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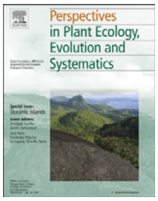

Research article

Predictive performance of plant species distribution models depends on species traits

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ABSTRACT

Predictive species distribution models are standard tools in ecological research and are used to address a variety of applied and conservation related issues. When making temporal or spatial predictions, uncertainty is inevitable and prediction errors may depend not only on data quality and the modelling algorithm used, but on species characteristics. Here, we applied a standard distribution modelling technique (generalized linear models) using European plant species distribution data and climatic parameters. Predictive performance was calculated using AUC, (Cohen's) Kappa and true skill statistic (TSS), that were subsequently correlated with biological and life-history traits. After accounting for phylogenetic dependence among species, model performance was poorest for species having a short life span and occurring in human disturbed habitats. Our results clearly indicate that the performance of distribution models can be dependent on functional traits and provide further evidence that a species' ecology is likely to affect the ability of models to predict its distribution. Biased and less reliable predictions could misguide policy decisions and the management and conservation of our natural heritage.

Introduction

Species distribution models (SDMs) are widely used tools in ecological research (Guisan and Zimmermann, 2000). Given the increasing importance of SDMs in ecological risk assessment, an evaluation of their predictive capacity is necessary (Barry and Elith, 2006). Within temporal or spatial predictions, model uncertainty is inevitable and thus prediction error needs to be assessed thoroughly in order to derive reasonable interpretation of the model results (Heikkinen et al., 2006).

Fielding and Bell (1997) distinguished between 'algorithmic' and 'biotic' prediction errors. Algorithmic errors have been widely studied (e.g. Segurado and Aráujo, 2004; Pearson et al., 2006; Meynard and Quinn, 2007) and are an artefact of the data-collection process or stem from limitations of the modelling approach. In contrast, biotic errors occur when ecological parameters are omitted from the modelling framework and lead to an inaccurate description of the species' distribution. SDMs are based on the assumption that species are in equilibrium with climate, i.e. they occur in all climatically suitable areas whilst being absent from all unsuitable ones (Guisan and Zimmermann, 2000). However, this assumption is violated by the influence of biotic interactions (Brown et al., 1996; Pearson and Dawson, 2003) and dispersal limitations (Svenning et al., 2008). Further, SDMs assume that species show no intraspecific variability regarding their niche but this is not always true, for example large-ranging species show adaptations to local conditions (Stockwell and Peterson, 2002). Distribution models commonly apply climatic predictors but other biologically relevant parameters such as land use, geological and pedological properties, groundwater influence and biotic interactions were, until recently, rarely considered mostly due to limited data availability. This has been addressed in recent studies and applications are promising (Heikkinen et al., 2007; Luoto et al., 2007; Pompe et al., 2008; Rickebusch et al., 2008; Schweiger et al., 2008).

Besides modelling algorithm and environmental parameters, predictive performance can be associated with species' traits. Geographical attributes of ranges (McPherson et al., 2004; Luoto et al., 2005) and climatic niche position (Kadmon et al., 2003; Hernandez et al., 2006) have been identified as correlates of predictive performance. The importance of range size for predictive performance is often studied although results are inconclusive. While some studies report that models of species with a high prevalence perform better compared to species with low prevalence (birds: Kadmon et al., 2003, artificial species: Meynard and Quinn, 2007), others found opposite results (birds: Stockwell and Peterson, 2002, butterflies: Luoto et al., 2005, various animal species: Hernandez et al., 2006). Furthermore, the influence of prevalence can be a statistical artefact because of the systematic dependence of modelling algorithms and accuracy

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measures on prevalence (McPherson et al., 2004; Allouche et al., 2006). Results concerning climatic niches are less ambiguous and models of species with clumped distributions (Luoto et al., 2005) and a narrow climatic niche are generally more accurate (Kadmon et al., 2003; Hernandez et al., 2006) than models of species with scattered distributions and wider climatic tolerance.

