea canadensis* in comparison to an ‘extended’ set of climate variables including four other climate parameters potentially better reflecting some critical aspects of the biology of *Elodea*. The main questions of this study are: (1) how successful are bioclimatic envelope models in predicting the distribution area and recent northward spread of *Elodea canadensis* in Europe?; (2) are there differences in the performance of models based on medium-term vs. long-term climate data, and models including three baseline climate variables vs. an extended set of climate variables?; (3) which climate variables are the best predictors of the distribution of *Elodea canadensis*?; and (4) does the model performance vary between the different models based on different sets of pseudo-absences, and is this variation more notable between models with an extended set of climate variables than between models with the three climate variables?

Methods

The study species

The study species, the Canadian waterweed *Elodea canadensis* Michaux, is a member of the family Hydrocharitaceae (Simpson 1984, Cook and Urmi-König 1985). *Elodea canadensis* is a submerged aquatic plant which is native only in the New World. The species occurs in inland lakes, ponds and slowly moving waters in rivers, streams and canals (Cook and Urmi-König 1985). It prefers cool water temperatures (tolerance ranging between 10–25°C), and calcium-rich eutrophic water (pH 6.5–10). In northern Europe it grows mainly in relatively firm, nutrient-rich sediments with a high mineral content (Weidema 2000). *Elodea canadensis* is able to form dense single-species stands and become a dominant species in water 0.1–1.5 m deep (Cook and Urmi-König 1985, Kozhova and Izhboldina 1993). It tolerates relatively high levels of light, but not frost. The species is able to recommence growth as soon as the temperature rises in spring. It fragments easily and disperses effectively by vegetative means, as the fragments have a high survival rate (Cook and Urmi-König 1985, Barrat-Segretain et al. 2002).

In optimal growing conditions *Elodea canadensis* can be a troublesome species. Dense stands of *Elodea* reduce temperature and oxygen concentrations of water, and

decomposing stands cause internal nutrient loading (Cook and Urmi-König 1985, Weidema 2000). In northern Europe, mass occurrences of the species may alter the whole lake ecosystem and turn the water hyper-eutrophic and muddy. In Norway, such mass occurrences have very probably caused disappearances of red listed plant species populations that inhabited certain lakes and ponds before the invasion of *Elodea canadensis* (Weidema 2000, pp. 98–99). Interestingly, after the establishment of the species in a given waterbody a cyclical trend has often occurred. Within the first 3–4 years, the species attains a pest position during which it can effectively exclude other macrophytes. However, after the next 3 to 10 years the populations often decline steadily, and thereafter the species remains as a small relict population, or may disappear for some time (Simpson 1984).

Several different dispersal mechanisms have been suggested for *Elodea canadensis*, including deliberate translocations in (botanical) gardens, aquarium trade, and fragments carried passively over with timber material or small recreational boats (Simpson 1984, Cook and Urmi-König 1985, Weidema 2000, Pienimäki and Leppäkoski 2004). In addition, the long-lasting fragments of the species disperse effectively via watercourses and may also be transported by waterfowl from one lake to another. Remarkably, only female plants of *Elodea canadensis* occur in northern Europe, meaning that there it is dispersed only by vegetative means, i.e. mainly via fragments that become rooted (Weidema 2000, p. 98).

Distribution data and range shifts

Elodea canadensis is (for most parts) native and widespread in temperate North America, the core distribution area extending in the north to ca. 55°N in Canada and southwards to about 35°N in Alabama, USA. The main occurrences of the species concentrate around the Great Lakes and the St. Lawrence Valley (Cook and Urmi-König 1985). The distribution of *Elodea canadensis* in North America was extracted from three sources: (i) the map published by Cook and Urmi-König (1985), (ii) Flora of North America, Vol. 22, Hydrocharitaceae (Committee 1993+; accessed via <http://www.fna.org/FNA/>), and (iii) the species distribution data base governed by USDA (United States Department of Agriculture; <http://plants.usda.gov/>). The presence records from these three sources were agglomerated and re-sampled into a lattice system using grid cells 0.5° × 0.5° in size, and a geographical window ranging from 20°N, 140°W to 70°N, 52°W. However, as the species occurs predominantly in inland water bodies, only mainland areas in North America and parts of Mexico from this window were included in the actual modelling (Fig 1a), resulting in a set of 9701 grid cells from which 2015 cells had the species.

In Europe, *Elodea canadensis* was introduced first to Northern Ireland in 1836, then in the 1840s to Scotland and England, and from 1850 onwards it spread rapidly over the British Isles (Simpson 1984, Cook and Urmi-König 1985). In 1850–1860, the species was introduced to Belgium, Germany and the Netherlands, from where it spread rapidly to several other central European countries. In the Nordic Countries,

except Norway, the species was first recorded in the late 19th century. The distribution data for *Elodea canadensis* in Europe were taken from Hultén and Fries (1986), and digitized using a lattice system with cells of $0.5^\circ \times 0.5^\circ$ in size. The European window used in this study ranged from 34.5°N , 10.5°W to 71.5°N , 45.0°E . Grid cells occurring in the sea areas were excluded from the data set, and 5083 grid cells were selected in the final European data set, including 1881 cells with known occurrences (Fig. 1b).

In Finland, *Elodea canadensis* was first planted in the Botanical Garden in Helsinki and other corresponding places but its spreading in Finland became rapid and aggressive only in the 20th century (Weidema 2000). By 1920, the species was recorded from several locations in southern Finland (Hintikka 1917). Since then, it has continued to expand its distribution range and has recently been recorded from relatively northern water bodies (Fig. 1c). The distribution data of *Elodea canadensis* in Finland was derived from the national atlas data base ‘Kastikka’ for vascular plants (Lampinen and Lahti 2007; <http://www.luomus.fi/kasviatlas>). The known presence points of the species were recorded using a uni-

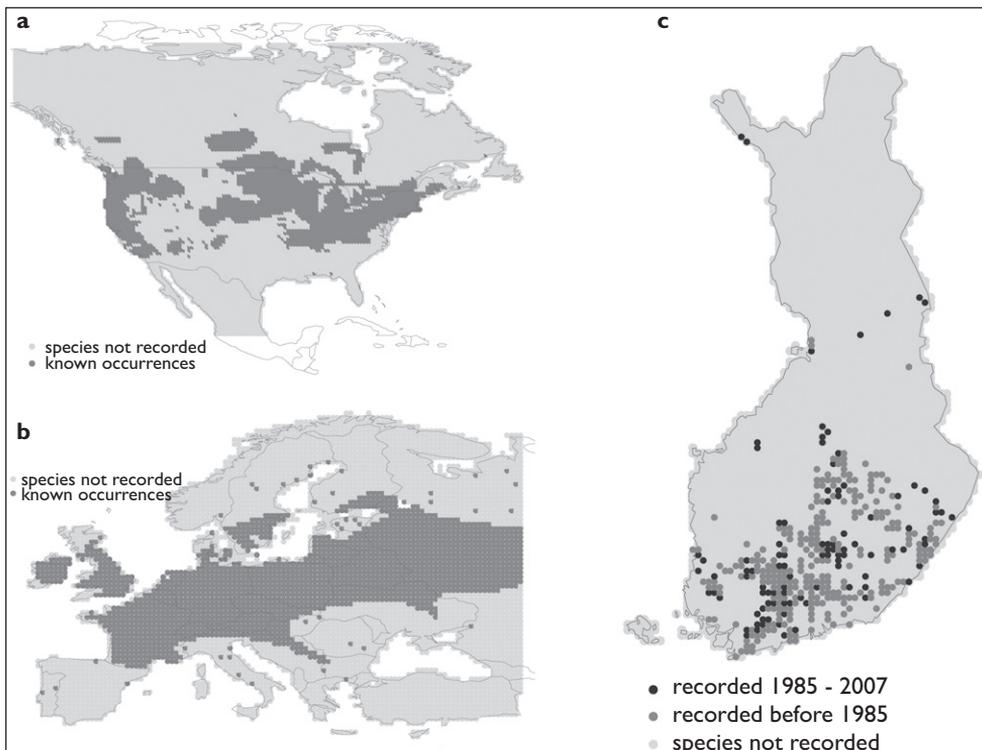


Figure 1. Distribution of *Elodea canadensis* in the three study areas. **(a)** Grid cells in North America with known occurrences ($n = 2015$, in dark grey) and cells in which the species has not been recorded ($n = 7686$, in light grey), **(b)** grid cells in Europe with known occurrences ($n = 1881$) and cells with no known occurrences ($n = 3202$), and **(c)** grid cells in Finland in 1961–1984 (in dark grey) and 1985–2006 (in black) with known occurrences ($n = 276$ and 375) and cells with no known occurrences (in light grey). For all the 10 data sets used in calibrating the models in North America, 2015 random pseudo-absence points were selected from the 7686 (presumed) absence grid cells.

