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The prediction of macrophyte species occurrence in Swiss ponds

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Abstract

The study attempted to model the abundance of aquatic plant species recorded in a range of ponds in Switzerland. A stratified sample of 80 ponds, distributed all over the country, provided input data for model development. Of the 154 species recorded, 45 were selected for modelling. A total of 14 environmental parameters were preselected as candidate explanatory variables. Two types of statistical tools were used to explore the data and to develop the predictive models: linear regression (LR) and generalized additive models (GAMs). Six LR species models had a reasonable predictive ability (30–50% of variance explained by the selected predictors). There was a gradient in the quality of the 45 GAM models. Ten species models exhibited both a good fit and statistical robustness: *Lemna minor, Phragmites australis, Lysimachia vulgaris, Galium palustre, Lysimachia nummularia, Iris pseudacorus, Lythrum salicaria, Lycopus europaeus, Phalaris arundinacea, Alisma plantago-aquatica, Schoenoplectus lacustris, Carex nigra.* Altitude appeared to be a key explanatory variable in most of the species models. In some cases, the degree to which the shore was shaded, connectivity between water bodies, pond area, mineral nitrogen levels, pond age, pond depth, and the extent of agriculture or pasture in the catchment were selected as additional explanatory variables. The species models demonstrated that it is possible to predict species abundance of aquatic macrophytes and that each species responded individually to distinct environmental variables.

Introduction

Hydrophytes play an important role in the freshwater ecosystem functioning of many shallow waterbodies: as primary producers, by providing structure in the habitat of many animal species, and provide shelter and food to invertebrates (e.g., Castella et al., 1984; Bänziger, 1998; Antoine, 2002) and fish (e.g., Rossier, 1995). The factors controlling the distribution of macrophytes in bodies of standing water have been investigated by many authors. The distribution of macrophytes is often related to water chemistry, especially as influenced by eutrophication (e.g., Lehmann & Lachavanne, 1999). The significance of parameters such as morphometry, water levels, perturbations and disturbances, composition of bottom substrates, land-use in the catchment and surroundings, connectivity between water bodies, as well as interactions with the fish fauna has also been demonstrated (e.g., Jupp & Spence, 1977; Rørslett, 1991; Wright et al., 1992; Bornette & Amoros, 1996; Lehmann et al., 1997; Lougheed et al., 2001; Oertli et al., 2002). Many of these studies are concerned with the relationships between species richness of aquatic macrophytes and environmental variables but few involve study of a high number of individual species (e.g., Heegaard et al., 2001; Bio et al., 2002).

The analysis of species–environment relationships is a central issue in ecology and provides the baseline information needed for habitat distribution modelling (see Scott et al., 2002). A wide range of models has been developed to cover aspects as diverse as biogeography, conservation biology and climate-change research (Guisan & Zimmermann, 2000). The development of predictive models for the occurrence of individual species is currently viewed as a way to increase the efficiency of habitat assessment and as tools for the management of endangered or invasive species (e.g., Lehmann et al., 2002; Overton et al., 2002). The species richness of different taxonomic groups of fauna and aquatic plants recorded in a range of 80 ponds in Switzerland was modelled with a set of environmental variables (Oertli et al., 2000). The selected model predicted that the species richness of aquatic plants involved altitude, area, mean depth and nitrogen concentration levels. Here, we explore the extent to which the abundance of individual aquatic plant species recorded in the ponds can be modelled. The task is to identify variables that have the highest explanatory potential. The results may aid pond managers in identification of parameters upon which they could act to enhance or limit certain species.

Study areas

A previously established inventory of 8000 ponds (Borgula et al., 1994) provided the baseline for a stratified sample of 80 ponds distributed fairly evenly with respect to altitude (210–2757 m.a.s.l), area (6–94000 m^2) and biogeographic regions (Jura, Swiss Plateau and Alps). Of these ponds 31 were known to have a natural origin with an age exceeding 4000 years (since the end of the last glaciation). The other 49 had various ages and were man-made (e.g., for gravel or clay extraction, fishing or nature conservation). The main pond characteristics are listed in Table 1.

