



Are niche-based species distribution models transferable in space?

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ABSTRACT

Aim To assess the geographical transferability of niche-based species distribution models fitted with two modelling techniques.

Location Two distinct geographical study areas in Switzerland and Austria, in the subalpine and alpine belts.

Methods Generalized linear and generalized additive models (GLM and GAM) with a binomial probability distribution and a logit link were fitted for 54 plant species, based on topoclimatic predictor variables. These models were then evaluated quantitatively and used for spatially explicit predictions within (internal evaluation and prediction) and between (external evaluation and prediction) the two regions. Comparisons of evaluations and spatial predictions between regions and models were conducted in order to test if species and methods meet the criteria of full transferability. By full transferability, we mean that: (1) the internal evaluation of models fitted in region A and B must be similar; (2) a model fitted in region A must at least retain a comparable external evaluation when projected into region B, and vice-versa; and (3) internal and external spatial predictions have to match within both regions.

Results The measures of model fit are, on average, 24% higher for GAMs than for GLMs in both regions. However, the differences between internal and external evaluations (AUC coefficient) are also higher for GAMs than for GLMs (a difference of 30% for models fitted in Switzerland and 54% for models fitted in Austria). Transferability, as measured with the AUC evaluation, fails for 68% of the species in Switzerland and 55% in Austria for GLMs (respectively for 67% and 53% of the species for GAMs). For both GAMs and GLMs, the agreement between internal and external predictions is rather weak on average (Kulczynski's coefficient in the range 0.3–0.4), but varies widely among individual species. The dominant pattern is an asymmetrical transferability between the two study regions (a mean decrease of 20% for the AUC coefficient when the models are transferred from Switzerland and 13% when they are transferred from Austria).

Main conclusions The large inter-specific variability observed among the 54 study species underlines the need to consider more than a few species to test properly the transferability of species distribution models. The pronounced asymmetry in transferability between the two study regions may be due to peculiarities of these regions, such as differences in the ranges of environmental predictors or the varied impact of land-use history, or to species-specific reasons like differential phenotypic plasticity, existence of ecotypes or varied dependence on biotic interactions that are not properly incorporated into niche-based models. The lower variation between internal and external evaluation of GLMs compared to GAMs further suggests that overfitting may reduce transferability.

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Abbreviations: SDM, species distribution model; GLM, generalized linear model; GAM, general additive model; CH, Switzerland; P/A, presence and absence; AT, Austria; GIS, geographic information system; DEM, digital elevation model; IDW, inverse distance weighting; IE, internal evaluation; EE, external evaluation; IP, internal prediction; EP, external prediction; AUC, metric based on the area under the curve of a receiver-operating characteristic plot (ROC plot); TI, transferability index.

Overall, a limited geographical transferability calls for caution when projecting niche-based models for assessing the fate of species in future environments.

Keywords

Austria, generality, generalized additive models (GAM), generalized linear models (GLM), geographical transferability, habitat distribution, model evaluation, predictions, spatial modelling, Switzerland.

INTRODUCTION

Niche-based species distribution models (SDM) (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005) are models that relate observations of species, gathered over a certain period of time, to various attributes of the environment such as topography, climate or geology. These environmental attributes, or predictors, arranged along a gradient from proximal to distal predictors (Austin, 2002), can have direct or indirect effects on species establishment and survival. As SDMs do not consider the time dimension, they are said to be static. Conceptually, they assume the fitted relationship to be an adequate representation of the realized niche of the species under a stable equilibrium constraint (Franklin, 1995; Guisan & Theurillat, 2000a).

In recent years, a large number of studies have used SDMs, developed for individual species at various spatial scales (for examples see Scott *et al.*, 2002). These models are not only of theoretical interest in biogeography, but are also valuable tools in conservation biology and species management (Miller, 1986; Carey & Brown, 1994; Godown & Peterson, 2000; Engler *et al.*, 2004). However, most published SDMs were developed for sections of a species' range and few models have been fitted at the global scale (Jeffree & Jeffree, 1994) or have used the full extent of a species' geographical range. Examples of the latter include models where regionally endemic species (Peterson *et al.*, 2000) or the whole native range for invasive alien species (Peterson *et al.*, 2003) were considered.

Furthermore, SDMs are usually evaluated and applied within the region in which they were fitted. As a result, their applicability to other parts of a species' geographical range (Thomas & Bovee, 1993; Fielding & Haworth, 1995; Glozier *et al.*, 1997; Ozesmi & Mitsch, 1997; Schröder & Richter, 1999; Kleyer, 2002) or to other time periods (Schröder & Richter, 1999; Araújo *et al.*, 2005b) was rarely assessed. This concept of geographical or temporal cross-applicability of models was defined as transferability (Thomas & Bovee, 1993; Glozier *et al.*, 1997; Schröder & Richter, 1999; Kleyer, 2002) or generality (Fielding & Haworth, 1995). Such transferability can be an important feature of SDMs, for instance if they are used for projections into new areas (transferability in space) or for predictions of climate-change responses (transferability in time) (Fielding & Haworth, 1995).

There could be potential obstacles to model transferability. According to Walter's law of relative habitat constancy (Walter

& Breckle, 1985), species can shift their apparent habitat – often defined with regard to indirect predictors such as topography or vegetation structure – to fit to their basic ecological requirements determined by direct, physiologically meaningful predictors (such as sum of temperature or water availability). As a result, transferability should be limited when indirect predictors are used, as these may fail to express the true habitat requirements of the species in distinct geographical areas. Using direct or resource predictors should allow a more universal, and thus more transferable, definition of a species' realized niche, but requires these predictors to be available in a spatially explicit form (Austin, 1980, 1985; Austin *et al.*, 1984; Austin & Smith, 1989; Guisan & Zimmermann, 2000). Models incorporating spatial or temporal autocorrelation may also be difficult to transfer into distinct geographical areas (Hampe, 2004; Araújo *et al.*, 2005a; Guisan & Thuiller, 2005). However, even when the abiotic conditions remain constant, changes in the regional species pools usually occur in distinct parts of a species' range, for instance as a result of different historical influences. Such local changes in biotic pressure are likely to generate local modifications of a species' realized niche (Pulliam, 2000), and thus to affect the geographical transferability of locally fitted models. The existence of ecotypes (climatic, edaphic, geographic, etc.) may also cause problems when transferring a model from one region to another (Walter & Breckle, 1985; Joshi *et al.*, 2001).

Moreover, it is well documented that species tend to thrive in a more varied array of habitats at the centre of their distribution, and to become rarer and more restricted to specialized habitats towards the margins (Brown *et al.*, 1995). In addition, landscape-scale population dynamic processes, such as mass effects and source–sink dynamics (Dias, 1996; Pulliam, 2000; Mouquet & Loreau, 2002, 2003), can inflate realized niches where species are abundant, whereas other processes, such as Allee effects, may shrink them where species are rare (Groom, 1998; Keitt *et al.*, 2001). Hence the position of the different study areas within the whole species' range is also likely to affect the way niche models are fitted (Peterson *et al.*, 2000). Furthermore, it has been shown for SDMs of plant species that spatial predictability depends on particular traits of individual species such as those that determine their colonization ability (Dirnböck & Dullinger, 2004).