form grid system with grid cells of 10×10 km in size ($n = 3544$) (Fig. 1c). These records were assigned into two temporally delimited data sets: records made in 1960–1984 and in 1985–2006. Based on the floristic resurveys of known occurrences, we made an assumption that all the 10-km grid cells that had occurrences of the species in the earlier surveys still had the species in the later time periods. Thus all the records made in 1960–1984 were also considered as valid positive records in 1985–2006, and records made before 1960 were included both in the 1960–1984 and the 1985–2006 species data. We acknowledge here that this assumption might be unrealistic for many short-lived species. However, for the occurrences of *Elodea canadensis* it is reasonable. This is because the species is able to develop long-lasting populations, regenerate vegetative and spread effectively within a particular waterbody (Cook and Urmi-König 1985, Kozhova and Izhboldina 1993). The data from the national atlas data base ‘Kastikka’ for vascular plants, as well as the empirical lake monitoring data collected by one of the authors (HT), suggest that the species is able to persist in the same regions or even the same lakes in Finland for at least 50–60 years.

Climate data

Mean monthly precipitation and temperature values on a grid with $0.5^\circ \times 0.5^\circ$ spatial resolution for North America and Europe matching the species data were extracted from the Climatic Research Unit (CRU) TS 2.0 dataset (New et al. 2002, Mitchell et al. 2003), and averaged over two time periods. The two time slices in North America were 1901–1990 (‘long-term’ climate data) and 1961–1990 (‘medium-term’ climate data), and in Europe 1901–1980 and 1951–1980, delimited to match in both continents with the probably latest recording years in the species data. Climate data for the years 1961–2006 on a 10×10 km grid covering the whole Finland was provided by the Finnish Meteorological Institute (Venäläinen et al. 2005) and averaged over two time slices corresponding with to those of the species data, 1961–1984 and 1985–2006 (interpolated values for Finland were not available before 1961).

For each of the three geographical areas and all the different time slices, we calculated two ‘competing’ sets of climate predictor variables. The first data set consisted of three ‘baseline’ climate variables that are considered to be among the most important broad-scale determinants of the ranges of terrestrial plants: (i) mean temperature of the coldest month (MTCO), growing degree days above 5°C (GDD5) and water balance (WB) (see Beerling et al. 1995, Huntley et al. 1995, Sykes et al. 1996). GDD5 were derived by estimating daily values from monthly mean temperatures using a sine curve interpolation (Brooks 1943). The water balance was calculated as the annual sum of the monthly differences between precipitation and potential evapotranspiration following Skov and Svenning (2004). The formulas applied were the following:

$$\text{WB} = \sum_{i=1}^{12} (P_i - PET_i) \quad (1)$$

where, P_i = mean precipitation in month i

PET_i = mean potential evapotranspiration in month $i = (58.93 \times T)/12$ [if $T_i > 0^\circ\text{C}$, else $PET_i = 0$]

where, T_i = mean temperature in month i

In the second case, we complemented the three baseline variables with four additional variables in order to investigate whether the extended set of climate variables would provide more accurate projections of the climatically suitable areas for the species. The four additional variables aimed to reflect some critical stage in the life cycle of *Elodea canadensis*, including: (i) mean temperature in spring (Temp_{MAM} ; March, April, May), (ii) mean July temperature (Temp_j), (iii) water deficit in (late) summer ('Defi_sum'; July, August, September), and annual water deficit ('Defi_ann'). Monthly water deficit values were calculated following Ohlemüller et al. (2006). The formula for measuring water deficit was almost the same as that used to calculate the water balance (Equation 1), the difference being that only those values and months are taken into account where PET_i exceeds the precipitation (P_i), otherwise $P_i - PET_i$ is let being 0. These monthly values were summed for July – September and for the whole year.

The first reasoning for including these variables was that mean temperatures in spring can be an important determinant for the distribution of *Elodea canadensis*. This is because the species is able to regenerate actively soon after the temperatures increase (Barrat-Segretain et al. 2002). Second, one factor potentially governing the southern range margin of the species is the water temperature during the warmest part of the growing season. In this study we used the July temperature and the water deficit in late summer as surrogates for direct measurements of the temperature in inland water bodies. Earlier studies have found especially the July air temperature to be a good predictor of maximum surface-water temperatures (Mohseni et al. 2003, Sharma et al. 2007). Water deficit in late summer summarises the interactions between temperature and precipitation and thus also has the potentiality to indicate landscapes where the water levels in many lakes can become low, and consequently growing conditions can become more readily overly warm for *Elodea canadensis*. Annual water deficiency provides an additional indication of the areas which may face an accumulative water deficit and heating effect and thus show high maximum surface-water temperatures.

Statistical analysis

We used generalized additive models (GAMs) in the bioclimatic envelope modelling of *Elodea canadensis*. Generalized additive models are flexible data-driven non-parametric extensions of generalized linear models (Hastie and Tibshirani 1990) that allow both linear and complex additive response curves to be fitted (Wood and Augustin 2002). All the GAM models were developed using the GRASP (Lehmann et al. 2003) user interface in S-Plus (Version 6.1 for Windows, Insightful Corp.).

The modelling process included several separate steps. In the very first step, following Beaumont et al. (2009), ten random selections of 2015 pseudo-absence grid cells were taken in North America from the 7686 grid cells with no records of *Elodea*. The 2015 grid cells with known presences were added into each of the ten random draws, and thus all the 10 combined random sets had the recommendable prevalence of 50% (McPherson et al. 2004, Meynard and Quinn 2007). Next, all the random sets were calibrated four times, i.e. using the species data and the four different climate data

sets. In total, 40 different GAMs were developed, by applying the 10 random data sets separately into four main types of GAM: (1) medium-term (1961–1990) climate data including 3 baseline variables, (2) long-term (1901–1990) climate data including 3 baseline variables, (3) medium-term climate data including an extended set of 7 variables, and (4) long-term climate data including an extended set of 7 variables.

All the GAMs were built using a stepwise procedure to select relevant explanatory variables and the level of complexity of the response shapes. A starting model including all continuous predictors smoothed with 3 degrees of freedom was fitted first. Following Bio et al. (2002), the variable dropping or conversion to linear form was tested using Bayesian information criterion (BIC) (Johnston and Omland 2004), which is more selective than the widely used Akaike's information criterion (AIC). All the predictor variables that were selected in the final model were required to make a model contribution (i.e. contribution of a given predictor within the selected models, as measured by GRASP; see Lehmann et al. 2003) of 5% or more. Moreover, from the pairs of highly (>0.90) correlated variables the one with lower model contribution was excluded from the model. Because the response variables represented binary data (presence or absence of the species), a binomial distribution of error via a logistic link function was applied (Lehmann et al. 2003).

The performance of the 40 GAMs in predicting the distribution of *Elodea canadensis* in North America was evaluated by four measures: (i) BIC (smaller values are indicative of a better fit to the data) (Venables and Ripley 2002), (ii) the amount of deviance explained (D^2) (i.e. the ratio of the explained deviance to the total deviance), (iii) the resubstitution method (or 'simple validation', see Lehmann et al. 2003) based on a plot of observed response values against the values predicted by the model, and the subsequent area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding and Bell 1997), and (iv) four-fold cross-validation, carried out with four random subsets of the entire dataset. In the four-fold cross-validation, each randomly selected subset was dropped from the model, the model was recalculated and predictions were made for the omitted data points. Combination of the predictions from the different subsets was then plotted against the observed data (Lehmann et al. 2003), and model performance was measured using the AUC of the ROC plot. The following interpretation of AUC-values was used (Swets 1988): $AUC > 0.9$: excellent agreement between observed and predicted distribution; $0.8 < AUC < 0.9$: good model accuracy; $0.7 < AUC < 0.8$: fair; $0.6 < AUC < 0.7$: poor; $AUC < 0.6$: fail. Differences between the four main types of GAMs with respect to the four model performance measures were analysed using a paired t-test (Quinn and Keough 2002).

