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Modelling the abundance of an endangered medicinal species, *Phellodendron amurense*: generalised linear model vs. generalised additive model

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ABSTRACT: Study of relations between medicinal plant species and the environment is important in plant ecology and for conservation of medicinal plants. The generalised linear model and generalised additive model were used to describe the species response to environmental gradients exhibited by a community of *Phellodendron amurense* (an endangered medicinal plant species) in the Xiaolongmen Forest Park, Beijing, China. Data of species abundance and environmental variables were obtained from 25 plots measuring 10 m × 10 m. The results showed that both the generalised linear model and the generalised additive model were effective in describing species-environment relations. The Gaussian model was more suitable in modelling the species response to environmental gradients. *Phellodendron amurense* was absolutely the most dominant tree species in the community. All dominant species in it showed a harmonious relationship. The distribution and abundance of *Ph. amurense* were significantly correlated with the elevation, slope position, aspect, litter thickness, etc. These must be considered for conservation of the studied species and community.

Keywords: species response, generalised linear model, generalised additive model, *Phellodendron amurense*, conservation

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INTRODUCTION

Regression is the most common statistical method used to relate a population with the environmental gradient. Linear regression is a linear approach for modeling the relationship between species abundance ***y*** (dependent variable) and one or more environmental factors ***x*** (independent variables). In ecological studies, our goal is usually to predict and forecast population variation, so simple linear regression can be used to fit a predictive model using the observed data set of ***y*** and ***x*** values. Responses of species to environmental gradients have been frequently modeled using the Gaussian (normal) function (ter Braak 1985; Karadžić *et al.* 1999), beta function (Austin 1987; Karadžić *et al.* 2003), or Huisman-Olff-Fresco functions (Huisman *et al.* 1993). The models can be performed using both quantitative and binary (presence, absence) data. In the case of binary data, we can use logistic regression (ter Braak 1985; James *et al.* 2013; Karadžić 2018).

Developed by Nelder & Wedderburn (1972), the generalised linear model (GLM) generalises linear regression by postulating that the linear model is related to the response variable through a link function and by assuming amplification of the variance of each measurement to be a function of its predicted value. It is a generalisation of ordinary linear regression that response variables can follow other (e.g., Poisson, binomial) dis-

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tribution models, but must not be a normal distribution (Nelder & Wedderburn 1972; McCullagh & Nelder 1989). The generalised additive model (GAM) formulated by Hastie & Tibshirani (1990) is an extension of the generalised linear model. The linear predictor in GAM does not have to be linear, but depends linearly on some smoothing functions, and our interest focuses on deduction about these smoothing functions for predictor variables (Marra & Wood 2011). Either GLM or GAM can be more suitable for simulating a population's response to environmental gradients (Huisman *et al.* 1993; Zhang *et al.* 2016).

Amur cork (*Phellodendron amurense* Rupr.) is a well-known major source of the traditional Chinese medicine 'Huangbo'. A member of the family Rutaceae, it is an endangered and protected tree species in China. The wild populations and communities have been seriously disturbed and damaged by human activities, such as collection of bark used as medicine. Studies of relations between populations and the environment can serve as the basis for its conservation and restoration. Song & Zhang (2017) analysed the relations of *Ph. amurense* communities and environmental gradients in the Xiaolongmen Forest Park by means of fuzzy set ordination and showed that elevation and litter thickness were important for community distribution. Zhang *et al.* (2009) studied the relations between *Ph. amurense* communities and environmental factors by means of PCA-CA co-inertia analysis (CoIA) and showed that community composition and diversity were significantly correlated with elevation and slope position. Zhang *et al.* (2013) investigated the variation of functional diversity and conservation of *Ph. amurense* communities in the Dongling Mountains of Beijing, China. The aim of the present work was to study dominant species responses to environmental gradients and test the effectiveness of GLM and GAM models in analysing relationships between the abundance of *Ph. amurense* and environmental gradients.