Despite these potential obstacles, several studies provided evidence supporting the idea that niche positions are more than merely regional phenomena (Thompson *et al.*, 1993; Hill

et al., 2000; Prinzing *et al.*, 2002). They showed that most species can occupy similar niche positions in distinct regions, and that geographical variation of the niche does not usually increase for species that are more susceptible to competitive displacement or ecophysiological stress. This is further supported by several previous studies that successfully tested spatial and temporal transferability of habitat models. However, these studies were restricted to a limited number of habitats and species within a restricted number of taxonomic groups, including arthropods in fens (Schröder & Richter, 1999), fish (Freeman *et al.*, 1997; Glozier *et al.*, 1997) or birds (Fielding & Haworth, 1995; Ozesmi & Mitsch, 1997). Comparisons across many species (Araújo *et al.*, 2005a) and separate regions should allow more general conclusions.

Testing of model transferability could prove particularly powerful for complementing standard procedures of model evaluation (for best practice techniques see Maggini *et al.*, 2006, this issue). The use of observations independent from the training data set has been recommended for a proper evaluation of models (Fielding & Bell, 1997; Guisan & Zimmermann, 2000). If the training and test data sets are restricted to the same spatial and temporal domains, internal evaluation techniques such as data partitioning or split sample approaches are sufficient. If the predictions are to be tested for their generality and robustness (accuracy and stability of predictions in a new situation), Fielding & Bell (1997) recommend using a geographically (Fielding & Haworth, 1995) or temporally (Boyce *et al.*, 2002; Araújo *et al.*, 2005b) independent data set for their external evaluation.

A large number of studies, involving many different modelling techniques, have been conducted to predict the potential distribution of species under changing environmental conditions (Huntley, 1995; Sykes & Prentice, 1995; Guisan & Theurillat, 2000b; Bakkenes *et al.*, 2002; Peterson *et al.*, 2002; Dirnböck *et al.*, 2003; Thuiller *et al.*, 2005; Araújo *et al.*, 2006) as well as in regions where such species do not yet occur (Weber, 2001). However, testing for proper geographical or temporal transferability of models and the related uncertainty has usually been neglected.

For full model transferability between two regions, we suggest that the three following conditions have to be fulfilled: (1) the internal evaluation of models fitted in region A and B must be similar, (2) a model fitted in region A must at least retain a comparable external evaluation when projected into region B, and (3) internal and external spatial predictions have to match within both regions; here internal prediction means that a model fitted in region A is used for predictions in region A, whereas external prediction means that a model fitted in region B is used for predictions in region A.

We hypothesize that some modelling techniques are likely to be more robust than others when transferred from one geographical region to another. For instance, the shape of response curves in generalized additive models (GAM; Hastie & Tibshirani, 1986), being based on smoothing techniques, is not predefined and thus allows modelling closer to the data (Guisan *et al.*, 2002; Lehmann *et al.*, 2002) than do generalized

linear models (GLM; McCullagh & Nelder, 1989), which are based on parametric (often polynomial) response curves. For this reason, and for an identical number of degrees of freedom allowed for each predictor in each technique, we expect GAMs to provide higher fits overall (as shown by Moisen & Frescino, 2002) but potentially at the cost of being less generalizable than GLMs to other situations, that is, showing weaker transferability in space and time.

In this study we propose a quantitative measure (a new index) and test of transferability. Our data set covers 54 alpine plant species in two distinct geographical regions of Switzerland and Austria. We conducted a cross-region assessment using two modelling techniques, GLMs and GAMs, to answer three main questions:

- 1 How can transferability best be quantified?
- 2 Are niche-based models fitted with GLMs and GAMs transferable in space?
- 3 Does model transferability depend on the modelling technique used (GLM vs. GAM)?

METHODS

Study areas

The two study areas cover parts of the alpine and forest-free subalpine zones of the western Swiss Alps (6°60' to 7°10' E; 46°10' to 46°30' N) and the north-eastern calcareous Alps in Austria (14°60' to 15°50' E; 47°30' to 47°50' N). A comparison of the environmental gradients realized within the two study areas is given in Table 1. Hereafter, the Swiss and Austrian study areas are abbreviated CH and AT, respectively.

In the CH region, elevations reach 3210 m a.s.l. at the top of the Diablerets chain where important glaciers are still found. Along the altitudinal gradient the sequence of vegetation belts is that typical for the calcareous Alps: colline belt with deciduous forests (mainly *Fagus sylvatica* L., European beech); montane belt with mixed forests (*F. sylvatica* and *Abies alba* Mill., silver fir); subalpine belt with coniferous forest [*Picea abies* (L.) Karsten, Norway spruce]; alpine belt with heath, meadow and grassland vegetation; and nival belt with sparse vegetation cover of characteristic high-elevation taxa. Vegetation has long been, and still is, under the influence of human land use: pasture is common in this region from the valley bottoms up to the subalpine and lower alpine areas.

The AT study area comprises four distinct mountains (Mt Hochschwab, Mt Schneealpe, Mt Rax and Mt Schneeberg). Summits vary between 1900 and 2300 m a.s.l. Vegetation belts are generally similar to the CH region, although the nival zone is lacking. As in CH, summer pastures are abundant (Dirnböck *et al.*, 2003).

In this study we focused on the subalpine to nival belts only. Accordingly, we set the lower limit of the study areas at 1300 m a.s.l. in both CH and AT. This altitude corresponds to the average lower elevation limit of the subalpine belt in the Alps (Ozenda, 1985).

Table 1 Environmental context of the two study areas

	Switzerland (CH)	Austria (AT)
Surface (km ²)	270	110
Number of vegetation plots	402	603
Altitudinal range (m)	1300–3210	1300–2273
Temperature range (°C)	–3.5–6	1–4.5
Temperature degree days (°C day year ⁻¹)	313–2346	788–1830
Precipitation range (mm)	1400–2400	1500–2500
Moisture index (average of monthly values June–August) (mm day ⁻¹)	–13–174	–7–160
Global solar radiation (average of monthly values June–August) (kJ m ⁻² day ⁻¹)	3264–30659	3267–30616
Number of days with snow cover per year (period 1980–2000)	75–347	130–237

CH, Swiss study area; AT, Austrian study area.

Species data

Data on the presence–absence of species originate from two separate data sets. The CH data comprise 402 vegetation plots sampled during 2002 and 2003. The data for AT were collected between 1994 and 2001 on a total of 603 plots. A random stratified sampling strategy restricted to open, non-woody vegetation (grassland, rock and scree vegetation) was applied in both study areas. The plot size was constant in CH (16 m²), whereas it varied from 5 to 30 m² in AT (Dirnböck *et al.*, 2003). From the overall species pool of these samples, a total of 54 species with more than 30 occurrences in both data sets were selected for modelling.

Environmental predictors

We generated a comparable set of environmental predictors for both study areas, using identical GIS algorithms and types of input data (Table 2). All GIS predictors were calculated with a 25-m spatial resolution as derived from the digital elevation models (DEM) available in each study area.