In the final part of analysis of the North American data, probability values were generated for the occurrence of *Elodea canadensis* in all the 9701 grid cells by fitting the developed 40 models to this full data set. The geographical patterns and variability of the probability values between the four main types of GAMs were visually investigated, both by comparing the mean probability of occurrence values averaged for each grid cell over the 10 random GAMs and their standard deviation, and by investigating the probabilities from the individual random GAMs.

In the second main step of the modelling, the 40 random GAMs calibrated using the North American data were fitted to the European data sets. Transferring of the models was done between the corresponding pairs of climate data sets, i.e. the 10 random GAMs based on the 1901–1990 climate data set and the three climate variables (MTCO, GDD5, WB) from North America were projected to the European climate data set averaged over 1901–1980 and including the same three variables, and so forth. The probability values for the occurrence of *Elodea canadensis* derived from the transferred models were compared with the distribution records extracted from Hultén and Fries (1986). As some parts of Europe were probably undersampled, we made the assumption that absence data was not available here (cf. Thuiller et al. 2005).

The accuracies of the transferred models were tested separately for each of the four main model types in Europe. Using a chi-square test, we compared the number of known presences of *Elodea* situated in areas predicted to be climatically suitable for the species by <80% (<8 models out of 10; the four main GAM types were tested separately) of the models versus the number of known presences in areas predicted suitable by >80% of the models (cf. Herborg et al. 2007). Prior to the chi-square tests, the probabilities generated by the GAMs were transformed into presence and absence values using a cut-off level defined by the prevalence of species in the model calibration data (here 0.50) (see McPherson et al. 2004, Liu et al. 2005). In addition to chi-square tests, the mean probability values in the 1881 grid cells with known occurrences of *Elodea canadensis* were calculated separately for the four main types of GAMs and their differences were compared. Finally, the geographical patterns and variability of the probability values in the full European data set with 5083 grid cells were visually investigated to reveal potential differences between the projections from the four main types of GAMs.

In the third main step of modelling, the 40 GAMs calibrated using North American data were fitted to the Finnish climate sets, both for the time periods of 1961–1984 and 1985–2006 and using the two types of climate predictor sets. The performance of the transferred GAMs with the Finnish data was evaluated as described for the whole European data sets.

Results

Models for North America

The amount of the explained deviance (D^2) in the 40 random GAMs varied between 0.441 and 0.531, being on average highest in the models based on medium-term climate data and the extended set of 7 climate variables (Table 1). With regard to AUC from the resubstitution validation and AUC from the cross-validation, all the 40 GAMs showed an excellent model performance (Table 1). On average, medium-term extended models showed the highest AUC values but the difference from the long-term extended models was marginal. In fact, there were no statistically significant differences among these two main model types according to any of the four model performance criteria. The medi-

Table 1. Modelling accuracy of the four main types of GAMs for *Elodea canadensis* in North America. Accuracy was measured by **(a)** Bayesian information criterion (BIC), **(b)** the amount of deviance explained (D^2), **(c)** AUC from resubstitution validation, and **(d)** AUC from four-fold cross-validation. The mean values and their standard deviation (and minimum – maximum) in the four accuracy criteria were based on 10 individual random GAMs that were built using different selections of pseudo-absences. Differences between the ‘medium-term baseline’ models vs. ‘long-term baseline’ models (t_1), ‘medium-term baseline’ models vs. ‘medium-term extended’ models (t_2), ‘long-term baseline’ models vs. ‘long-term extended’ models (t_3) and ‘medium-term extended’ models vs. ‘long-term extended’ models (t_4) were tested with paired t-tests.

Accuracy criterion	Main type of GAM								t_4
	Medium-term baseline models	Long-term baseline models	Medium-term extended models	Long-term extended models	t_1	t_2	t_3	t_4	
(a) BIC	3138.57 ± 48.56	3133.15 ± 48.84	2855.83 ± 65.60	2860.33 ± 57.00	5.581***	16.560***	23.205***	-0.354 ^{ns}	
	(3049.50 – 3189.89)	(3043.55 – 3185.12)	(2758.93 – 2969.67)	(2754.59 – 2976.26)					
(b) explained deviance	0.450 ± 0.008	0.454 ± 0.009	0.510 ± 0.014	0.511 ± 0.012	-1.611 ^{ns}	-18.096***	-12.598***	-0.221 ^{ns}	
	(0.441 – 0.466)	(0.442 – 0.467)	(0.486 – 0.531)	(0.484 – 0.529)					
(c) AUC resubstitution	0.908 ± 0.003	0.908 ± 0.003	0.926 ± 0.005	0.923 ± 0.004	1.500 ^{ns}	-13.791***	-16.155***	-0.498 ^{ns}	
	(0.905 – 0.913)	(0.903 – 0.912)	(0.917 – 0.931)	(0.915 – 0.930)					
(d) AUC cross-validation	0.906 ± 0.003	0.907 ± 0.003	0.923 ± 0.006	0.923 ± 0.004	-1.406 ^{ns}	-12.194***	-16.665***	-0.365 ^{ns}	
	(0.903 – 0.912)	(0.904 – 0.912)	(0.915 – 0.930)	(0.914 – 0.929)					
Time slice	1961 – 1990	1901 – 1990	1961 – 1990	1901 – 1990					
Included climate variables	MTCO, GDD5, WB	MTCO, GDD5, WB	MTCO, GDD5, WB, Temp _{MAM} , Def_sum, Def_ann	MTCO, GDD5, WB, Temp _{MAM} , Def_sum, Def_ann					

um-term and long-term baseline models differed significantly only with regard to their BIC values. However, the medium-term extended models performed significantly better on the basis of all four criteria than the medium-term baseline models, and similarly, the long-term extended models out-competed the long-term baseline models (Table 1).

Both in the medium-term baseline and long-term baseline GAMs, the three climate variables (MTCO, GDD5, WB) were selected in all models, and in each model GDD5 showed the highest model contribution. However, the medium-term and long-term extended GAMs were more variable in terms of the selected climate variables (Table 2). GDD5 and Defi_ann were selected in all the 20 extended models, followed closely by WB and Defi_sum (18 extended models). In the extended models, GDD5 and Defi_sum appeared as the two most significant predictors of the distribution of *Elodea canadensis*, showing the highest model contributions (Table 2).

Visual examination of the mean probabilities provided by the four main types of GAMs showed that the projections from the two baseline models differed very little, and those from the two extended models were also very similar to each other (Fig. 2). Extended models differed slightly from baseline models, for example, in that generally they did not predict suitable areas for the species in Mexico, whereas the baseline models did (Fig 2). Despite their high performance, all the four types of main models failed to predict part of the northernmost known occurrences of the species correctly. However, they agreed in suggesting that *Elodea canadensis* has not yet spread into all the climatically suitable areas (with mean probability value ≥ 0.50) in North America.

Variability (standard deviation) in the per-grid-cell probability values between the random GAMs indicated that the projections from the extended models vary more than projections from the baseline models. The standard deviation of the probability values in the medium-term baseline models ranged from 0.005 to 0.048 (Fig. 3a), in the medium-term extended models from 0.015 to 0.251 (Fig. 3b), and in the long-term baseline and long-term extended models from 0.006 to 0.048 and from 0.011 to 0.181, respectively.

Table 2. Contributions of climate variables in the ‘extended’ models for *Elodea canadensis* in North America. **(a)** The number of times each climate predictor variable was selected in the 20 extended random GAMs based on medium-term (1961–1990) or long-term (1901–1990) time slices and an ‘extended’ set of seven climate variables, and **(b)** the number of times a given variable showed the highest model contribution in the models. The models were built separately 10 times both for medium-term climate data and long-term climate data.