Table 1. Mean values and ranges of preselected variables characterising the 80 ponds

	Variables		Units	Mean	Minimum	Maximum	Median
Local scale	Morphometry	Log10 (area)		3.31	0.78	4.98	3.26
		Area	m^2	8817	6	94346	1834
		Mean depth	cm	172	26	850	114.5
		Shoreline development^a		1.50	1.02	3.27	1.34
	Physical and chemical variables	Water transparency	cm	43	4	60	51
		Conductivity	μS cm^{-1}	383	6.2	1367	396
		pH-class (1 = acid, 2 = neutral-basic)		1.9	1	2	2
		Eutrophic class P^b (total P classes, according to Wetzel, 1983)		–	1	4	2
		Eutrophic class N^b (Nmin classes, according to Wetzel, 1983)		–	1	4	2
	Others	Age	Years	–	1	>4000	100
		Altitude	m. asl	1008	210	2757	733
		Extent of shade cover by trees on the shoreline	%	3.1	1	6	3
Larger scale	Catchment area	Proportion of agriculture in the catchment area	%	30	0	100	7.5
	Surroundings	Fraction of the surroundings (within 50 m of the pond) forested	%	35	0	100	32
	Connectivity^c	Within a radius of 1 km		3.22	0	7.72	4.06

[a] Ratio of the length of the shoreline to the circumference of a circle of area equal to that of the pond (Wetzel, 1983).

[b] Eutrophic class P and N: 1 = oligotrophic, 2 = mesotrophic, 3 = eutrophic, 4 = hypertrophic, Nmin = Inorganic nitrogen (sum of nitrate, nitrite and ammonia).

[c] Measure of pond isolation. This measure takes into account the number and size of ponds within a radius of 1000 m and their distance from the studied pond. Large values indicate low degrees of isolation.

Methods

Survey of flora

Using quadrat samples (0.5×0.5 m), floristic composition was assessed in the 80 ponds during the summer months (1996–1999). Quadrats were positioned in the water at 5 m intervals along transects perpendicular to the longest axis of each pond. Transects were located every 5 m for small ponds and every 20 m for large ponds. In each quadrat sample the abundance of submerged, floating-leaved and emergent macrophytes was assessed using five classes. The number of quadrats sampled was proportional to the pond surface. A mean abundance was calculated (sum of abundance in the quadrats/number of quadrats) for the species recorded in each pond. Mean species abundances were used as a response variable in the analyses. Plants considered here as aquatic are the 254 phanerogams listed in the highest humidity class (=5) of Landolt (1977): this includes true aquatics (species submerged or with floating leaves) and most of the emergents. To this "aquatic" species pool, a set of 22 of the most frequently recorded helophytes (listed by Landolt under class 4), Bryophyta and 8 taxa of Characeae were added. Species nomenclature follows Aeschimann & Heitz (1996) and Corillion (1975).

Environmental variables

In total, 14 environmental variables were used to characterise each pond (Table 1). These predictor variables were preselected according to their potential importance to aquatic vegetation.

Data analysis

Linear Regression (LR e.g., Draper & Smith, 1981) and Generalised Additive Models (GAM: Hastie & Tibshirani, 1990) were used to model the relationship between species and the environmental variables. Linear Regression is a very popular tool and is often used for modelling species occurrences and distributions. It estimates only one statistical parameter for each variable in the model, the slope, which is an advantage with small sample size. A stepwise procedure was used in the LR regression and the explanatory variables were selected using the Fischer test with a threshold of $p = 0.01$. This method relies on linear relationships between species and ecological variables. Nevertheless, species responses in their natural environment might differ from frequently assumed linear relationships. The Generalised Additive Model (Hastie & Tibshirani, 1990) is a more powerful tool because the non-parametric characteristics of the GAM allow modelling of any shape of response curve (e.g., sigmoid, plateau-shaped, etc.) without having to assume particular relationship between the dependent (plant species) and the independent variables (environmental variables). This technique has been used with success in many studies in the last decade (e.g. Austin & Meyers, 1996; Lehmann, 1998; Bio et al., 1998, 2002).