First, we calculated the slope from the DEMs to account for gravitational processes such as snow avalanches and rockfalls (Guisan *et al.*, 1998; Dirnböck *et al.*, 2003) and their

impact on vegetation. Second, we calculated linear lapse rates for long-term (1961–90) monthly mean temperature and monthly rainfall taken from the national meteorological networks of Switzerland and Austria (MeteoSuisse and ZAMG). Next, we normalized the monthly values to 0 m a.s.l., using the regression lapse rates, and interpolated the 0-m data to the whole surface of both study areas using inverse distance weighted interpolations (IDW). Finally, the spatially interpolated values (representing locally adjusted regression intercepts) were reprojected to actual elevations using the 25-m DEM of each study area and the regression lapse rates. This method differs from the approach of Zimmermann & Kienast (1999) in using IDW rather than thin-plate splines for the interpolation. These basic climatic variables were then transformed into three physiologically more meaningful bioclimatic predictors: the growing degree-days (with 0 °C threshold), moisture index over the growing season (difference between precipitation and potential evapotranspiration from June to August), and potential global solar radiation during the growing season (Table 2 and references therein). Additionally, the spatially distributed hydrological model PREVAH (Gurtz *et al.*, 2003) was used to obtain a physically based predictor for snow-cover duration in both Swiss and Austrian study sites.

Table 2 Physiologically meaningful environmental predictors used to model the distribution of species

Variables	Units	Details	Method	References
Temperature degree days	°C day year ⁻¹	Sum of days multiplied by temperature > 0 °C	ARCInfo AML	Zimmermann & Kienast (1999)
Moisture index (average of monthly values June–August)	mm day ⁻¹	Monthly average of daily atmospheric H ₂ O balance	ARCInfo AML	Zimmermann & Kienast (1999)
Global solar radiation (average of monthly values June–August)	kJ m ⁻² day ⁻¹	Monthly average of daily global solar radiation	ARCInfo AML	Kumar <i>et al.</i> (1997)
Snow cover	days	Number of days with snow cover for the period 1980–2000	PREVAH HRU model	Gurtz <i>et al.</i> (1999)
Slope	degrees	Slope inclination	DEM, ARCInfo GRID routine	Anon (2004)

As the latter model has not yet been used in any similar biogeographical study, we provide more details here. PREVAH has been used previously for simulation of the hydrological behaviour of catchments at different spatial scales (Zappa, 2002) and, among other model applications, checked against point observations of snow water equivalent and remotely sensed maps of snow cover distribution (M. Zappa, unpublished data). In the present application, the hydrological model is forced by interpolated daily values of observed climatic variables collected by MeteoSuisse and ZAMG. Data for five meteorological variables (precipitation, air temperature, relative sunshine duration, wind speed and water vapour pressure) have been used for the period 1979–2000. Global radiation was estimated as described by Schulla (1997). Both temperature and radiation are locally adjusted to take into account slope, aspect and shade. 1979 was adopted as the initialization period. The parameters controlling snow accumulation, snowmelt and runoff generation were then calibrated for the 6-year period 1980–85, and spatially distributed maps of cumulative snow cover duration were finally summarized for the 20-year period 1980–99.

All these environmental variables are expected to have a major direct ecophysiological impact on plant species (Pearson *et al.*, 2002; Dirnböck *et al.*, 2003; Körner, 2003), as required for successful transferability.

Analytical design

All steps of the analyses are summarized in Fig. 1. We divided the analytical design into three main parts: (1) model fitting, (2) model evaluation, and (3) model prediction.

Model fitting

Two separate models were fitted for each species in the *s-PLUS* 2000 software (MathSoft, 1999), with presence/absence values

in each regional data set, using GLMs (McCullagh & Nelder, 1989) and GAMs (Hastie & Tibshirani, 1986) with a binomial variance and a logistic link function. In both GLMs and GAMs, an Akaike information criterion (AIC)-based stepwise procedure in both directions was used to select the most significant predictors (Akaike, 1973). Up to second-order polynomials (linear and quadratic terms) were allowed for each predictor in GLMs, with the linear term being forced in the model each time the quadratic term was retained. Up to four degrees of freedom were allowed for the smooth functions in GAMs. The fit of GLMs and GAMs was measured with the Nagelkerke R^2 (Guisan & Zimmermann, 2000). Model fits within and between models (GLMs and GAMs) and regions (CH and AT) were compared for the 54 species with Wilcoxon signed-rank tests (treating the samples as grouped by species).

Spatial predictions

For both GLMs and GAMs, spatial predictions were made over the full geographical domains in *s-PLUS* using custom codes, then mapped using the ARCGIS 9.0 software (ESRI, 2004). Predictions in CH were made from both the model fitted in CH (internal predictions, IP) and the model fitted in AT (external predictions, EP), and reciprocally for predictions in AT.

Model evaluation

Comparisons of predicted (probability scale) and observed (presence–absence) values were based on the area under the curve (AUC) of a receiver-operating characteristic plot (ROC; Fielding & Bell, 1997) and the Kappa coefficient maximized over the full range of possible probability thresholds (hereafter max Kappa; Huntley, 1995; Guisan *et al.*, 1998). AUC takes values between 0 and 1 with 0.5 meaning no agreement; 0 an

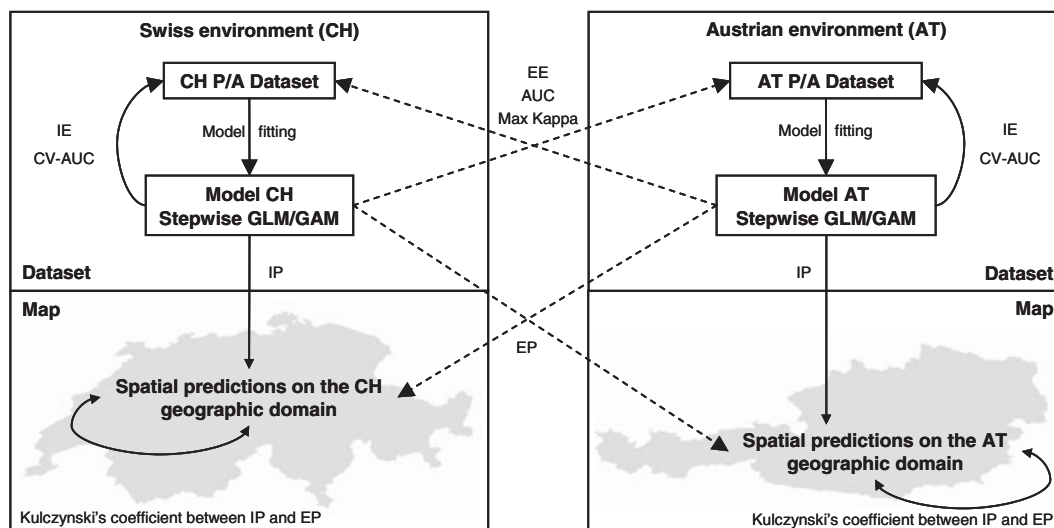


Figure 1 Experimental design. Generalized linear and generalized additive models (GLMs and GAMs) of each species were evaluated with the Switzerland (CH) and Austria (AT) presence/absence data sets and then applied to the geographical domains of both regions (—, IE = internal evaluation; —, IP = internal prediction; ---, EE = external evaluation; ---, EP = external prediction).

inverse relationship (errors better predicted); and 1 perfect agreement. Max Kappa takes values between -1 and +1, with 0 meaning no correlation, -1 an inverse relationship and +1 a perfect agreement.