Predictors	(a) selected in the models	(b) highest model contribution
MTCO	8	0
GDD5	20	8
WB	18	0
Temp _{MAM}	11	0
Temp _j	2	0
Defi_sum	18	12
Defi_ann	20	0

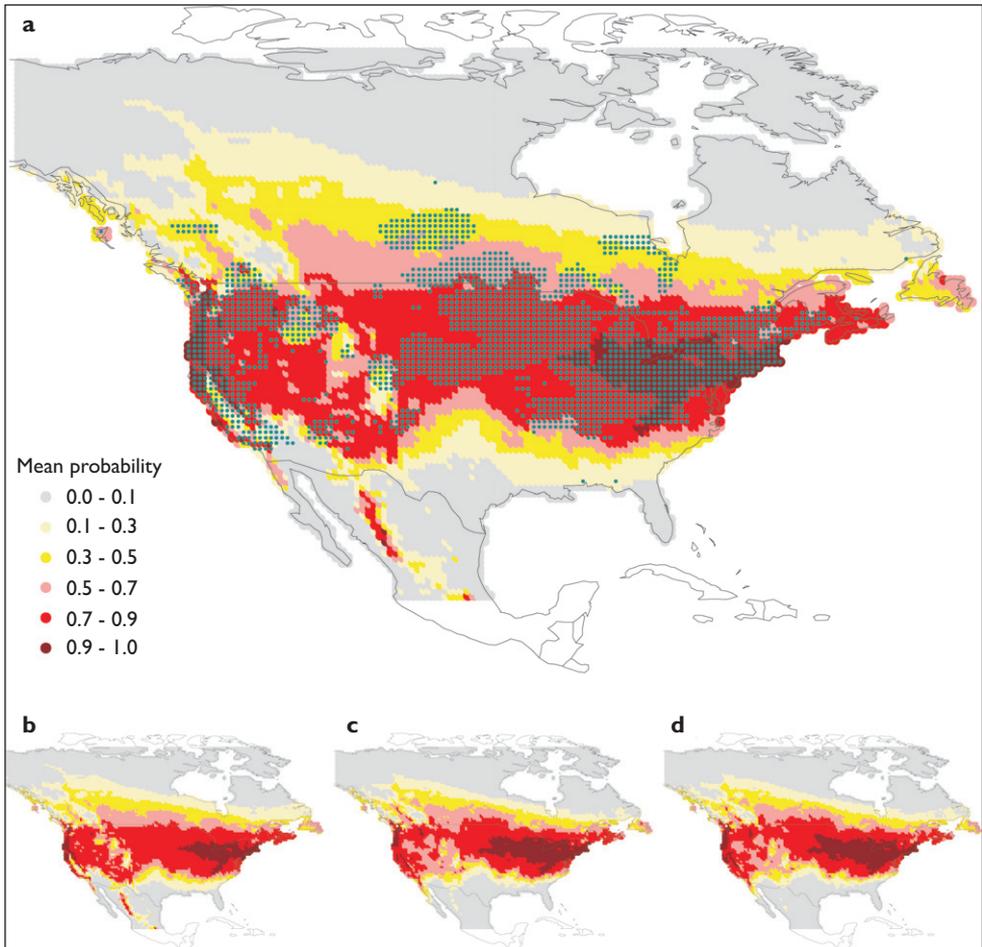


Figure 2. Projected distribution of *Elodea canadensis* in North America based on four different modelling approaches. The maps show the mean probability of occurrence derived from 10 random GAMs based on **(a)** medium-term climate data including 3 baseline variables, **(b)** long-term climate data including 3 baseline variables, **(c)** medium-term climate data including an extended set of 7 variables, and **(d)** long-term climate data including an extended set of 7 variables. Known occurrence points for *Elodea canadensis* are shown in (a) with green dots. The maps are in the same scale. Probabilities ≥ 0.5 indicate areas where the species is projected to occur.

Consequently, the projections between the individual random-set GAMs based on extended climate data differed to some extent, particularly in the geographically marginal areas, for example between random-set 2 (Fig. 3c) and random-set 5 (Fig. 3d).

Models for Europe

All the four main types of models developed for *Elodea canadensis* in North America predicted the known distribution in Europe very well. In the best case, the medium-term baseline models, only 2.7% of the known occurrences (51 out of 1881 occupied

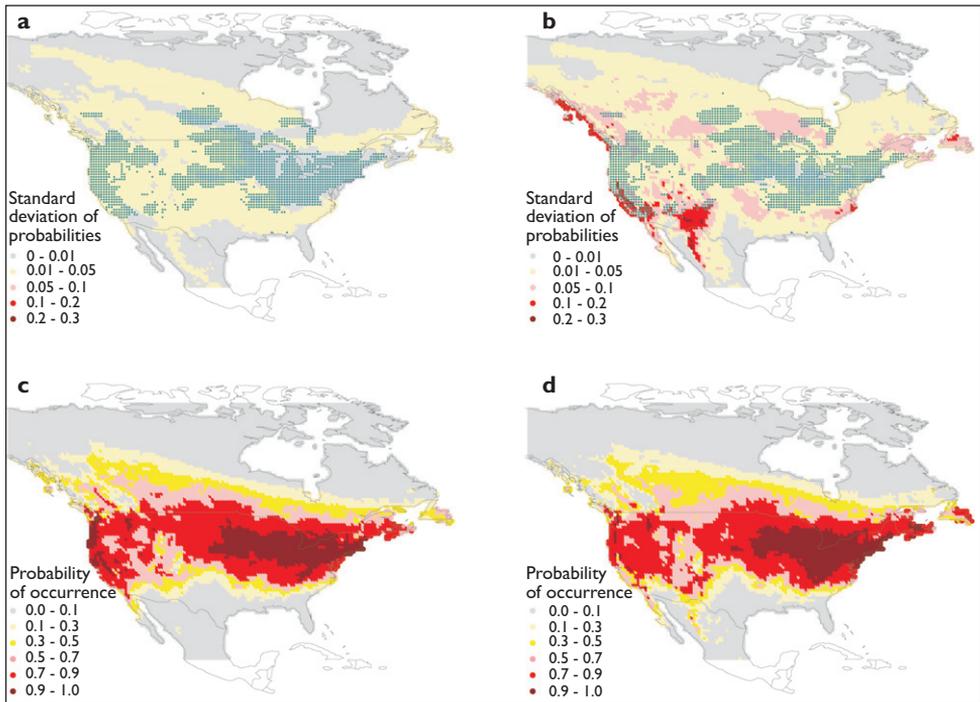


Figure 3. Variation in probability values and probabilities of occurrence from two individual models in North America. The per-grid-cell variation shows the standard deviation of probability values for the occurrence of *Elodea canadensis* derived from the 10 random GAMs based on (a) medium-term baseline climate data, (b) medium-term extended climate data. Probabilities of occurrence based on two individual medium-term extended models were derived from (c) a model based on pseudo-absence set 2, and (d) a model based on pseudo-absence set 5. Known occurrence points are shown in (a) and (b) with green dots.

grid cells; Table 3) were in areas predicted to be climatically suitable by < 80% of the random-set GAMs, whereas 97.3% of the occurrences of the species were in grid cells predicted as suitable by $\geq 80\%$ of the random GAMs ($df = 1$, chi-square = 1682.5, $p < 0.001$). However, the differences between model types were marginal, as the other three main model types also showed a significantly high predictive ability (Table 3). The mean probabilities in the European grid cells with known occurrences were highest in the long-term extended GAMs and lowest in the medium-term baseline GAMs (Table 3). The two statistically significant differences were that medium-term baseline GAMs had significantly lower mean probabilities in the grid cells with occurrences than the medium-term extended GAMs (paired t-test, $df = 1880$, $t = -9.29$, $p < 0.001$) and the long-term baseline GAMs ($df = 1880$, $t = -30.80$, $p < 0.001$). This discrepancy between the results of chi-square tests and mean probabilities in the occupied grid cells was caused by the higher variability in the performance of (separate) extended GAMs (Table 3). For example, the number of grid cells with known occurrences in Europe but predicted not to have the species varied in the separate medium-term extended GAMs from 46 to 85, but in the medium-term baseline GAMs from 49 to 53.