Since range and niche characteristics within these studies were derived from the data used for modelling, they strongly resemble data characteristics within the study area and do not necessarily depict true species characteristics. Independent data on species' traits have only been correlated with prediction errors for birds (Seoane et al., 2005; Carrascal et al., 2006; McPherson and Jetz, 2007), butterflies (Pöyry et al., 2008) and trees (Guisan et al., 2007). A low model accuracy was reported for fast growing, early successional tree species (Guisan et al., 2007) and locally scarce and inconspicuous bird species (Seoane et al., 2005). In contrast, Carrascal et al. (2006) found poor models for ubiquitous species, as well as species with very variable distributions, i.e. expanding/shrinking with climatic fluctuation. Distribution models for butterflies revealed a better predictive performance for large, more easily detectable, and less mobile species that are less influenced by stochasticity. Furthermore, the habitat in which species predominantly occur also influences the predictive power of distribution models (Pöyry et al., 2008).

It is evident, therefore, that the knowledge of the relationship between plant species traits and the predictive performance of SDMs is poor and requires further examination (Guisan et al., 2007). In our study, we use a standard distribution modelling technique and a widely used species distribution dataset to test the relationship between model performance and plant species traits. We hypothesise that the following traits will affect the quality/predictive performance of plant species distribution models:

- Life span/life form: The absence of short-lived species in a mapping unit may result from true climatic unsuitability but may also be caused by the failure to detect the species or by the absence of natural habitat in the mapping unit (e.g. following human disturbance) (Guisan and Thuiller, 2005). The distribution and occurrence of long-lived and conspicuous species are more likely to be recorded (Seoane et al., 2005). As modelling accuracy improves with data quality, we hypothesise that SDMs for these species will have a greater predictive power.
- Ecological strategy type (after Grime, 1979)/habitat dependence: Species ranges are not only restricted by environmental parameters but by biotic interactions (Gaston, 2003). We hypothesise that a slow growth rate and a good competitive ability promotes filling of the climatic niche and a longer persistence in the landscape and thus improves the predictive performance of SDMs (Guisan et al., 2007); or vice versa: if the occurrence of a species is prevented by competition with another species and the SDM does not include the interaction, it will tend to overestimate the species distribution (McPherson and Jetz, 2007). We also hypothesise that species with a lower competitive ability are associated with specific habitat types (e.g. extreme habitats, disturbances, pioneer species). The absence of such species may not indicate unsuitability and SDMs will therefore have a lower predictive quality.
- Dispersal type: It is assumed that trees (Svenning and Skov, 2004) and forest herbs (Svenning et al., 2008) in Europe have not yet reached their post-glacial equilibrium with climate. Species with low dispersal ability may not have filled their climatic niches and thus the predictive performance of these SDMs is reduced.
- Pollination type: Relative frequencies of pollination types are dependent on specific climatic and non-climatic factors (Kühn et al., 2006). Insect pollination is strongly dependent on land use, topology and geology (Kühn et al., 2006), wind pollination is facilitated by open vegetation (Culley et al., 2002) and a moderate wind speed (Whitehead, 1983) and selfing is regarded to be favoured when the environment is variable (e.g. due to disturbances), climatic conditions are poor or mates are absent (Baker, 1955). Dependence of a pollination type on non-climatic parameters or climatic parameters commonly not included in SDMs (e.g. wind speed, disturbance) would probably reduce predictive performance of SDMs for species having this pollination type.
- Niche width/habitat tolerance: Beside the prime importance of growth rate, Guisan et al. (2007) reported a low predictive performance for generalist trees, i.e. trees with wider elevation ranges. We hypothesise that this holds for other plant species with a low degree of specialization. The lack of ecological contrast among occupied and unoccupied mapping units should constrain a statistical description of the species' distribution.