MATERIALS AND METHODS

Amur cork data. The study area, located at 115° 26' - 115° 40' E and 40° 00' - 40° 05' N, is in the Xiaolongmen Forest Park in Beijing, China. This park is 120 km away from the city centre of Beijing and is a well-known region of ecological tourism in Beijing. The climate of this area is temperate and semi humid with continental characteristics and controlled by a seasonal monsoon. The mean annual precipitation varies from 500 to 650 mm, 70% of precipitation falling from June to September. The annual mean temperature in this area is about 7°C. The mean temperature of the coldest month is -7.8°C, and the mean temperature of the warmest month is 21.1°C. The altitude varies from 800 m to 1600 m a.s.l. (above sea level). Cinnamon soil, mountain cinnamon soil, and brown forest soil can be found in the mountainous area. Secondary forests with some plantations are the main vegetation types in this park. The dominant tree species are *Betula dahurica*, *B. platyphylla, Larix principis-rupprechtii, Quercus wutaishanica*, *Pinus tabulaeformis*, and *Juglans mandshurica* (Zhang *et al.* 2009).

The Xiaolongmen Forest Park is a good area for distribution of the studied species, *Ph. amurense,* and its community in Beijing (Zhang *et al.* 2009; Song & Zhang 2017). A comprehensive survey was carried out before sampling. Twenty-five sampling plots (10 m × 10 m) of *Ph. amurense* communities were set up and investigated. Sampling plots covered all of the area of distribution of *Ph. amurense*. The species name, coverage, average height, diameter at breast height (DBH), and individual number for dominant tree species were measured and recorded on each plot (Song & Zhang 2017). Species coverage was estimated visually by three investigators at the same time and the average value was used. Tree height was measured using a clinometer. The DBH of trees was measured with a caliper. Environmental factors including elevation, slope, aspect, soil depth, litter thickness, and slope position were also investigated and recorded on each plot. Elevation was measured using an eTrex Venture C GPS (Garmin Corporation), while slope and aspect were measured using a compass meter. Soil depth was measured with a penetrometer, and litter thickness was measured using a ruler. Elevation, slope, soil depth, and litter thickness were continuous variables. Slope position was classified from 1 to 5, representing hill ridge, upper location, middle location, lower location, and valley bottom, respectively. Aspect measurements were classified from 1 to 8 in the following way: 1 (337.6-22.5°), 2 (22.6-67.5°), 3 (292.6-337.5°), 4 (67.6-112.5°), 5 (247.6-292.5°), 6 (112.6-157.5°), 7 (202.6-247.5°), and 8 (157.6-202.5°) (Zhang *et al.* 2016).

The importance value (IV) for dominant tree species on a plot was calculated and used as species abundance in the analysis. The importance value was calculated as follows (Zhang 2011; Zhang *et al.* 2016):

$$IV = (R_A + R_H + R_D)/3 \quad (1)$$

$\boldsymbol{R_A}$, $\boldsymbol{R_H}$ and $\boldsymbol{R_D}$ refer to relative abundance, relative height, and relative dominance, respectively. Dominance refers to species trunk area at breast height.

Environmental gradients. We analysed the response of *Ph. amurense* in relation to elevation, aspect, litter thickness, soil depth, slope, and slope position. In addition, using the first axis of canonical correspondence analysis (ter Braak 1986), we analysed the response of *Ph. amurense* along a comprehensive gradient of elevation, slope, aspect, and slope position.

Statistical analyses. In order to summarise ecological information, we performed CCA analysis and used the first CCA axis as the independent variable in all GLM and GAM models (for details, see Zhang *et al.* 2009; and Song & Zhang 2017). The CANOCO software was used for CCA analysis and GLM and GAM modelling (ter Braak & Smilauer 2012). Importance values were used as the dependent variable in all GLM and GAM models. We tested three distributions--normal, Poisson, and gamma--for both regression models, GLM and GAM. In order to compare different models and find the model that best describes the relation between abundance of *Ph. amurense* and environmental variables, we used the Akaike Information Criterion (AIC), which estimates the quality of each model relative to each of the other models. Thus, AIC provides a way of comparing models:

$$AIC = 2k - 2\ln(L) \tag{2}$$

where $\boldsymbol{k}$ is the number of estimated parameters in the model. Let $\boldsymbol{L}$ be the maximum value of the likelihood function for the model. The lower the AIC value, the better the model performs (Hastie & Tibshirani 1990).