Table 3. Performance of the four main types of models for *Elodea canadensis* in Europe. The number of the grid cells with known occurrences of the species **(a)** predicted to have the species by < 80% of the random GAMs, **(b)** predicted to have the species by \geq 80% of the random GAMs, **(c)** range (min – max) in (a) among the 10 individual random GAMs, **(d)** statistics from the chi-square test for (a) vs. (b), and **(e)** mean probability of occurrences averaged across the 1881 grid cells with known occurrences.

Main model type	(a) No of Cells<80%	(b) No of Cells>80%	(c) Range	(d) X ²	(e) Mean probability
Medium-term baseline models	51	1830	49–53	1682.53***	0.815
Long-term baseline models	54	1827	47–53	1671.20***	0.823
Medium-term extended models	73	1808	46–85	1600.33***	0.823
Long-term extended models	52	1829	42–65	1678.75***	0.824

Mean occurrence probabilities for *Elodea canadensis* in Europe from the 10 medium-term baseline GAMs and 10 long-term baseline GAMs showed a high spatial agreement (Fig. 4a–b). By contrast, long-term extended GAMs provided on average higher probability values than the medium-term extended GAMs (Fig. 4c–d). All the four main types of models identified the favourable northern range margin for the species very well (using the probability of 0.50 as a cut-off level for distinguishing which grid cells are climatically suitable for the species and which are not), and at maximum only 11 records occurred in areas predicted to be climatically unsuitable by the four model types. The models also agreed in predicting that the climatically suitable areas for the species extend into much wider areas in the Mediterranean countries and areas next to the Black Sea than indicated by the range map of Hultén and Fries (1986) (Fig. 4).

The probabilities generated for all the 5083 grid cells in Europe showed much more variation among the individual extended models than the baseline models. For example, the standard deviation of the per-grid-cell probabilities in the medium-term extended models ranged from 0.005 to 0.351, whereas in the corresponding medium-term baseline GAMs the range was from 0.002 to 0.057 (Fig. 5a–b). The areas where the probabilities varied maximally were geographically and climatically marginal areas in the European study window. Consequently, the projections from solitary GAMs based on extended climate data differed occasionally considerably in these areas (Fig. 5c–d).

Models for Finland

All the four main types of models showed a high predictive ability (chi-square = 264.13 – 272.14, $p < 0.001$: Table 4) for the climatically suitable areas for *Elodea canadensis* in Finland on the basis of the climate and species data from 1961–1984. In the two extended models, 99.6% (275 out of 276) of the grid cells with occurrences of *Elodea canadensis* were predicted to have the species by \geq 80% of the random GAMs, and the two baseline models performed almost equally well (Table 4). The mean probabilities derived from the two baseline types of models were very similar to each other (Fig. 6a–b), but the projections derived from the extended models differed slightly in some areas

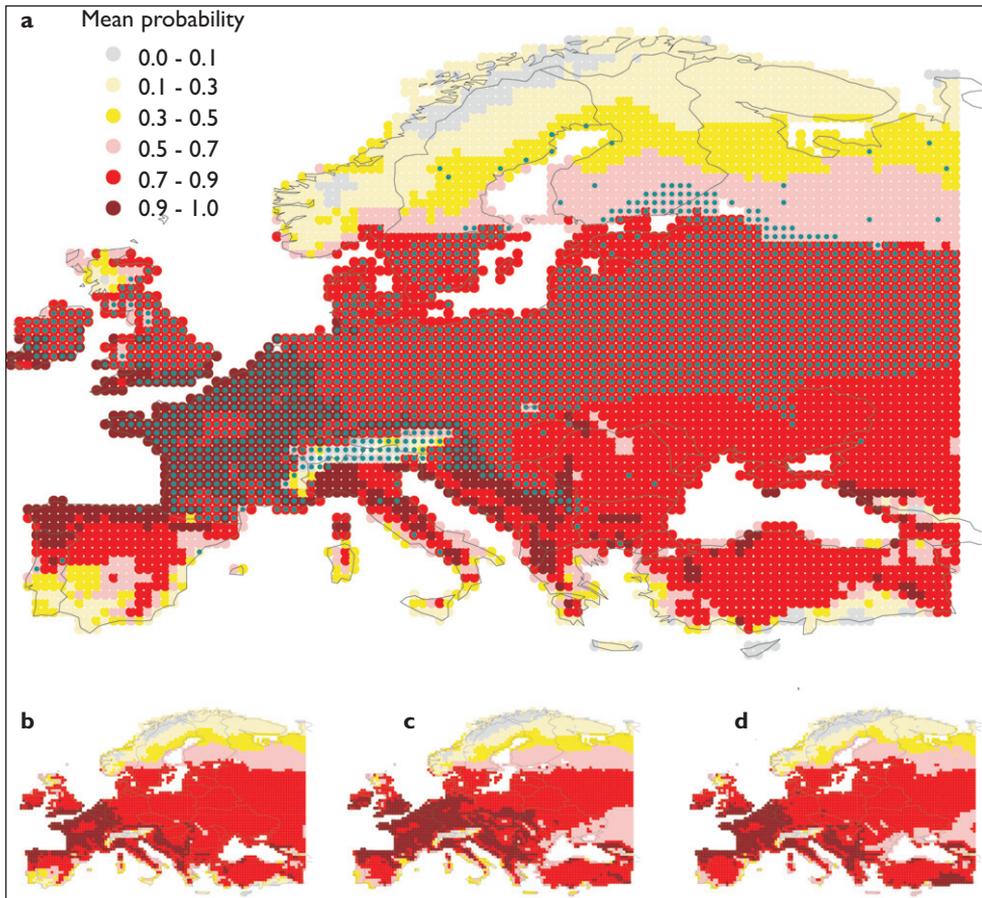


Figure 4. Projected distribution of *Elodea canadensis* in Europe based on four different modelling approaches. The maps show the mean probability of occurrence derived from 10 random GAMs calibrated with species and climate data from North America and transferred into Europe: **(a)** medium-term baseline models, **(b)** long-term baseline models, **(c)** medium-term extended models, and **(d)** long-term extended models. Known occurrence points are shown in (a) with green dots. The maps are in the same scale.

(Fig. 6c–d). The area predicted as climatically suitable by the extended models extended ca. 100–200 km further north than in the baseline models. However, there was more variation in the probability values derived from extended models than in those from the baseline models. Moreover, projections from the individual extended GAMs differed occasionally considerably (Fig. 6e–h), as also did the number of grid cells with known occurrences but predicted not to have the species by the individual models (Table 4).

Transferring the models into the climate and species data from 1984–2006 indicated that the four types of models also have a high predictive ability in predicting the most recent distribution of *Elodea canadensis* in Finland (chi-square = 347.52 – 352.38, $p < 0.001$; Table 5). The majority of the new records for *Elodea canadensis* in Finland discovered in 1985–2006 were located in the areas projected as climatically suitable, but 6 or 7 new records occurred in the 10-km grid cells situated northwards from the area predicted as climatically