Methods

Data

Species distribution data of vascular plants were obtained from the Atlas Florae Europaeae database (AFE) maintained by the Botanical Museum, University of Helsinki, at a resolution of 50 km × 50 km. Species traits were derived from BiolFlor (Klotz et al., 2002), a database of biological and ecological traits for Central European plant species and from a dataset on dispersal type (Frank and Klotz, 1990). We extracted all AFE species with available trait information. We used the following traits to address our hypotheses: dispersal type, life span, life form, pollination type, strategy type, number of vegetation units a species is affiliated to and hemerobic level (see Table 1 for details). Although the BiolFlor database covers Central Europe only, we associated the data with models covering the whole of Europe, as the chosen traits are generally stable and show low intraspecific variability. Hence, this spatial mismatch should not influence the results. The AFE database covers approximately 20% of the European flora but does not provide distribution data on some species rich herb families such as Asteraceae, Poaceae, Cyperaceae and Fabaceae. Preliminary tests for regions with known distributions of the full flora revealed that our modelled species are generally adequate to represent the trait compositions of the whole flora (Hanspach et al., unpublished). Species with less than 50 presences or absences in the AFE database were excluded to allow for reliable modelling (Kadmon et al., 2003). Data on recent climate (1961–1990) were taken from Mitchell et al. (2004) and were aggregated from the original resolution of 10 min × 10 min onto the 50 km × 50 km resolution of the AFE data. We derived a set of 17 standard climatic variables (see Appendix Table 1).

Modelling of species distribution

We used generalized linear models (GLMs) with a binomial error distribution to model the distribution of 638 plant species. Recently, authors have suggested that several methods be combined in an ensemble to minimize algorithmic errors (Araújo and New, 2007; Marmion et al., 2009). GLMs are, however, among the methods with a good performance (Elith et al., 2006). They are more robust to overfitting and have a better transferability or

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Table 1
Traits used in the analysis of predictive performance extracted from the BiolFlor database (Klotz et al. 2002). The number of species (*N*) differed in each analysis. Significance levels relate to single-variable models (n.s. not significant, $^{**}p < 0.01$, $^{***}p < 0.001$).

Trait	Description	*N*	AUC	Kappa	TSS
Prevalence	Proportion of presences compared to all grid cells	645	***	***	***
Dispersal type	Wind-, self-, water-, animal dispersal	356	n.s.	n.s.	n.s.
Life span	Annual, biennial, perennial	588	***	***	**
Life form	Classification based on Raunkier (1934)[a]	525	***	***	***
Strategy type	Ecological strategy type according to Grime (1979): ruderals, competitors, stress-tolerators and mixed types	606	***	***	**
Pollination type	Wind-, self-, insect pollination	499	***	***	n.s.
Number of vegetation units	Number of vegetation units a species is affiliated to according to Schubert et al. (2001)	612	n.s.	***	***
Hemerobic level	Species' affiliation to vegetation influenced by humans at different levels[b]	603	***	***	***

[a] Definitions of life forms: therophyte—summer annuals, which can only reproduce by means of generative diaspores; geophyte—resting buds are subterranean, often on storing organs protected within the soil; hemicryptophyte—resting buds are situated on herbaceous shoots close to the soil surface protected by foliage or dead leaves; chamaephyte—resting buds are situated on herbaceous or only slightly lignified shoots some centimetres above the soil surface protected by parts of the plant itself and/or by snow cover (especially cushion plants); nanophanerophyte—resting buds are situated on woody shoots, which form a stemless shoot system with strong basal ramification; hemiphanerophyte—resting buds are situated on woody, basally ramified shoots up to a height of ca. 50 cm (dwarf shrub) or on the only basally lignified parts of higher shoots, which do not become lignified in their upper parts but die down periodically; macrophanerophyte—resting buds are situated on woody shoots, the medial and apical ramifications of a woody trunk form a crown.