Generalised linear model and generalised additive model. The general linear model (GLM) decomposes variability of dependent variable $\boldsymbol{y}$ into variability that can be explained by the model ($\hat{y}$) and error component $\boldsymbol{e}$:

$$y = \hat{y} + e = Xb + e \tag{3}$$

where $\hat{y}=Xb$ is the vector of the predicted response, $\boldsymbol{X}$ is the vector of predictors, and $\boldsymbol{b}$ is the vector of linear equation components:

$$\hat{y}_i = b_0 + b_1 x_{i,1} + b_2 x_{i,2} + \ldots + b_m x_{i,m} \tag{4}$$

Variables representing predictors in $\boldsymbol{X}$ can be either quantitative or categorical. Depending on the type of independent variables (predictors), GLM calls for ANOVA, ANCOVA, regression analysis, and other univariate statistical methods.

Despite its great generality, the GLM has serious limitations. There are many relationships that cannot be adequately summarised by a simple linear equation. The dependent variable can have a non-continuous distribution, and the predicted values thus should also follow the respective distribution. Moreover, the linear model can be inadequate to describe a non-linear relationship between predictors and dependent variable(s).

Nelder & Wedderburn (1972) and McCullagh & Nelder (1989) described the generalised linear model (GLZM), which can be used to predict responses both for dependent variables with discrete distributions and for dependent variables which are nonlinearly related to the predictors.

In the GLZM, the distribution of the dependent or response variable can be (explicitly) non-normal and does not have to be continuous (i.e., it can be a binomial, a Poisson negative binomial, etc.). The GLZM predicts dependent variable values from a linear combination of predictor variables, which are "connected" to the dependent variable via a link function.

Hastie & Tibshirani (1986) described the generalised additive model, which represents a nonlinear extension of the GLM:

$$\hat{y}_i = b_0 + b_1 x_{i,1} + b_2 x_{i,2} + \ldots + b_m x_{i,m} + e_i \tag{5}$$

It can be modified to allow for a non-linear relationship among dependent and predictor variables if we replace each linear component $b_1 x_{i,j}$ with a smooth non-linear function $f(x_{i,j})$. Using this concept, Hastie & Tibshirani (1990) proposed the following form of the generalised additive model:

$$y_i = b_0 + \sum_{j=1}^{m} f(x_{i,j}) + e_i \tag{6}$$

RESULTS

In order to get a comprehensive environmental gradient, canonical correspondence analysis (CCA) ordination was used to summarise ecological information (Fig. 1). The first CCA axis was significantly correlated with elevation (with a correlation coefficient of 0.755, P<0.001), slope position (0.580, P<0.001), and aspect (0.560, P<0.001) and was a comprehensive gradient of these variables (Song & Zhang 2017).

The response of the importance value of *Ph. amurense* to the first CCA axis was subjected to GLM and GAM modelling at different distributions and the results were all significant in describing species-environment relationships (Table 1). There was no significant difference between simulated results of the GLM and GAM models (Table 1).

To judge from AIC values and probabilities, the normal distribution best described the variation of *Ph. amurense* along a comprehensive environmental gradient obtained using the GLM and GAM models in the Xiaolongmen Forest Park, although the Poisson and gamma distributions were also significant (Table 1, Figs. 2, 3). The variation of *Ph. amurense* abundance showed a unimodal curve of response to environmental change.