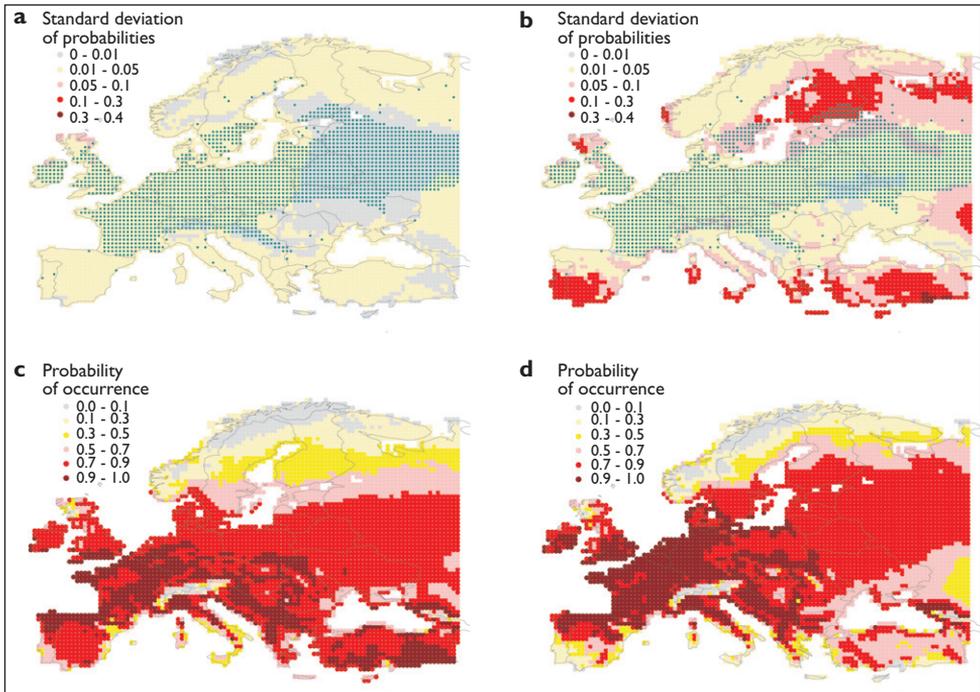


Figure 5. Variation in probability values and probabilities of occurrence from two individual models in Europe. The per-grid-cell variation shows the standard deviation of probability values for the occurrence of *Elodea canadensis* derived from the 10 random GAMs based on (a) medium-term baseline climate data, (b) medium-term extended climate data. Probabilities of occurrence based on two individual medium-term extended models were derived from (c) a model based on pseudo-absence set 2, and (d) a model based on pseudo-absence set 5. Known occurrences are shown in (a) and (b) with green dots.

Table 4. Performance of the four main types of models in Finland with data from 1961 - 1984. The number of the grid cells with known occurrences of *Elodea canadensis* (a) predicted to have the species by < 80% of the random GAMs, (b) predicted to have the species by $\geq 80\%$ of the random GAMs, (c) range (min – max) in (a) among the 10 individual random GAMs, (d) statistics from the chi-square test for (a) vs. (b), and (e) mean probability of occurrences averaged across the 276 grid cells with known occurrences.

Main model type	(a) No of Cells<80%	(b) No of Cells>80%	(c) Range	(d) X ²	(e) Mean probability
Medium-term baseline models	3	273	3–3	264.13***	0.645
Long-term baseline models	2	274	1–3	268.05***	0.669
Medium-term extended models	1	275	0–3	272.01***	0.698
Long-term extended models	1	275	1–33	272.01***	0.669

suitable (Fig. 7). Similarly as with the 1961–1984 data, the area predicted as climatically suitable extended further north in the extended models than in the baseline models, the extended models showed higher variation in their probability values, and projections from the solitary extended models differed occasionally considerably (Fig. 7, Table 5).

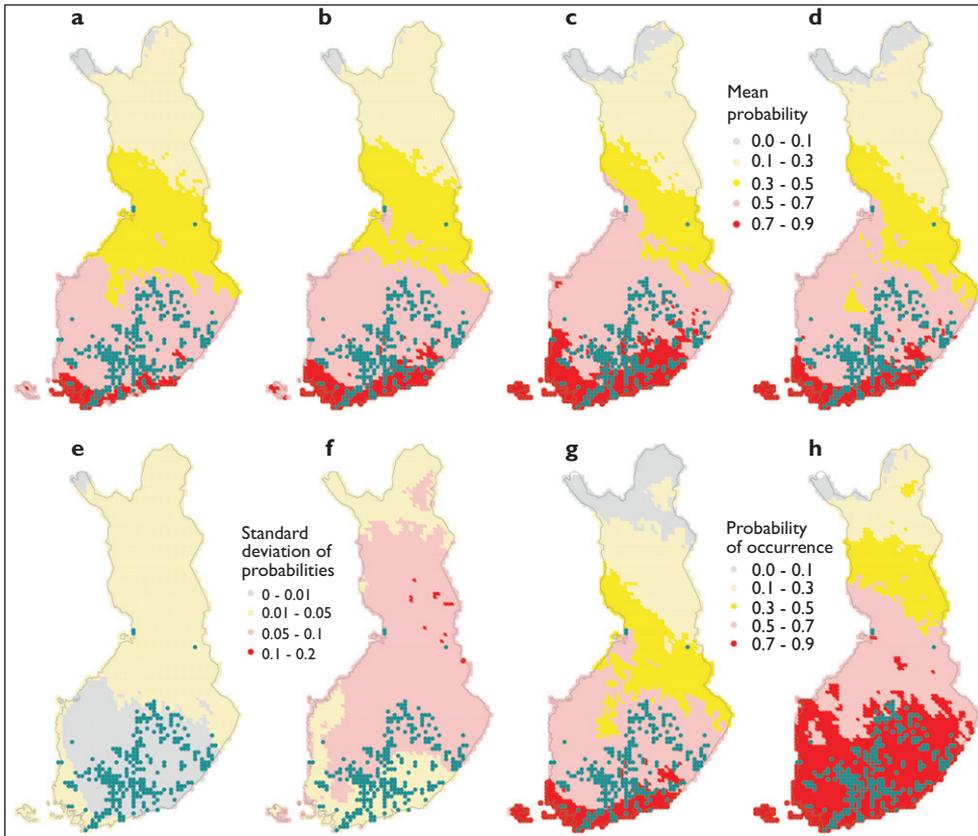


Figure 6. Projected distributions, variation in probability values and probabilities of occurrence from two individual models in Finland. Projected distributions show mean probability of occurrence for *Elodea canadensis* in Finland, based on 10 random GAMs fitted to climate data from 1961–1984: (a) medium-term baseline models, (b) long-term baseline models, (c) medium-term extended models, and (d) long-term extended models. The standard deviation of per-grid-cell probabilities derived from 10 random GAMs is shown for (e) the medium-term baseline models, and (f) the medium-term extended models. Probabilities of occurrence based on two individual medium-term extended models were derived from (g) a model based on pseudo-absence set 2, and (h) a model based on pseudo-absence set 5. Known occurrence points from < 1985 are shown with green dots. The maps are in the same scale in (a) – (d), in (e) and (f), and in (g) and (h).

Discussion

According to Rahel and Olden (2008) there are few examples of geographic range shifts consistent with recent changes in climate in freshwater organisms, in contrast to several examples in terrestrial and marine species. Sporadic data includes observations of the recent invasion of *Ranunculus trichophyllus* in high-elevation lakes in the Himalayas, considered as a signal of a warming climate (Lacoul and Freedman 2006), poleward range shifts in four freshwater taxa in UK during the recent period of climate warming (Hickling et al. 2006), and some solitary observations of new occurrences at high latitudes (for

Table 5. Performance of the four main types of models in Finland with data from 1985 – 2007. The number of the grid cells with known occurrences of *Elodea canadensis* (a) predicted to have the species by < 80% of the random GAMs, (b) predicted to have the species by \geq 80% of the random GAMs, (c) range (min – max) in (a) among the 10 individual random GAMs, (d) statistics from the chi-square test for (a) vs. (b), and (e) mean probability of occurrences averaged across the 375 grid cells with known occurrences.

Main model type	(a) No of Cells<80%	(b) No of Cells>80%	(c) Range	(d) X ²	(e) Mean probability
Medium-term baseline models	7	368	6–8	347.52***	0.691
Long-term baseline models	6	369	6–6	351.38***	0.711
Medium-term extended models	7	368	2–7	347.52***	0.749
Long-term extended models	6	369	6–40	351.38***	0.703

a review see Heino et al. 2009). This study contributes to this accumulating evidence and shows that *Elodea canadensis*, an introduced freshwater plant species, has recently spread northwards in northernmost Europe, in Finland, in concert with the recent climatic changes and in agreement with the predictions from bioclimatic envelope models.

A number of earlier studies have reported the ability of ecological niche models and bioclimatic envelope models to predict the geographic occurrences of invasive freshwater species in their native and introduced range, mainly for fish species (Iguchi et al. 2004, Chen et al. 2007) and more rarely for aquatic plants (Peterson 2003a, Peterson et al. 2003). However, some recent studies have reported notable mismatches between the model projections developed for the invaded areas and the observed occurrences therein (Broennimann et al. 2007, Fitzpatrick et al. 2007). Such discrepancies may reflect the potentiality of invasive species to occupy climatically distinct niche spaces in the invaded areas (Broennimann et al. 2007), a phenomenon which would decrease the usefulness of niche –based models to assess the potential spread of introduced species. However, such mismatches did not occur in our results. Thus bioclimatic envelope models appear to have the potentiality to produce useful first-filter predictions for the distribution of *Elodea canadensis*, and to identify the broad-scale geographical limits to the species' spread and areas most vulnerable to invasions (cf. Peterson 2003a, Peterson et al. 2003, Herborg et al. 2007).