[b] Hemerobic levels: 1—no influence, 2—low (e.g. grazing, airborne/water immissions), 3—intermediate (e.g. clearing, rare ploughing, rare fertilization), 4—increased (e.g. fertilization, liming, use of biocides), 5—high (e.g. levelling, tillage, mineral fertilization), 6—very high (e.g. deep tillage, intensive use of biocides and fertilizers, permanent drainage), 7—completely disturbed.

generalizability in space than comparable techniques like generalized additive models (Randin et al., 2006). Furthermore, Guisan et al. (2007) showed that variance across species was higher than across techniques. Thus, considering more techniques would not be expected to change the results on which species' traits explain predictive performance across models of all species. We defined 2219 cells of the AFE grid covering most European countries as the study region (i.e. European Union EU 27 plus Albania and the countries of former Yugoslavia except Serbia and Montenegro). We performed a principal components analysis with all standardized climatic variables to account for collinearity. The first five principal components (explained variance 90.1%, see Appendix Table 1) were included as independent variables in the models, allowing for linear and quadratic effects.

We applied a ten-fold cross-validation for every model by randomly splitting the data into 10 parts. We successively omitted one tenth of the data when performing model calibration and validated the model on the excluded tenth of the data. To evaluate the predictive performance of the models we calculated the mean values of AUC (area under receiver operating characteristic curve; Hanley and McNeil, 1982), mean maximum values of Cohen's Kappa (Cohen, 1960) and mean values of true skill statistic (TSS, Allouche et al., 2006). Kappa was maximized by successively calculating Kappa values in steps of 0.0005 across the entire probability range from 0 to 1 and subsequently selecting the threshold with the maximum value. AUC values can range between 0 (no agreement) and 1 (total agreement) and Kappa/TSS between -1 (no agreement) and 1 (total agreement). TSS was calculated as the sum of sensitivity (true presences/all observed presences) and specificity (true absences/all observed absences) minus one. Values of AUC and Kappa were assessed according to Monserud and Leemans (1992) and Hosmer and Lemeshow (2000).

Modelling predictive performance with traits

The relationships between species traits and Kappa, AUC and TSS were primarily estimated using analysis of variance (ANOVA) and linear regressions in single variable models for each trait. Since trait information was not complete, species numbers differed between models (Table 1).

Traits that were significant in the single-variable models were included in a multi-variable model (375 species), at the same time accounting for the effect of prevalence and phylogenetic dependencies. Prevalence was repeatedly reported as blurring the true predictive performance of models and Kappa values, in particular, showed a strong systematic dependence on prevalence (McPherson et al., 2004). To control for its influence on predictive performance we included species' prevalence from the SDMs as an explanatory variable. Prevalence was standardized to reduce collinearity and then included as a linear and a quadratic term. Traits are dependent between species according to phylogenetic structure (Freckleton et al., 2002). These dependencies would violate the assumption of independent data points and also may mask ecological patterns (McPherson and Jetz, 2007). We therefore accounted for phylogenetic structure by calculating a patristic distance matrix from a phylogenetic supertree (Durka, 2002), representing the sum of the branch lengths between each combination of species. In the absence of information on branch lengths, we set them to one (Faith, 1992). The patristic distance matrix was subject to a principal coordinate analysis. The first five principal coordinates (total explained variance: 76.3%; explained variance of the first axis: 30.1%, second: 21.3%, third: 16.5%, fourth: 4.9%, fifth: 3.5%; principal coordinates are henceforth termed as phylogenetic axes) were added as explanatory variables (Diniz-Filho et al., 1998, Desdevises et al., 2003). Hemerobic level was incorporated into the multi-variable model as a metric variable. We also incorporated it as a categorical variable in another model (results not shown), although this lost information on the ranks of the levels. Both results lead in the same direction, but the results of the metrically defined hemerobic level gave a better fit. We performed post-hoc Tukey multiple comparisons between levels of all traits with significant ANOVA models. Error probabilities were adjusted to control for inflated type I error rates (Hothorn et al., 2008). We assessed the collinearity of traits among species by calculating a principal coordinates analysis based on Gower dissimilarities. Subsequently, scores of the species traits for the first four axes (explained variance 68%) were derived by fitting the traits onto the ordination (see Appendix Table 2).