The quality of the models was evaluated through the explained deviance (D^2) and its stability by simple correlation (r_1) and five-fold cross-validation correlation (r_2). The sample was randomly split into five approximately equal-sized groups. Models were recalculated for four of these groups and validated on the fifth. The higher the r^2-value, the higher is the stability of the models. The GAMs were performed using S-PLUS (Mathsoft) and a set of functions developed for generalised regressions and spatial predictions (GRASP; Lehmann et al., 2002). A cubic-spline smoother was used as a function to smooth the environmental variables (X_j), with three degrees of freedom (d.f.). Mean species abundances were transformed in order to be able to use a quasi-binomial distribution (0 = absence; abundance 1 = 0.2; 2 = 0.4; 3 = 0.6; 4 = 0.8; 5 = 1.0). A forward stepwise procedure was used. The explanatory variables were selected using the Fischer test with a threshold of $p = 0.01$.

Results

Although the 80 ponds studied represented only a very small fraction of the number of ponds estimated to occur in Switzerland, 154 aquatic plant species were recorded, representing about 54% of the Swiss aquatic plant flora. Only 45 species occurred in more than 10 ponds. The majority of them were helophytes and a few species were floating or submerged macrophytes (*Chara globularis*, *C. vulgaris*, *Lemna minor*, *Nymphaea* *alba*, *Potamogeton alpinus, P. natans*, *P. pectinatus*, *P.* gr. *pusillus, Ranunculus trichophyllus*). Most of these species are considered as common and non-threatened in Switzerland. The most frequent plants recorded were *Phragmites australis* (51%), *Caltha palustris* (34%), *Lythrum salicaria* (34%), *Mentha aquatica* (34%), *Carex rostrata* (33%), *Typha latifolia* (33%) and *Carex nigra* (31%).

Models LR

The LR models for 45 individual species had explained variance (R^2) ranging from 0 to 51%. Only six species had 32–51% of the variance explained (Table 2). Altitude, the variable the most frequently selected in LR, was involved in five of the six species models and had a negative effect on the abundance of two species. The rise of pond area increased the abundance of *Phragmites australis* and *Lythrum salicaria* and the extent of shade cover of the shore had a negative effect on their abundance. High values of total phosphorus content in the water increased the abundance of *Juncus filiformis* and *Typha latifolia*. Some other variables were involved positively or negatively, depending of the species, in a few models.

Models GAM

There was a gradient in the quality of the Generalised Additive Models. *Calliergonella cuspidata*, *Carex flava*, *Equisetum palustre*, *Glyceria fluitans* and *Polygonum amphibium* could not be modelled with the environmental variables tested. In total, 40 species models had 16–99% of total deviance in abundance explained and a cross-validation coefficient r_2 varying between 0 and 0.82. A set of 10 models had 87–99% deviance explained and very high simple-validation coefficients. These models included many predictor variables ("over-fitting") and have very low confidence (cross-validation coefficients). *Chara vulgaris*, *Nymphaea alba*, *Potamogeton alpinus* and *P. pectinatus* for example belong to this group and were modelled with low accuracy. Models incorporating one (generally altitude) or two variables had generally low deviance in abundance explained (*Chara globularis*, *Potamogeton* gr. *pusillus* or *Mentha aquatica* for instance). Ten models (Table 3), including three to five variables, showed a high degree of explained variation (more than 50% of the deviance explained) and relatively high stability (cross-validation above 0.46). Five other models were close to these arbitrary limits (*Alisma plantago-aquatica*, *Lycopus europaeus*, *Lysimachia vulgaris*, *Potamogeton natans* and *Typha latifolia*).