All the four main types of models applied in this study provided accurate and statistically highly significant predictions of the occurrences of *Elodea canadensis* both in the native and invaded range. In Europe, the most notable mismatches between the model projections and the distribution map of *Elodea canadensis* by Hultén and Fries (1986) occurred in the Alps and in southernmost areas in Europe and adjacent areas around the Black Sea. All the four main model types predicted that there are no climatically suitable areas for the species in the Alps, whereas Hultén and Fries (1986) reported that the species occurs throughout this area. This discrepancy may be based on possible errors in the expert-drawn delineation of historical range of *Elodea canadensis* in areas with few known occurrence points (Habib et al. 2003, Graham et al. 2008), in other words, exaggerating the extent of occurrences in the Alps. Alternatively, the

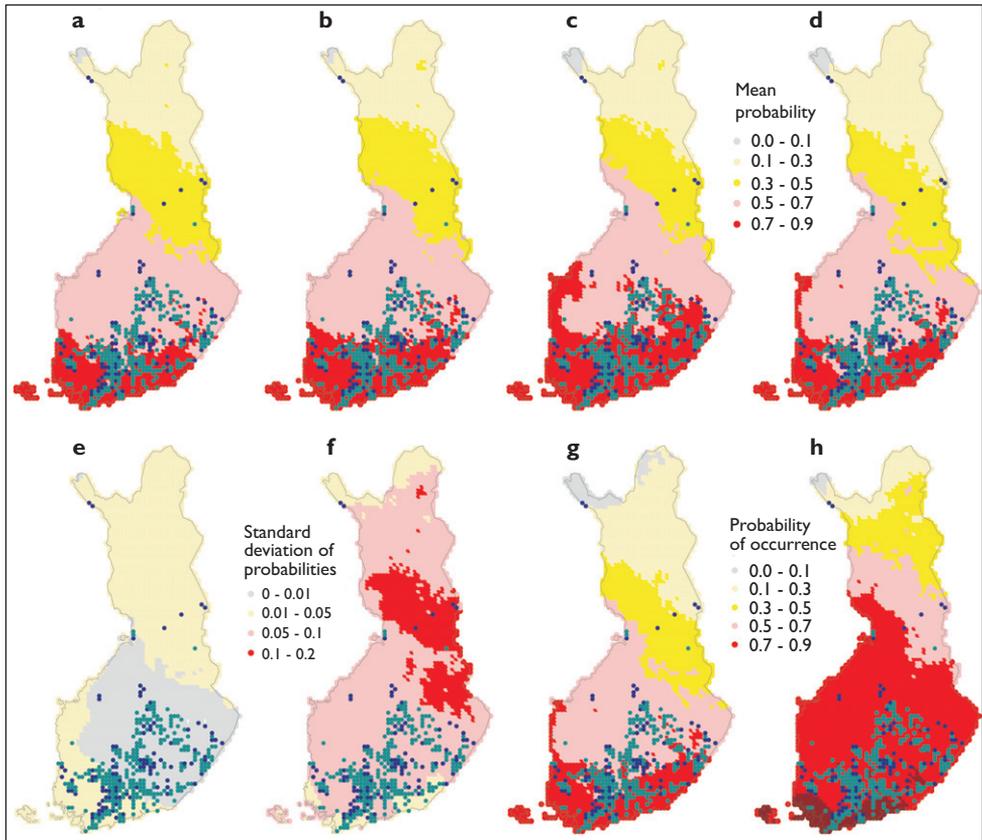


Figure 7. Projected distributions, variation in probability values and probabilities of occurrence from two individual models in Finland. Projected distributions show mean probability of occurrence for *Elodea canadensis* in Finland, based on 10 random GAMs fitted to climate data from 1985–2006: **(a)** medium-term baseline models, **(b)** long-term baseline models, **(c)** medium-term extended models, and **(d)** long-term extended models. The standard deviation of per-grid-cell probabilities derived from 10 random GAMs is shown for **(e)** the medium-term baseline models, and **(f)** the medium-term extended models. Probabilities of occurrence based on two individual medium-term extended models were derived from **(g)** a model based on pseudo-absence set 2, and **(h)** a model based on pseudo-absence set 5. Known occurrence points from < 1985 are shown with green dots, and from 1985–2006 with blue dots.

species may have been recorded to occur in the Alps in lakes situated in microclimatically sheltered valleys and at the base of the mountains, at altitudes over 750 meters a.s.l. (Unni 1977, Dubois et al. 1988). Bioclimatic envelope models generally use the mean values of climate variables averaged over the whole grid cell, and thus in topographically heterogeneous landscapes they may fail to detect the existence of sheltered, climatically suitable sites for the appearance of lowland species (cf. Peterson 2003b, Luoto and Heikkinen 2008).

Our models suggested that the climatically suitable area for *Elodea canadensis* covers much larger areas in southern Europe than those where the species was mapped by

Hultén and Fries (1986). This disagreement may be a result of the poor ability of our models to detect the southern range limit of the species, leading to consequent over-predictions in the model projections. However, more probably the species had not yet spread to these climatically suitable areas before the map of Hultén and Fries was published, as indicated by the recent observations of the species from Turkey (Akbulut et al. 2001) and northern Africa (Vilá et al. 1999). Thus although *Elodea canadensis* was introduced in Europe in the 1830s and has spread effectively since then, it apparently still had not reached all climatically suitable areas in Europe and adjacent areas by the 1980s. This suggests that the delimitation of the full climatic limits for the species can be subject to biases if made only on the basis of the invaded range. In a similar vein, Welk (2004) argued that a reliable prediction of the invaded range of *Lythrum salicaria* in North America was only possible using a large cumulative data set compiled during ca. 150 years of monitoring of the species range changes in North America. This calls for special caution in ecological niche modelling of recently introduced species based on invaded range only.

Interestingly, in Finland about half a dozen new observations of *Elodea canadensis* discovered in 1985–2006 occurred up to a maximum of 300 km north from the areas predicted as climatically suitable. These new records suggest that either the species has been able to accelerate its spread towards northernmost Europe during recent years more than simulated by the bioclimatic models, or that a series of unusually warm years during the last ca. 15 years in Finland (Tuomenvirta 2004, Pöyry et al. 2009) and elsewhere in Europe (Della-Marta et al. 2007) has enabled *Elodea canadensis* to make major dispersal jumps. Indeed, the northernmost records have been made quite recently, one in 1994 and the other in 2001, and thus these observations probably reflect the accumulating effect of the recent warm years.

Three factors potentially affecting the performance of the bioclimatic envelope models were examined here: temporal delimitation of the climate data, selection of climate variables, and interactions between multiple sets of pseudo-absences and increasing the number of predictor variables. Several studies have used climate data averaged over a 30 year period (e.g. Huntley et al. 1995, Sykes et al. 1996, Hartley et al. 2006), although the species data might have been collected over a much longer time slice. We used climate predictor variables that were averaged both over a 30 year period and over a 80- (Europe) or 90- (North America) year period. However, the use of longer-term climate data (which better covered the time slice when the species occurrence records were made) did not significantly improve the model accuracy or affect the geographical predictions of suitable areas. Thus climate data averaged over a 30 year time slice also appear to offer in our case useful predictors for species data collected over a longer time slice. However, it is not possible to assess the generality of this finding, i.e. whether it is a special case or could be applied to other corresponding bioclimatic modelling studies as well. Similar results are likely to emerge in studies where the climate data averaged over a shorter time period do not deviate much from the data averaged over a longer time period. If the two climate data sets deviate notably, differences in the model outputs may occur especially when the models are fitted to the climate scenario data to assess potential future species distributions.