Both original data and model residuals were checked visually (histograms) and statistically (Kolmogorov–Smirnov test) for deviation from normal distribution. Model simplification was conducted using a manual backward selection procedure that excluded all explanatory variables which did not significantly contribute to the fit when we compared models using ANOVAs. We performed a hierarchical partitioning to obtain the

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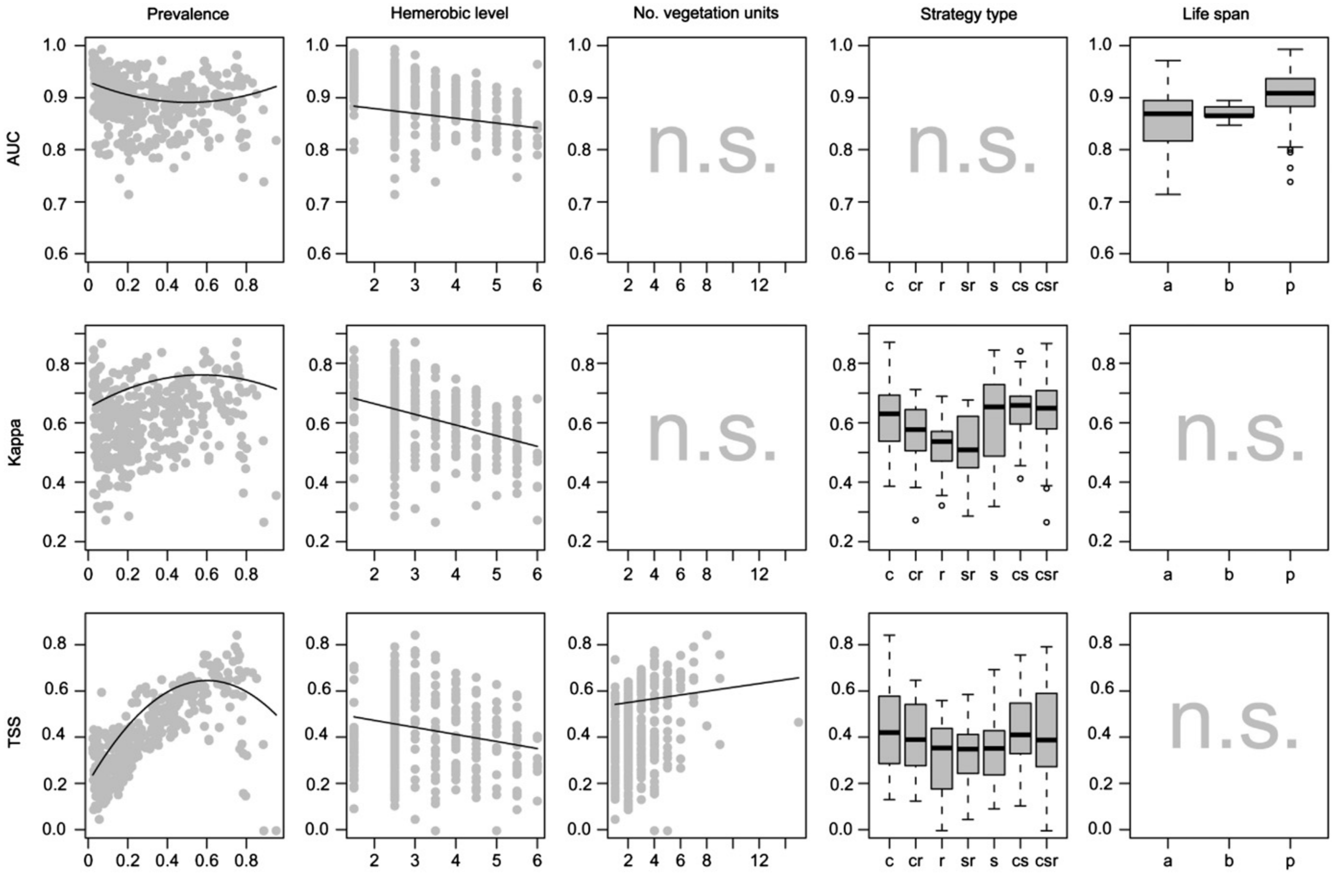