In the GAMs, altitude was involved in 90% of the best models and was the main explanatory variable for the majority of the species (Table 3). The extent of shade on the shore and connectivity were concerned with more than half of the models. Area, mineral nitrogen and total phosphorus content of the water, and pond age were involved in about one-third of the models. Shore sinuosity and pH were not included in the best species models.

Table 2. Standardised contribution coefficients of LR selected explanatory variables to the six best models (more than 30% explained variance ($p < 0.05$))

	Freq %	Alt	Area	Shore shade	Ptot	Age	Shore dev	pH	Nvar	R^2
Carex nigra	25	0.72							1	0.51
Phragmites australis	41	−0.64	0.34	−0.26			0.19		4	0.49
Juncus filiformis	12	0.47			0.29			−0.30	3	0.37
Lythrum salicaria	27	−0.65	0.28	−0.42					3	0.37
Eriophorum angustifolium	10	0.63						0.29	2	0.35
Typha latifolia	26				0.25	−0.51	−0.28		3	0.32

alt: altitude; area: $\log_{10}$(area); shore shade-class: percentage of the shore shaded; shore dev: shoreline sinuosity; Ptot: eutrophication class P; age: age-class; shore dev: shore sinuosity index. Number of selected predictors in species model (Nvar), percentage of explained variance (R^2).

Table 3. Contribution of GAMs selected explanatory variables to the 10 most accurate models and validation diagnostic

Species	Freq %	Alt	Area	Depth	Shore shade	Nmin	Ptot	Connect	Agri catch	Forest env	Age	Cond	Trans	Nvar in GAM	Null dev	Resid dev	%D	r_1	r_2
Lemna minor	26	10.9		4.3	4.3			5.7						4	49.5	22.9	54	0.74	0.46
Phragmites australis	51	18.3	9.4		6.8						4.5			4	75.2	33.0	56	0.79	0.67
Galium palustre	28	6.8				7.3	3.5							3	30.3	11.9	61	0.83	0.67
Lysimachia nummularia	20	3.2				3.1	1.7	1.7						4	20.1	7.4	63	0.75	0.55
Iris pseudacorus	29				3.7	3.6				3.6	1.9			4	30.5	10.6	65	0.80	0.59
Lythrum salicaria	34	7.4	3.2		3.5				2.0					4	24.0	8.1	66	0.83	0.62
Phalaris arundinacea	28	7.2	2.0		4.8		4.5	2.5						5	35.9	9.6	73	0.90	0.60
Schoenoplectus lacustris	18	18.9		9.5					4.5	9.2	3.5			5	45.1	9.6	79	0.92	0.66
Carex nigra	31	10.6			3.8			2.6				2.0		4	46.2	9.3	80	0.90	0.72
Eriophorum angustifolium	13	7.5						2.5					1.6	3	17.8	3.4	81	0.94	0.82

Number of selected predictors in species model (Nvar in GAM), null deviance (null dev), residual deviance (resid dev), percentage of explained deviance (% D), simple validation coefficient (r_1) and cross-validation coefficient (r_2). All models were selected with threshold $p < 0.01$.

alt: altitude; area: $\log_{10}$(area); depth: mean depth (m); shore shade-class: percentage of the shore shaded; Nmin: eutrophic class N; Ptot: eutrophic class P; connect: connectivity within a radius of 1 km; agri catch: agricultural catchment; forested env: % of forested surface in the close surrounding of the pond (50 m); age: age-class; cond: conductivity; trans: transparency of the water.

Comparison of the Phragmites australis *models*

Four variables were included in the LR and GAM models. They explained respectively 49% of the variance and 56% of the deviance. Three variables were common to both models: altitude, size and shade and gave the same level of contribution. Age, the fourth and the least contributive variable in the GAM was not integrated in the LR. In contrast, the shore development was included in the LR but not in the GAM. The response curves in the GAM showed that relationships between *Phragmites australis* abundance and the four variables selected were not linear but fitted plateau-shape or sigmoid curves. This close fit to the data explain why GAMs gave more information than LRs and included different variables, although the main contributive variables were the same in both models. The GAM model indicated that high abundance of *Phragmites australis* would occur in big ponds older than 40 years, located at low altitude and with low shade on the shore.