The AUC values were interpreted using the classification of Araújo *et al.* (2005a) adapted from Swets (1988): excellent $AUC > 0.90$; good $0.80 > AUC < 0.90$; fair $0.70 > AUC < 0.80$; poor $0.60 > AUC < 0.70$; fail $0.50 > AUC < 0.60$. The Kappa values were interpreted using the ranges of agreement of Araújo *et al.* (2005a) adapted from Landis & Koch (1977): excellent $K > 0.75$; good $0.40 > K < 0.75$; poor $K < 0.40$. We assumed that the geographical transferability fail for models which have an internal evaluation (=IE) > 0.7 for the AUC coefficient (> 0.4 for Kappa) and which have an external evaluation (=EE) < 0.7 for the AUC (< 0.4 for Kappa).

The internal evaluation of the models was made by running a 10-fold cross-validation (van Houwelingen & Le Cessie, 1990) on the training data set. During the cross-validation procedure, the original prevalence of the species presences and absences in the data set was maintained in each fold.

The external evaluation was made by projecting each model in the other area and comparing predictions with geographically independent observations using AUC and max Kappa. This represents a fully independent evaluation as recommended by Fielding & Bell (1997).

Internal and external evaluations were compared within and between models and regions for the 54 species using paired *t*-tests.

Measuring and testing transferability

According to our previous definition of full model transferability (see *Introduction*) three conditions have to be fulfilled, based on comparisons of model fit; model evaluation; and spatial predictions. Whereas comparison of model fit is straightforward (one measure for each model in each region), comparison of evaluation measures is more complex. To achieve this, we developed an index (equation 1) that numerically assesses the transferability of an SDM across two regions:

$$TI = \frac{\frac{1}{2} \left(\left(1 - \frac{|AUC_{regA \rightarrow regA} - AUC_{regA \rightarrow regB}|}{0.5} \right) + \left(1 - \frac{|AUC_{regB \rightarrow regB} - AUC_{regB \rightarrow regA}|}{0.5} \right) \right)}{1 + \left| \frac{AUC_{regA \rightarrow regA} - AUC_{regA \rightarrow regB}}{0.5} - \frac{AUC_{regB \rightarrow regB} - AUC_{regB \rightarrow regA}}{0.5} \right|} \quad (1)$$

where $AUC_{regA \rightarrow regA}$ means that the model is fitted in region A and evaluated in the same region. The transferability index (TI) is based on the decrease of the AUC coefficient when switching from the internal ($AUC_{regA \rightarrow regA}$ and $AUC_{regB \rightarrow regB}$) to the external ($AUC_{regA \rightarrow regB}$ and $AUC_{regB \rightarrow regA}$) evaluation for both regions. The TI varies from 0 to 1 and is at its maximum when the difference between

IE and EE is null. Note that this index is based only on the AUC evaluation measure, and does not include assessment of reciprocal spatial predictions. Thus it provides information only on criteria 1 and 2 when assessing the full transferability.

Four potential relationships implying this TI and various species or model properties were tested with linear models across the whole set of species, for both GLMs and GAMs: TI as a function of (1) the differences between prevalences in Switzerland and Austria, (2) the differences in degrees of freedom between the models fitted in CH and in AT, (3) the differences between the adjusted deviance of models fitted in CH and in AT, and (4) the similarities between models compositions in CH and in AT.

In addition, we tested separately the difference in degrees of freedom between GLMs and GAMs as a function of [(IE - EE) of GLMs] - [(IE - EE) of GAMs] in each region with a linear regression. The prevalence of a species in one region was calculated using the ratio of the occurrences of the species to the total number of observations. The similarity between the model compositions in CH and AT was calculated with the simple matching coefficient (Legendre & Legendre, 1983).

To assess the third criterion of full model transferability, the agreement between IP and EP maps was calculated with an asymmetrical distance version of Kulczynski's coefficient (KC; Legendre & Legendre, 1983). The KC for comparison of map *j* vs. *k*, (here IP vs. EP for a given region) D_{jk} , is:

$$KC_{jk} = \frac{\sum_{i=1}^n X_{ij} - \sum_{i=1}^n \min(X_{ij}, X_{ik})}{\sum_{i=1}^n X_{ij}} \quad (2)$$

where X_{ij} and X_{jk} are the habitat suitability for cell *i* for maps *j* and *k*, respectively, and *n* is the number of cells. Similarly, KC_{kj} can be calculated for *k* vs. *j*, and KC_{kj} is not, in general, equal to KC_{jk} . The KC varies from 0 to 1 and is at its maximum when the difference between IP and EP is null. The KCs were then compared within and between models and regions with Wilcoxon signed-rank tests. Overall trends between models and regions across species were assessed using boxplots and standard pairwise tests.

RESULTS

The measures of model fit are, on average, 24% higher for GAMs than for GLMs in both CH and AT regions. On average, GLMs and GAMs have a higher fit in CH than in AT (83% higher for GLMs and 78% for GAMs; Table 3, Fig. 2). In addition, the range of values for the explained deviance

Table 3 Global comparisons, using Wilcoxon signed-rank tests, of the adjusted deviance of the 54 species models between generalized linear and generalized additive models (GLMs and GAMs) (IDs 1 and 2) and between Switzerland (CH) and Austria (AT) (IDs 3 and 4) (IDs correspond to numbers in Fig. 2)

	ID	x	Test	y	P
Comparisons between GLMs and GAMs	1	GLM.CH	<	GAM.CH	< 0.001
	2	GLM.AT	<	GAM.AT	< 0.001
Comparisons between CH and AT	3	GLM.CH	>	GLM.AT	0.007
	4	GAM.CH	>	GAM.AT	0.001

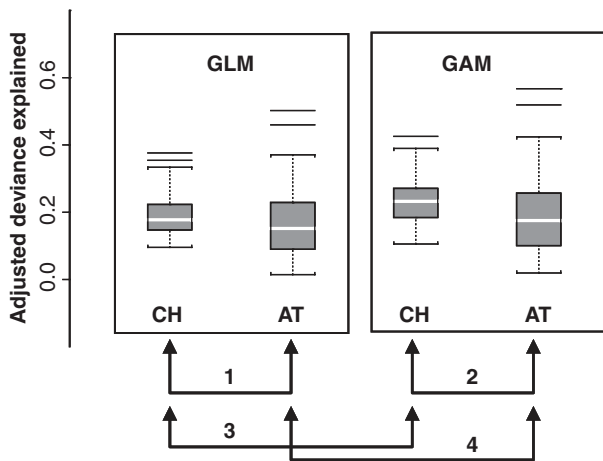


Figure 2 Boxplots of the adjusted D^2 explained by generalized linear and generalized additive models (GLMs and GAMs) in Switzerland (CH) and Austria (AT) for the 54 species. None of the differences in the adjusted D^2 within models between the two regions (arrows 1 and 2), and between GLMs and GAMs within regions (arrows 3 and 4), is significant (Wilcoxon signed-rank tests with P values of 0.898/0.951 and 0.770/0.051, respectively).

(adj- D^2) is narrower in CH than in AT for both GLMs and GAMs (Fig. 2). Results of comparisons across regions and across methods are given in Table 4. Hereafter, reference numbers given in the text for each type of comparison (C1–C6) are as explained in Table 4.

The IE is systematically higher than the EE for both GLMs and GAMs, between and within regions (C1 and C2). When comparing the two methods (C3) using the Kappa coefficient, IE for GLMs is higher than for GAMs in AT, whereas no significant difference is observed with the AUC coefficient. In CH, comparing the IE of GLMs and GAMs using either the AUC or the Kappa coefficients yields no significant difference.