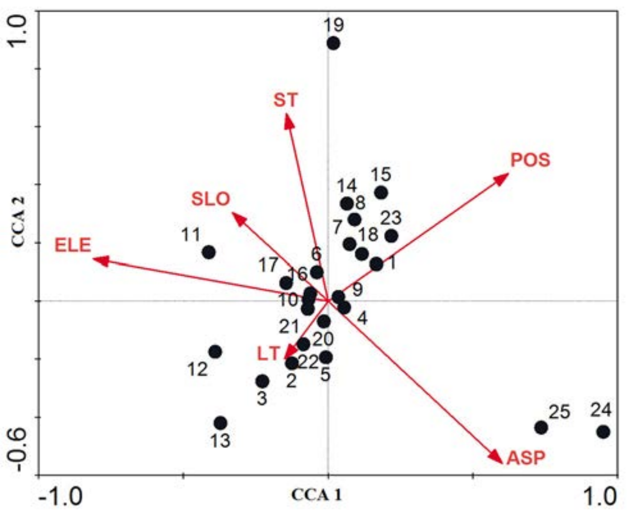

Fig. 1. Canonical correspondence analysis (CCA) of 25 plots and six environmental variables of *Ph. amurense* communities in the Xiaolongmen Forest Park, Beijing, China. ELE, SLO, POS, ASP, ST, and LT refer to elevation, slope, slope position, aspect, soil thickness, and litter thickness respectively.

Four dominant tree species, viz., *Ph. amurense, Acer truncatum, Fraxinus rhynchophylla*, and *Juglans mandshurica,* had different response curves, which means that they play different roles in community construction and composition (Fig. 4). Similar results of GLM and GAM modelling were obtained, with little statistical difference (Fig. 5). Comparing the GLM with the GAM, we note that the results obtained using the GLM seem better at describing the unimodal response (Figs. 4, 5).

For different single environmental gradients, the GLM and GAM performed differently in modelling the response of *Ph. amurense* abundance (Figs. 6, 7). The GLM results can be easily interpreted in terms of ecological meanings. *Phellodendron amurense* abundance showed a unimodal curve along each environmental gradient. The GAM revealed some linear relations of abundance and individual environmental gradients. The species distribution and abundance were significantly correlated with elevation, aspect, and slope position (Table 2, Figs. 6, 7), and slope position with the lowest AIC value performed best in modelling (Table 2). Slope, litter thickness, and soil depth also played important roles in species abundance and distribution. However, the effects of different environmental variables on population and community were diverse. Elevation was more significant for community composition and structure, and slope position and aspect were more important for dominant species.

DISCUSSION

The generalised linear model and generalised additive model were both useful in modelling the responses of *Ph. amurense* and dominant tree species abundances