Additional factors which might critically affect the model performance are the time slice and the climate conditions under which the species data in the invaded range have been collected. In particular, if several occurrences have been made in climatically extreme years that have enabled notable dispersal jumps for the species, models based on climate data sets averaged over several decades can fail to predict correctly such abrupt changes in distribution range (Baker et al. 2000, Heikkinen et al. 2006b). Thus in projecting the models to the invaded range, it should be noted that changes in the range margins may be related to climatically highly optimal short-term time periods and associated dispersal jumps of the species (cf. Mitikka et al. 2008), as also suggested by our results.

Insufficient attention has been paid to the potential impacts of selection of climatic variables (Beaumont et al. 2005, Heikkinen et al. 2006b, Beaumont et al. 2007), although the observed discrepancies between model predictions and invaded ranges may be caused by the choice of climatic predictors or climate data sets used in the modelling (Peterson and Nakazawa 2008). Here, the extended models including seven climate variables showed significantly better model performance in North America (and in Finland) than the baseline models with three climate variables. The differences in spatial projections of the climatically suitable areas between the baseline and extended models were slight in North America, but showed a tendency to become more noticeable when the models were transferred to Europe, particularly to Finland (cf. Thuiller 2003). In general, the success of the attempts to transfer species distribution models from one continent or region to another has varied between the studies. Some studies have reported a high success for the projections of the transferred models (e.g. Peterson 2003a, Iguchi et al. 2004, Chen et al. 2007), while some other studies have shown notable differences between the model predictions and observed species distributions (e.g. Fitzpatrick et al. 2007, Broennimann et al. 2007, Beaumont et al. 2009). Recent studies suggest that habitat models based on essential functional resources for the studied species could be transferred better in space than models that use indirect environmental variables, such as biotope types (Vanreusel et al. 2007), and that the transferability may be reduced due to the peculiarities of the study areas, such as differences in the ranges of environmental factors and the varied impact of land-use history between the model calibration and model evaluation areas (Randin et al. 2006).

With regard to individual climate variables, GDD5 was among the two most important predictors of the distribution of *Elodea canadensis* in all models. GDD5 has been successfully employed in broad-scale modelling of the distribution of terrestrial plant species (Beerling et al. 1995, Huntley et al. 1995, Sykes et al. 1996), and it also appears to provide a useful predictor of the range limits and climatically suitable areas for invasive aquatic plants as well. In North America, Welk (2004) concluded that *Lythrum salicaria*, an invasive wetland species, is sensitive especially to variation in length of the growing season. Growing degree days, which is an indicator for the length and thermal intensity of the growing season, can thus be a highly useful predictor in delimiting the northern range boundaries for a wide range of plant species from different habitats. By contrast, mean temperature of the coldest month (MTCO) was

in most cases replaced in the extended models by one or more of the four additional variables. The lower explanatory power of MTCO for aquatic plants in comparison to terrestrial species is probably related to the fact that water bodies tend to mitigate the effects of extreme minimum temperatures, and moreover, ice cover isolates the overwintering submerged aquatic plants from the effects of extreme cold periods. Annual water balance (WB) was selected almost equally as often as the two water deficit variables into the extended models, but made a lower model contribution than the two water deficit variables.

Contrary to our expectations, July temperature did not appear as a significant predictor for *Elodea canadensis*. It is possible that the two water deficient variables that combine the impacts of temperature and precipitation better reflect the areas where water temperatures in inland watercourses are exposed to critical levels of warming, whereas the northern range limit for the species is more accurately determined by GDD5 than by July temperature.

Overall, the improvements in model performance observed here between the baseline models and the extended models support the conclusions reached by Beaumont et al. (2005): more consideration should be paid to the selection of variables in order to identify those that have the greatest predictive power, and knowledge on the biology of the modelled species should be used as much as possible during the variable selection. In particular, the use of one baseline set of environmental variables which is readily at hand in multispecies modelling studies (instead of careful species-specific selection of variables) may result in suboptimal models being generated for some, or even many, of the species (Heikkinen et al. 2006b).

However, inclusion of more predictor variables in ecological niche models can also cause drawbacks. Most importantly, excessive inclusion of predictors may complicate the interpretation of the importance and effect of individual predictor variables (Heikkinen et al. 2004, Hartley et al. 2006), and result in over-fitting and overly complex models (Hartley et al. 2006). In addition, our results show that increasing the number of candidate predictors increases the uncertainty in model predictions in a hitherto rarely acknowledged way, i.e. via its interaction with the use of pseudo-absences. There are several approaches for generating pseudo-absence points (Pearce and Boyce 2006), including selecting points randomly (McPherson et al. 2004), randomly with case-weighting to reduce the effective sample size of pseudo-absences (Guisan et al. 2007), or via environmentally weighted random sampling (Zaniewski et al. 2002). This selection of approach can affect the outcomes of the models (Engler et al. 2004), but the pros and cons of different approaches remain open to debate (Chefaoui and Lobo 2008). Here, following McPherson et al. (2004), the pseudo-absences were selected randomly. Our results show that increasing the number of predictors may notably increase the variability of the model projections based on different random sets of pseudo-absences, due to the varying combinations of climate variables that were selected in the different extended GAMs. This variability between the individual extended models caused increased variation in the per-grid-cell probability values and in the spatial predictions of the suitable areas between the individual models (Fig. 3, 5, 7 and 9).

This suggests that in order to lower the risk of choosing an inappropriate set of pseudo-absence points and generating suboptimal models, multiple sets of pseudo-absences should be generated instead of using only one selection (Engler et al. 2004), as well as averages calculated across multiple models to provide consensus predictions (Hartley et al. 2006). Projections from multiple models allow quantification of the uncertainty in model predictions, which in turn assists the making of management decisions with greater certainty (Hartley et al. 2006). In our case, mapping the standard deviation of the per-grid-cell probability values provided a simple way to visualise where the predictions from the individual extended GAMs differed most and where they agreed most.

It is obvious that identification of the detailed locations most at risk to the invasions by *Elodea canadensis* would benefit from including information on other factors in addition to climate (cf. Rahel and Olden 2008). Potentially useful additional predictors include factors describing the degree of human influence (population density, land transformation, presence of infrastructures etc.) (Ficetola et al. 2007), and physical and chemical characteristics of water bodies (cf. Buchan and Padilla 2000). In the case of *Elodea canadensis* particularly water chemistry might matter. Although the species has a relatively wide tolerance for water pH, it favours calcium- and nutrient-rich eutrophic waters (Weidema 2000).

It is very likely that *Elodea canadensis* will continue to spread further north in Finland and elsewhere in northernmost Europe. This is because the magnitude of the projected climate change is particularly high in northern latitudes (ACIA 2005). Warming climate can reduce the extent of ice cover and cause warmer water temperatures in high latitude water bodies, and thus allow the further expansion of invasive aquatic species such as *Elodea* (Rahel and Olden 2008). In general, freshwater organisms are less capable of tracking the geographic shifts in climatic optima than terrestrial organisms (Rahel and Olden 2008). However, *Elodea canadensis* is probably better equipped to pass the four main barriers in the process of species invasion into new areas (see Hellmann et al. 2008) than aquatic species in general: i.e. effective passing of (1) Geography–barrier (many dispersal vectors, long-lasting fragments), (2) Abiotic conditions –barrier (survives in invaded areas due to relatively wide tolerance capability), (3) Biotic interactions –barrier (able to compete effectively with native macrophytes and become dominant), and (4) Landscape factors –barrier (vegetative fragments spreading via watercourses and passive transportation by human activities and waterfowl) (Goodwin et al. 1999, Barrat-Segretain et al. 2002, Richardson et al. 2007).

Conclusions

Our results suggest that bioclimatic envelope models can provide a useful first-step tool for the identification of areas most at risk to colonization by *Elodea canadensis*, and possibly also for other similar aquatic invasive species. Such models may help in targeting early preventive or ameliorative measures in a timely manner (Kriticos et al. 2003), planning and prioritizing of control measures (Weber 2001, Roura-Pascual et al. 2004), and inform us as to the potential further spread of the species across the new landscape (Chen et al. 2007). However, increasing attention should

be targeted to careful consideration and selection of environmental variables included in the models, generating consensus predictions based on multiple models (especially when employing pseudo-absences), and investigating and quantifying the geographic patterns of the uncertainties in the model predictions. These actions would help in improving the usefulness of bioclimatic envelope models, and ecological niche models in general, in predicting the distributions and range shifts of invasive aquatic species.

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