The comparisons of regions (C4) show that the IE of GLMs and GAMs is higher in CH than in AT. Furthermore, GLMs fitted in CH have higher EE with the Kappa coefficient than GAMs fitted in CH when both are transferred to AT (C5), whereas no significant difference is observed with the AUC coefficient. However, no such significant differences exist between EE of GLMs and GAMs when they are transferred from AT to CH. The EE of GAMs transferred from AT to CH is higher, on average, than that of GAMs transferred from CH to AT (Table 5).

The histograms (Fig. 4) show an important difference between the IE and EE of GLMs and GAMs in both regions. When testing transferability with the AUC metric, the transferability failed for 68% of the species models fitted in Switzerland and for 55% of the models fitted in Austria for GLMs, and for 67% (CH) and 53% (AT) of the models for GAMs. These values are even higher when evaluated with the Kappa coefficient: 82% of the GLMs fitted in CH failed and 100% of the GAMs, whereas all the models fitted in AT and 91% of the GAMs failed. The distribution of the AUC coefficients on the EE histograms (Fig. 3) shows that, globally, GLMs are only slightly – yet significantly – more robust to transferability than GAM models.

The results of the linear regressions in Table 5 show no relationships between the TI of GLMs and GAMs and the difference of prevalence, degrees of freedom and adjusted deviance between the two regions. There is also no relation between the TI and the similarity of models, in terms of predictor composition, between CH and AT.

The number of degrees of freedom used in GAMs is higher, on average, than in GLMs in both CH and AT (Wilcoxon signed-rank tests: $P < 0.001$), but the linear regressions show no relationship between the difference in IE and EE between GLM and GAM [(IE – EE)_{GLM} – (IE – EE)_{GAM}] and the difference in degrees of freedom between GLMs and GAMs in both regions ($R^2 < 0.01$).

Regarding spatial predictions, the Wilcoxon signed-rank tests on the agreement between prediction maps (KC) show no significant differences between GLMs and GAMs within CH (Fig. 5, arrow 1 below the graph) and within models across regions (Fig. 5, arrows 3 and 4). On the other hand, the agreements between IP and EP of GAMs are higher, on average, than those of GLMs in AT (Fig. 5, arrow 2, $P < 0.01$). In general, the agreement between IP and EP is rather weak (average value of the coefficient between 0.3 and 0.39) and the variation across species is considerable (from 0 to 0.97).

The four examples in Fig. 6 illustrate the different types of pattern of GLM transferability across regions. In order to be comparable across regions, the four selected species have a similar adjusted deviance in CH and AT. The results of GAM models are not presented because they show exactly the same patterns. Three scenarios are possible. A few species, such as *Thesium alpinum* L., meet all the criteria for full transferability (Fig. 6a). For other species, such as *Luzula multiflora* (Retz.) Lej. and *Hypericum maculatum* Crantz s.str., models transfer

Table 4 Comparison by paired *t*-tests of internal evaluation (IE) and external evaluation (EE) for generalized linear and generalized additive models (GLMs and GAMs) in Switzerland (CH) and Austria (AT) (e.g. GLMCHAT = GLM fitted in CH and evaluated with the AT data set)

	AUC				maxKappa			
	<i>x</i>	Test	<i>y</i>	<i>P</i>	<i>x</i>	Test	<i>y</i>	<i>P</i>
<i>Transposability</i>								
C1: Comparisons of IE with EE across regions within models	GLM.CH.ON.CH	>	GLM.CH.ON.AT	< 0.001	GLM.CH.ON.CH	>	GLM.CH.ON.AT	< 0.001
	GAM.CH.ON.CH	>	GAM.CH.ON.AT	< 0.001	GAM.CH.ON.CH	>	GAM.CH.ON.AT	< 0.001
	GLM.AT.ON.AT	>	GLM.AT.ON.CH	< 0.001	GLM.AT.ON.AT	>	GLM.AT.ON.CH	< 0.001
	GAM.AT.ON.AT	>	GAM.AT.ON.CH	< 0.001	GAM.AT.ON.AT	>	GAM.AT.ON.CH	0.023
C2: Comparisons of IE with EE within regions and models	GLM.CH.ON.CH	>	GLM.AT.ON.CH	< 0.001	GLM.CH.ON.CH	>	GLM.AT.ON.CH	< 0.001
	GAM.CH.ON.CH	>	GAM.AT.ON.CH	< 0.001	GAM.CH.ON.CH	>	GAM.AT.ON.CH	< 0.001
	GLM.AT.ON.AT	>	GLM.CH.ON.AT	< 0.001	GLM.AT.ON.AT	>	GLM.CH.ON.AT	< 0.001
	GAM.AT.ON.AT	>	GAM.CH.ON.AT	< 0.001	GAM.AT.ON.AT	>	GAM.CH.ON.AT	< 0.001
<i>Methods</i>								
C3: Comparisons of IE within regions between models	GLM.CH.ON.CH	=	GAM.CH.ON.CH	0.27	GLM.CH.ON.CH	=	GAM.CH.ON.CH	0.48
	GLM.AT.ON.AT	=	GAM.AT.ON.AT	0.14	GLM.AT.ON.AT	>	GAM.AT.ON.AT	0.004
C4: Comparisons of IE across regions within models	GLM.CH.ON.CH	>	GLM.AT.ON.AT	< 0.001	GLM.CH.ON.CH	>	GLM.AT.ON.AT	0.019
	GAM.CH.ON.CH	>	GAM.AT.ON.AT	< 0.001	GAM.CH.ON.CH	>	GAM.AT.ON.AT	0.001
<i>Transposability by methods</i>								
C5: Comparisons of EE within regions between models	GLM.CH.ON.AT	=	GAM.CH.ON.AT	0.82	GLM.CH.ON.AT	>	GAM.CH.ON.AT	0.010
	GLM.AT.ON.CH	=	GAM.AT.ON.CH	0.65	GLM.AT.ON.CH	=	GAM.AT.ON.CH	0.99
C6: Comparisons of EE across regions within models	GLM.CH.ON.AT	=	GLM.AT.ON.CH	0.61	GLM.CH.ON.AT	=	GLM.AT.ON.CH	0.12
	GAM.CH.ON.AT	<	GAM.AT.ON.CH	0.015	GAM.CH.ON.AT	<	GAM.AT.ON.CH	0.002

Table 5 Results of linear regressions correlating the transferability index to: difference of the prevalence of species between the two study regions; difference in degrees of freedom between generalized linear and generalized additive models (GLMs and GAMs); difference of adjusted D^2 of the models; and similarity of model composition between the two regions

<i>Y/X</i>	CH-AT							
	Prevalence		Adjusted D^2		d.f.		Similarity	
	R^2	<i>P</i>	R^2	<i>P</i>	R^2	<i>P</i>	R^2	<i>P</i>
Transferability index (TI)								
GLM	1.66E-03	7.69E-01	4.19E-04	8.83E-01	1.30E-02	4.10E-01	6.89E-04	8.50E-01
GAM	2.71E-03	7.081E-01	4.23E-02	1.35E-01	8.79E-03	5.00E-01	1.23E-05	9.79E-01

well from one region to another but not *vice versa* (asymmetrical transferability; Fig. 6b,c). This asymmetrical transferability represents the predominant pattern across our 54 species.