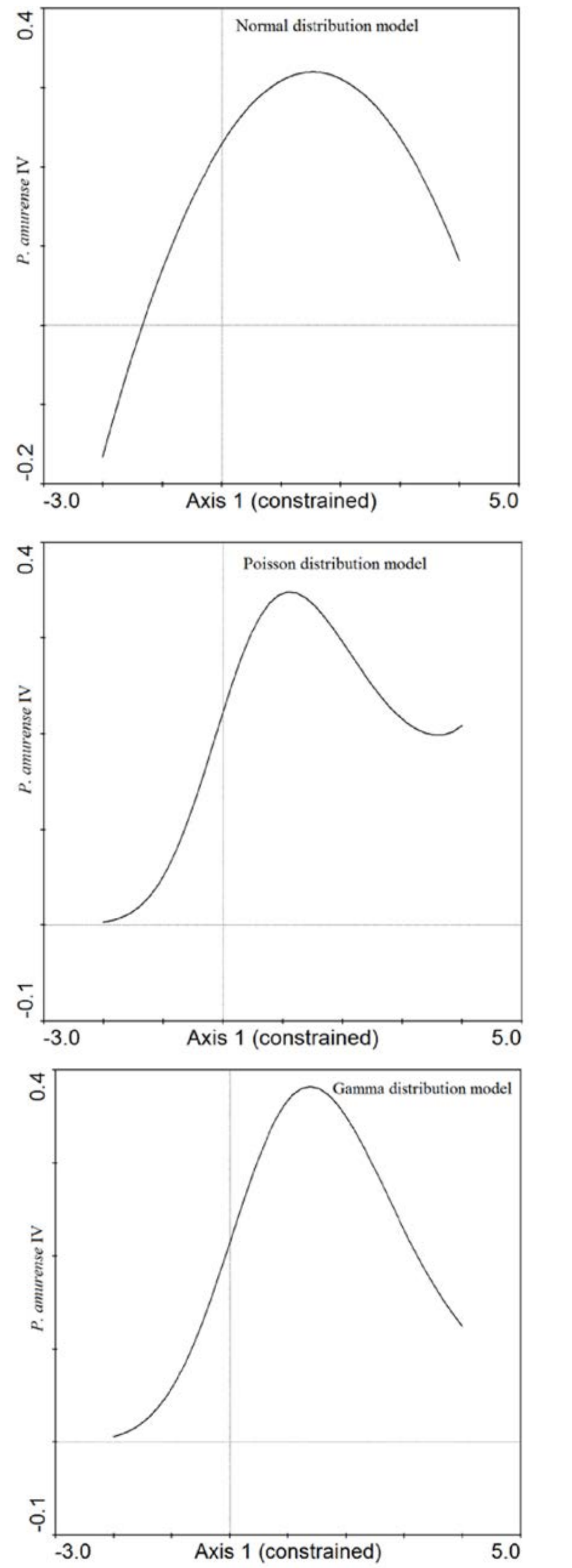

Fig. 2. Generalised linear model simulation curves of importance value of *Ph. amurense* along a comprehensive gradient (the first CCA axis) for three different distribution models in the Xiaolongmen Forest Park, Beijing, China.

Table 1. Summary of modelling the population of *Ph. amurense* in the Xiaolongmen Forest Park, Beijing, China, using different regression and distribution models.

Regression model	Distribution model	F	P	AIC
Generalised linear model	Normal	6.49	0.003	0.291
	Poisson	11.75	<0.001	1.117
	Gamma	17.48	<0.001	6.109
Generalised additive model	Normal	10.13	<0.001	0.269
	Poisson	15.19	<0.001	1.146
	Gamma	22.12	<0.001	6.348

Table 2. Summary of modelling the response of *Ph. amurense* abundance to single environmental gradients in the Xiaolongmen Forest Park, Beijing, China, using the GLM.

Environmental variables	Fitted model deviation	F	P	AIC
Aspect	0.403	0.062	0.026	0.513
Elevation	0.372	0.628	0.039	0.514
Litter thickness	0.357	0.947	0.435	0.493
Slope position	0.016	170.44	0.000	0.022
Slope	0.380	0.470	0.293	0.525
Soil depth	0.353	1.040	0.394	0.478

to environmental gradients, which is consistent with the results of other studies (Chen 2009; Zhang 2011). There were no significant differences in modelling the response of *Ph. amurense* abundance to environmental gradients in the Xiaolongmen Forest Park. However, the GLM seemed better than the GAM and should be the first choice in future studies. For a comprehensive gradient (the CCA axis), the GLM and GAM performed similarly in modelling species responses. For single environmental gradients, they yielded different results. The results obtained using the GLM were closer to ecological relations (Figs. 6, 7) (ter Braak & Smilauer 2012). The GLM and GAM offer a more effective choice for regressions of species-environment relations (Chen *et al.* 2010). The Gaussian (normal) distribution proved to be more suitable for modelling the response of the studied species to environmental gradients than the Poisson and gamma distributions in the present study. This is possibly because the distribution scale for the *Ph. amurense* population and community is comparatively small and mainly focused in one valley with generally stable habitat conditions in the Xiaolongmen Forest Park (Zhang *et al.* 2009; Song & Zhang 2017). In practical studies, responses of species to environmental gradients have been modelled much more frequently using the Gaussian (normal) function than the Poisson and gamma functions (ter Braak 1985; Karadžić *et al.* 1999).