Fig. 1. Association of species traits retained in the simplified multi-variable models with AUC (upper row), Kappa (middle row) and TSS (lower row): prevalence; hemerobic level (median values of species' affiliation to vegetation influenced by humans at levels between 1—no influence and 7—completely disturbed); number of vegetation units a species is affiliated to; ecological strategy type according to Grime (1979): c—competitors, r—ruderals, s—stress-tolerators and mixed types; life span: a—annual, b—biennial, p—perennial. Traits not retained are marked with n.s. (not significant). Regression lines were derived from the model estimates. Association of phylogenetic axes with validation values are not shown.

independent effect of each variable on model fit (Mac Nally, 1996). Statistical analysis was performed using the R software (R Development Core Team, 2008).

Results

The SDMs had a mean explained deviance of 49.7% ± 13.5 (mean ± standard deviation) and a predictive performance that can be considered as good (AUC: 0.89 ± 0.05; Kappa: 0.59 ± 0.12). TSS had a mean value of 0.39 ± 0.17. In the single-variable models we clearly identified an association of AUC, Kappa and TSS values with all traits except dispersal type (models of AUC, Kappa and TSS), number of vegetation units (model of AUC) and pollination type (model of TSS; see Table 1).

In all simplified multi-variable models prevalence (linear and quadratic terms), hemerobic level and the third and fifth phylogenetic axis were retained (Table 2). Additionally, the following variables remained in the models: number of vegetation units (model of TSS), strategy type (model of Kappa and TSS) and life span (model of AUC). While AUC was described by a positive quadratic function of prevalence, the function for Kappa and TSS was hump-shaped (Fig. 1). In all models, predictive performance decreased with increasing association to human disturbance. TSS increased when species were affiliated with many vegetation units. The post-hoc test for life span revealed significantly lower values of AUC for annual species compared to perennials. Kappa values of the strategy type 'stress tolerator-ruderal' were significantly lower than for the type 'competitor-ruderal'. There were no significant differences for the model of TSS. The models of AUC and Kappa explained more than a quarter and the model of TSS more than two thirds of the total variation. Hierarchical partitioning (Fig. 2) showed a strong contribution of hemerobic level (AUC, Kappa), life span (AUC) and strategy type (Kappa) to this variation. Prevalence contributed most strongly to the explanation of TSS. Response variables and residuals did not deviate significantly from normality (Kolmogorov–Smirnov test, visual inspection).

Discussion

Our results show that specific life-history traits of plant species have a significant effect on model performance. We confirmed our hypothesis of the low predictive model performance of short-lived species. This was not only reflected by the results of life span, but also hemerobic level (species with a high hemerobic level (above four) are predominantly annuals, see Appendix Table 2) and partially by strategy type. Ruderals are defined by a short reproduction time and good dispersal abilities, which are characteristic adaptations to unstable habitats (Grime, 1979). These results extend the findings of Guisan et al. (2007), who reported a low predictive performance for fast growing trees that are typical of early successional stages. Sites sustaining early successional species are difficult to map and may not be available over the whole landscape. Further, a high propagule pressure and

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Table 2
Results from the simplified multi-variable species' trait models. The predictive performance of species distribution models across Europe is measured as AUC, Kappa and TSS (adjusted R^2: model of AUC 0.28, model of Kappa 0.27, model of TSS 0.7; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