Finally, the models of some species are not adequately transferable in either direction (Fig. 6d). However, even when the first two criteria for full transferability are met (see *Introduction*), the agreement between IP and EP remains very low in a significant number of cases (*c.* 10% of species).

DISCUSSION

General patterns in transferability

The average transferability of our models across all species is weak compared with other studies (Thomas & Bovee, 1993; Schröder & Richter, 1999; Mäki-Petäys *et al.*, 2002). The

external evaluation failed for more than 50% of the species. Considerable discrepancies among species are observed for trans-geographical predictions (between IP and EP maps). Overall, prediction agreement (measured by the KC) across all species and between methods is, on average, weak. Fielding & Haworth (1995) reached the same conclusion, namely that there is a lack of generality in their models. Taken together, these results suggest that care should be taken when these models are projected to future climates (Araújo *et al.*, 2005b). However, the capacity for transferability is highly species-specific. Models for some species meet the criteria for full transferability (e.g. *T. alpinum*, Fig. 6a), whereas many others do not, showing either asymmetrical transferability or none at all (e.g. *Arabis alpina* L., Fig. 6d).

Our study highlights the importance of testing transferability on a large number of species. Moreover, it reveals a

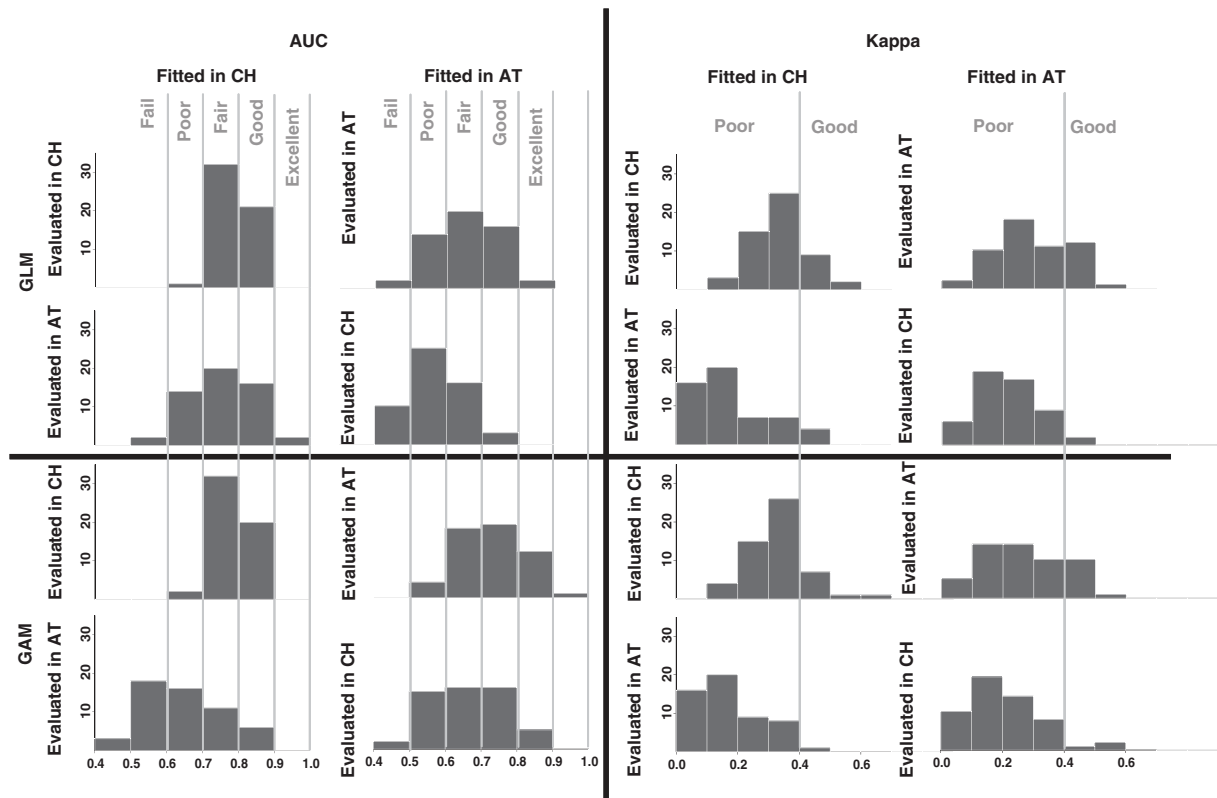


Figure 3 Histograms of the distribution of the area under the curve of a receiver-operating characteristic plot (AUC) and Kappa coefficients for the internal and external evaluation in Switzerland and Austria.

considerable variation in the transferability of SDMs between regions and between modelling techniques. The causes for this limited transferability and high variability cannot be unveiled directly from our results. However, aspects of our results can be used to help identify potential reasons and propose hypotheses for guiding further investigation.

From an inspection of our models, we could not find evidence in support of the idea that differences in the degrees of freedom and in the selected predictors have an effect on the TI. Thus we focus our discussion on the predominant pattern of asymmetrical transferability. Possible causes may be separated into two categories: (1) environmental causes, which are specific to differences between geographical regions, and (2) biotic causes, which are intrinsic to each individual species being modelled and to the regional species pool with which it is interacting.

Environmental and biotic limitations to full transferability

With respect to geographical differences, asymmetrical transferability might depend on the predictor variables in the model and their range in the training region compared with their range in the test region. From a transferability perspective, a model with predictors that cover the same or a wider range in the training region is more likely to give accurate predictions

in the test region than the reverse. Hence differences in the size and upper limit of the altitudinal range between the two regions (McPherson *et al.*, 2004) may have truncated the response curves of alpine and subalpine species to temperature-related predictors in AT, but not in CH: for example, true alpine species could have a linear response to degree-days in AT and a unimodal response in CH. This is equivalent to the problem of extrapolating beyond the realized range of one or more gradients within the training region (Van Horn, 2002), which is an important issue in general for the geographical transferability of models.

Transferability is obviously sensitive to where, within the distributional and environmental range of a species, a model was developed and parameterized: the variability of transferability is more pronounced when models are transferred from CH to AT.

Larger-scale effects, such as the geographical situation of the study areas (e.g. north–south vs. east–west oriented valleys) and differences in land-use practices, could also affect transferability (Fielding & Haworth, 1995). Dirnböck *et al.* (2003) showed that, for many alpine species, land use (history) is a significant predictor of regional distribution patterns. This kind of qualitative variable is, however, extremely difficult to standardize across regions that have different human traditions and agricultural practices.