Discussion

Linear regression gave relatively low prediction of species abundance, with only six models explaining more than 30% of the variance. As expected, GAMs described and quantified better than LR the relation between individual plant species and characteristics of their habitat. Indeed, a higher number of species were successfully modelled by GAMs and the four species modelled by both methods had better accuracy with GAMs than LRs. GAMs can produce accurate models, as revealed by the good fits and the high cross-validation coefficients. The best models are the ones that simultaneously account for the most variation in the data with the fewest terms (Burnham & Anderson, 1998). Ten models showed a high level of explanation of species abundance (>50% explained deviance) including two to five variables and high stability (cross-validation >0.4). Four other models were close to these arbitrary limits (*Lycopus europaeus*, *Lysimachia vulgaris*, *Potamogeton natans* and *Typha latifolia*) and could be improved with additional data. Species with lower frequencies were usually unsuccessfully modelled and the chance for a species to be modelled with accuracy increased with its frequency. However, species like *Mentha aquatica* and *Caltha palustris* (present in 34% of ponds) failed to be modelled with accuracy. The reasons might be insufficient occurrences in each abundance class (*C. palustris* is present only at low densities) and/or lack of sensitivity of the species to the environmental variables tested in this study.

As the models were cross-validated they do not need to be re-evaluated by an independent dataset. A cross-validation on five subsets is like the sum of five independent evaluations but has the advantage of using, in the final model, the entire information available.

According to Stockwell & Peterson (2002), the number of ponds sampled in this study (80) was reasonable enough to ensure the accuracy of prediction. These authors explored sample size needs for accurate modelling for three predictive modelling methods and found that logistic regression (data in presence/absence) can develop accurate models based on about 50–100 samples. Moreover, abundance data contain more information than presence/absence data so our models based on 80 units should be more accurate than those based on occurrence data only.

Each species responded individually to distinct combination of environmental variables. Species reacted to local characteristics of their habitat (nitrogen, phosphorus, conductivity, water transparency, pond age, pond area, depth of the water, shade cover and sinuosity of the shore) but also to variables performing at other spatial scales (altitude, land-use in the surroundings and in the catchment area and pond connectivity). Altitude appeared as a key explanatory variable for most species and was generally the variable contributing most in the models. This result is not surprising because altitude summarises climatic components (temperature, light, precipitation), known to be major factors for plant growth.

Statistically good models tell us that the variables selected in the final model are related to the abundance of the species but cannot prove that the models are ecologically significant. The results showed that the model of *Phragmites australis* abundance was valid statistically. Examination of the response curves revealed that the model was also quite ecologically significant. For the other species statistically accurately modelled, the ecological influence of some of the selected variables must still be validated. Therefore, expert knowledge remains essential to analyse the ecological pertinence of the model.

Conclusion

The species models generated demonstrate that it is possible to predict species abundance of aquatic macrophytes. GAMs were able to produce statistically valid response models for 11 species. Species with robust models are among the most frequent plants, but generally it is the most rare species that give rise to conservation concerns. In that context it would be desirable to produce models to manage endangered or invasive species. Two species threatened in Switzerland were present in our data set but none was significantly explained by the variables tested (*Nymphaea alba* (18%) and *Potamogeton* gr. *pusillus* (*P. pusillus* and *P. berchtoldii*) (16%)) (Moser et al., 2002). Reliable models for species like *Phragmites australis* and *Lythrum salicaria* or *Myriophyllum spicatum* would also help the development of strategies to control these plants, native in Europe but behaving as invasive in North America (e.g. Buchan & Padilla, 2000, Blossey et al., 2001; Tewksbury et al., 2002). Statistical tools like GAMs show considerable potential in construction of models for application in the management of the habitat of particular species. However, in the absence of observational data, expert knowledge can be used to predict species occurrence and abundance (e.g., Keddy, 2000; Willby et al., 2000).

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