	Sum of squares	Degrees of freedom	*F*-value	*p*-value
Model of AUC				
Intercept	16.5425	1	9370.4177	***
Prevalence	0.0525	1	29.7455	***
Prevalence^2	0.0248	1	14.0295	***
Hemerobic level	0.0227	1	12.8685	***
Life span	0.0222	2	6.2791	**
Third phylogenetic axis	0.0134	1	7.5978	**
Fifth phylogenetic axis	0.0093	1	5.2635	*
Residuals	0.6461	366		
Model of Kappa				
Intercept	18.5175	1	1953.1648	***
Prevalence	0.3322	1	35.038	***
Prevalence^2	0.0886	1	9.3471	**
Hemerobic level	0.2389	1	25.1942	***
Strategy type	0.1643	6	2.8882	**
Third phylogenetic axis	0.1312	1	13.8359	***
Fifth phylogenetic axis	0.0789	1	8.3253	**
Residuals	3.432	362		
Model of TSS				
Intercept	6.411	1	763.2249	***
Prevalence	5.1958	1	618.5515	***
Prevalence^2	1.2932	1	153.9495	***
Number of vegetation units	0.0578	1	6.8865	**
Hemerobic level	0.1686	1	20.0696	***
Strategy type	0.1449	6	2.8745	**
Third phylogenetic axis	0.074	1	8.815	**
Fifth phylogenetic axis	0.1501	1	17.8654	***
Residuals	3.0324	361		

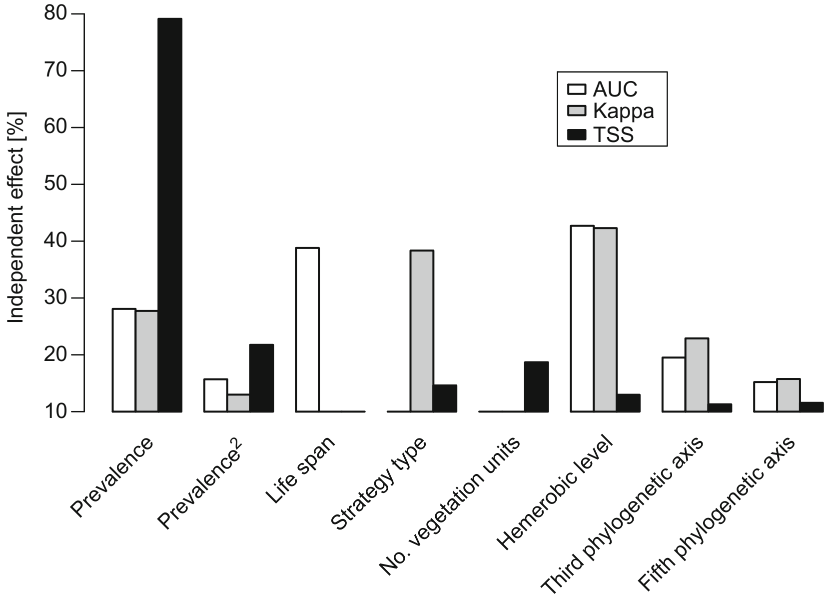

Fig. 2. The independent effects of each explanatory variable to the overall fit of the simplified multi-variable models for AUC, Kappa and TSS (adjusted R^2: model of AUC 0.28, model of Kappa 0.27, model of TSS 0.7) calculated using hierarchical partitioning.

good dispersal ability leads to a high mobility, which decreased the predictive power of SDMs when modelling butterflies in Finland (Pöyry et al., 2008).

We found no evidence that very long-lived life forms such as phanerophytes (i.e. trees) showed different performance compared to other perennials. Our methodologies may, however, lack the sensitivity required to detect such patterns. The performance of models of species classified as competitors were not as superior as expected, though performance for these species was better than for ruderals. We assume that this is due to the coarse resolution of the data which hindered the detection of biotic interactions. Moreover, competitors are typical for late successional stages and are characterized by a low dispersal ability, which might trigger a restricted niche filling. Generally,

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the application of statistical models for species that are not in equilibrium with climate is difficult (Guisan and Zimmermann, 2000).

We hypothesised a low predictive performance of species with the strategy type stress-tolerator, since they mainly depend on non-climatic environmental parameters such as geology and topography. These species tolerate stress that is induced by nutrient or oxygen deficiency in soils, high salt concentrations or water deficiency (Grime, 1979). Our results supported this hypothesis only partially, but data resolution may have been too low to detect such habitat dependencies (Pearson and Dawson, 2003). The comparably good performance of the strategy type stress tolerator may have been caused by the coincidence of some habitats with climate, e.g. saline habitats with oceanic climate or dry habitats with continental climate.