Shifts in the microclimatic niches of species from one region to another can be understood as a response to climatic

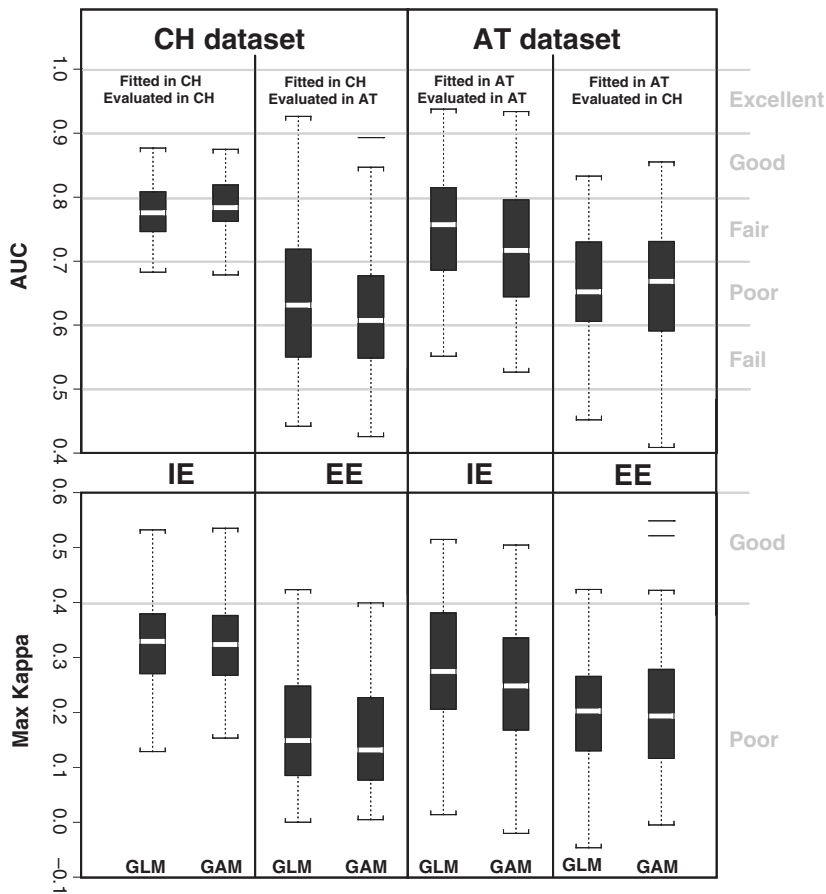


Figure 4 Boxplots of the metric based on the area under the curve of a receiver-operating characteristic plot (AUC) and max Kappa metrics for the internal and external evaluations of generalized linear and generalized additive models (GLMs and GAMs) in Switzerland (CH) and Austria (AT).

differences between regions: the niche requirements of the species are met by occupying different types of site (Walter & Breckle, 1985). However, some differences in local microclimatic conditions may not have been captured by the interpolated environmental variables used in this study. For example, a displacement in the geological or edaphic gradient (Coudun *et al.*, 2006, this issue) that may be required to recover the water conditions could not have been taken into account with our set of predictors. In our case, the 25-m resolution of the predictors may not be appropriate to capture processes such as snow accumulations, rockfalls or microtopographical refuges (Gottfried *et al.*, 1998; T. Lassueur, S. Joost and C. F. Randin, unpublished data).

Another reason for asymmetrical transferability may be that species whose abundance is highly unequal in the two regions may have their niches deformed in divergent directions. For instance, whereas high regional abundances may drive a niche inflation due to mass effects or source–sink systems (Dias, 1996; Pulliam, 2000), regional rarity may cause a niche restriction due to Allee effects (Groom, 1998) or dispersal limitations (Pulliam, 2000; Dirnböck & Dullinger, 2004). However, such discussion remains speculative as long as these effects cannot be revealed by specifically designed observational studies of field experiments.

Differences in phenotypic plasticity and the presence of distinct ecotypes in the two regions may also have an influence on transferability (Joshi *et al.*, 2001). Solving this would have

required genetic analyses to be performed, which was beyond the scope of our study, but it constitutes an interesting direction for future research.

Asymmetrical transferability may also be caused by external biotic factors. Although some authors argue that competitive displacement affects a species' geographical range only rarely (Thompson *et al.*, 1993; Hill *et al.*, 2000; Prinzing *et al.*, 2002), others suggest that biotic interactions play quite an important role in limiting species ranges (Zobel, 1997; Odland & Birks, 1999). More generally, Ozesmi & Mitsch, 1997) suppose that transferability is difficult to assess without taking the main interspecific interactions into account. These different points of view may be the result of studies having been carried out at different resolutions, and thus may be a question of scale. If the resolution used does not correspond to that at which competition potentially takes place (if the competing species can co-occur in the same cell without actually competing for resources), such competitive effects on species range may not be detectable (Guisan & Thuiller, 2005).

As the capacity for transferability appears to depend largely on the species being modelled, further investigations should focus on individual species properties, such as the relationship between species traits or full functional types and their transferability (Kleyer, 2002). In this respect, preliminary results on the relationship between plant traits and the robustness/accuracy of SDMs are promising (Dirnböck & Dullinger, 2004; Thuiller *et al.*, 2004; Thuiller, 2004). For

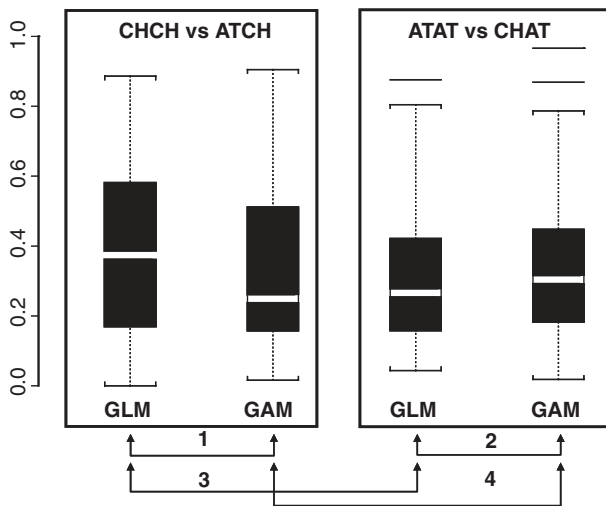


Figure 5 Boxplots of the agreement (Kulczynski's coefficient) between internal and external prediction maps (Fig. 1) within the same geographical domain. CHCH vs. ATCH, agreement between the model fitted in Switzerland (CH) and predicted on the CH geographical domain and the model fitted in Austria (AT) and predicted on the CH geographical domain. No significant difference was observed, on average, between agreements of generalized linear and generalized additive models (GLMs and GAMs) within CH (arrow 1, Wilcoxon signed-rank test, $P = 0.179$), whereas Kulczynski's coefficients of GAMs are, on average, greater than those of GLMs within AT (arrow 2, Wilcoxon signed-rank test, $P = 0.002$). No significant difference was observed in the average for agreements of either GLMs or GAMs between the two ranges (arrows 3 and 4, Wilcoxon signed-rank test, $P = 0.123$ and 0.770 , respectively).

instance, by controlling the proportion of the realized niche that a species was able to colonize, the dispersal capacity can influence the distribution of alpine plant species and their niche breadth along environmental gradients, and thus also affect the transferability of models.

Modelling techniques and choice of predictors

The scores of the external evaluation are globally higher for GLMs than for GAMs when models are transferred from CH to AT, and the scores of the EPs are higher for GLMs in both directions of transferability. Moreover, the variability of the EP is, on average, slightly less pronounced with GLMs, which suggests that models fitted with this technique are more robust when transferred than are GAMs. This result is in line with our hypothesis that overfitting can reduce transferability, with GLMs being less prone to overfitting and thus more generalizable. It is, however, in contradiction with results obtained by Araújo *et al.* (2005b) who found GAM to show superior transferability, in time, to GLMs. Such results are highly dependent on the way GLMs and GAMs are fitted. If polynomial orders higher than quadratic are allowed, GLMs could well show more pronounced overfitting than GAMs. At least, for the same number of degrees of freedom allowed for

each predictor (e.g. third order in GLM; smoothing with three degrees of freedom in GAM), GAMs, as non-parametric models, will always tend to be closer to the data, more sensitive to the peculiarities of particular samples, and thus more prone to overfitting.

Another methodological issue with transferability, although very difficult to assess, may be the quality of the predictor variables and the way each method deals with these. For instance, as GAMs tend to be closer to the data, one could expect them to be more sensitive to measurement or modelling errors in the predictors. However, although these errors may well weaken the models, and thus limit their transferability, they are unlikely to cause the asymmetrical transferability observed in our study. An additional problem here is that the exact level of error is usually unknown for individual predictors. As a result, a proper error assessment can be difficult to conduct in this type of study. Nevertheless, in future studies attempts should be made to pay more attention to the quality and type of predictor variables. According to other studies using similar predictors, those used here are supposedly of a rather proximal nature. However, they still might not be the most proximal and physiologically meaningful ones, and thus may have potentially contributed to causing limited transferability. Further efforts should be made to improve the accuracy of the environmental predictors used to fit this type of model, their spatial resolution and their proximality (in the sense of closeness to causality; Austin, 2002), especially in complex landscapes such as mountain ecosystems.

CONCLUSIONS

Overall, we observed a weak geographical transferability for the 54 SDMs, with considerable variation among species. In this regard, our TI proved useful in providing a quantitative estimate of the geographical transferability across regions. Furthermore, none of the differences in the degrees of freedom, in the composition of models, or in species prevalence across regions appeared to have an effect on the transferability values. The proposed index thus seems useful, but requires more thorough testing and evaluation than possible in this single study.

Only a minority of species met the criteria of full transferability, while asymmetrical transferability was the predominant pattern. The pronounced variability across species calls for additional multi-species assessments in order to test the transferability of SDMs properly. From our set of species, we suggest that several factors (region- or species-specific) may explain the partial transferability or even total lack of transferability for some species. The slightly better transferability of GLMs compared with GAMs further suggests that overfitting may reduce transferability. This also requires further investigation.

Overall, we conclude that transferability is an important component of model evaluation, particularly when models are to be projected in space or time. Other sources of uncertainty have already been shown to weaken the suitability of SDMs for

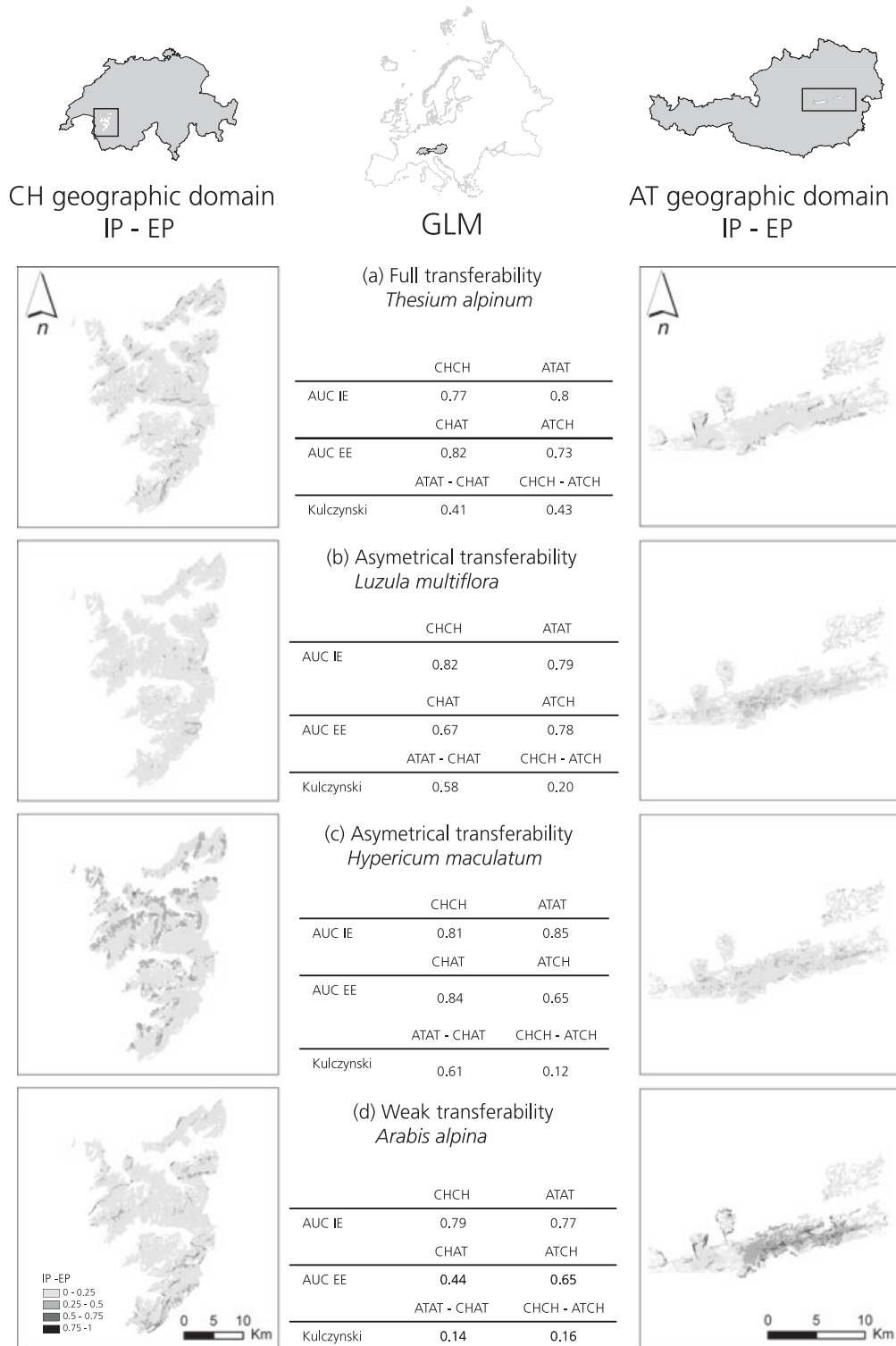


Figure 6 Four examples of generalized linear model (GLM) transferability across regions. Full transferability gives good external evaluations (AUC) in both regions. *Thesium alpinum* meets all the transferability criteria. Models of other species (*Luzula multiflora* and *Hypericum maculatum*) are only transferable from one region to another but not *vice versa* (asymmetrical transferability), whereas the last group of species does not meet transferability criteria in any direction (*Arabis alpina*). The differences between internal and external predictions of GLMs (difference between continuous predictions) are represented on a map for each region. These patterns are the same for the generalized additive models (GAMs). The variation of predictions between internal prediction (IP) and external prediction (EP) can be very high, even if the conditions for transferability are fully met. For the four examples, the Kappa values and maps show an important variation between IP and EP.

climate-change projections (Thuiller *et al.*, 2004; Thuiller, 2004; Araújo *et al.*, 2005b, 2006; Pearson *et al.*, 2006). Here we demonstrate that failure to achieve full transferability in space can constitute an additional – yet very important – component of the uncertainty associated with these projections. Their robustness to transferability and the related uncertainty should thus be estimated first, then provided alongside the projections themselves in order to allow nature managers and conservationists to make informed decisions.

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