We could not support our hypothesis regarding the influence of dispersal type on predictive performance, but propose that mechanisms of dispersal are still important in terms of future environmental change. Dispersal ability plays a key role in tracking climate change (Pitelka et al., 1997; Davis et al., 1998; Thuiller et al., 2008) and incorporating genuine rates of dispersal could prove valuable in future SDMs. Further, we found no influence of pollination type on predictive performance. We assume that our spatial resolution was too coarse to detect when important parameters, such as land use or geological conditions, were missing (Pearson and Dawson, 2003; Kühn et al., 2006).

Species' affiliation to human disturbance showed the most consistent results over the three measures of predictive performance. A species' dependence on human disturbance may at least partly uncouple its occurrence from climatic parameters and in such a way decrease predictive performance. This is supported by the low co-variation of urban areas and arable lands with climatic variables found in Europe (Thuiller et al., 2004). The high importance of hemerobic levels may indicate the lack of appropriate environmental parameters within the SDMs. Incorporating information on human influence on ecosystems, e.g. occurrence or cover of specific land cover types, may improve models of these species. At the 50 km × 50 km resolution, Thuiller et al. (2004) could not show a superior predictive performance when including land cover variables into SDMs, though explanatory power was enhanced. Improvements of predictive performance were shown, however, at finer spatial resolution (Pearson et al., 2004; Luoto et al., 2007; Pompe et al., 2008).

The influence of prevalence on predictive performance showed ambiguous results. The negative linear effect of prevalence on AUC is in line with results from previous studies, which show that species with wider ranges are less well predicted (Segurado and Aráujo, 2004; Luoto et al., 2005; McPherson and Jetz, 2007). In contrast, the slight increase of AUC values with increasing prevalence may be a statistical artefact, since data with high prevalence were scarce. Kadmon et al. (2003) found that a wide climatic niche was negatively correlated with predictive performance, as data on species with wide ranges and broad niches seem to lack strong ecological contrast to allow for meaningful species distribution modelling. Furthermore, the hump-shaped response of Kappa to prevalence has been shown to be a statistical artefact (McPherson et al., 2004). TSS showed the strongest response to prevalence, although it was reported to be independent of prevalence (Allouche et al., 2006). If this could be attributed to an ecological relationship, one would expect a consistent pattern with AUC, but this was not the case. We attribute this pattern to the threshold selection technique that was used, because thresholds to convert probabilities of occurrence into presence/absence, which are derived by maximizing Kappa, cause a systematic dependence of sensitivity and specificity on prevalence (Liu et al., 2005). This directly translates into biased values of TSS.

The interpretation of trait syndromes (e.g. ruderals are predominantly annuals; see Appendix Table 2) remains difficult and is particularly challenging, as an experimental approach is required to determine specific causal relationships. Our approach aimed at providing improvements of SDMs in general, in terms of a priori species selection or post-hoc model interpretation. Although we did not use ensemble methods but only GLMs, the general dependence of model performance on species characteristics should be valid across algorithms. Further, the significant effects of the phylogenetic axes indicate that species relatedness plays a role within the analysis (McPherson and Jetz, 2007). Interpretation of such an axis is difficult because it represents an artificial dimension of the phylogenetic space. Possibly, it is a surrogate for an influential but unmeasured trait or combination of traits. The decomposition of the axis into the respective species and their relative contribution is mathematically straightforward, albeit systematically/ecologically difficult to comprehend due to the complex nature of reduction in dimensionality involved.

In conclusion, we suggest taking the extent of the prediction errors of SDMs into account, by testing their relative performance in regard to their specific life-history traits. Species richness patterns which are derived by summarizing results of large numbers of SDMs are most probably impaired by models of low predictive performance. We recommend an evaluation of prediction errors to help understand underlying ecological processes or methodological shortcomings. In addition, assessing prediction error may also help to improve low quality prediction models through the inclusion of additional predictor variables. We suggest that species or species groups with low quality predictions should be excluded or down-weighted in compound analyses when establishing management decisions or nature conservation strategies.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2010.04.002.

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