Along the comprehensive gradient, *Ph. amurense* abundance increased gradually and reached maximum, then decreased gradually, which is in keeping with results obtained using the Gaussian model for species-environment relations (Marra & Wood 2011). This means that the given population occupied all suitable habitats in this area (Chen *et al.* 2010). For single environmental variables, this species performed in different ways, i.e., its abundance was greater at elevations above 1000 m, at medium soil depth and litter thickness, and on shady hills with less slope and lower slope position (Fig. 6). The abundance of *Ph. amurense* was closely related to these environmental gradients, which is consistent with the results of community-environment relation analyses previously conducted in the studied area (Zhang *et al.* 2009; Zhang *et al.* 2013; Song & Zhang 2017). This means that the endangered medicinal species played an important role in community composition, structure, and function (Li 2008). Environmental conditions in the Xiaolongmen Forest Park are suitable for growth and development of the *Ph. amurense* population and community (Li 2008; Zhang *et al.* 2009). For conservation of this species and its community, it is necessary to ensure protection of conditions favourable for its survival (Chen *et al.* 2010; Sadia *et al.* 2017).

The response curves for the four dominant tree species were different and illustrate the relationships be-

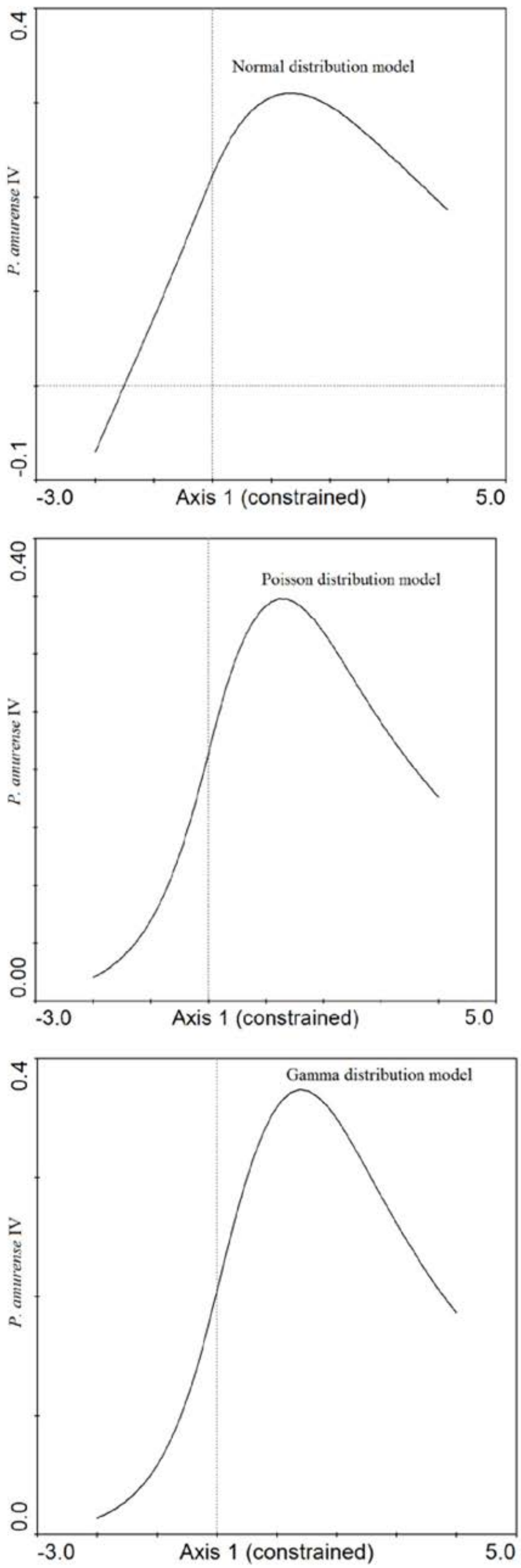

Fig. 3. Generalised additive model simulation curves of importance value of *Ph. amurense* along a comprehensive gradient (the first CCA axis) for three different distribution models in the Xiaolongmen Forest Park, Beijing, China.

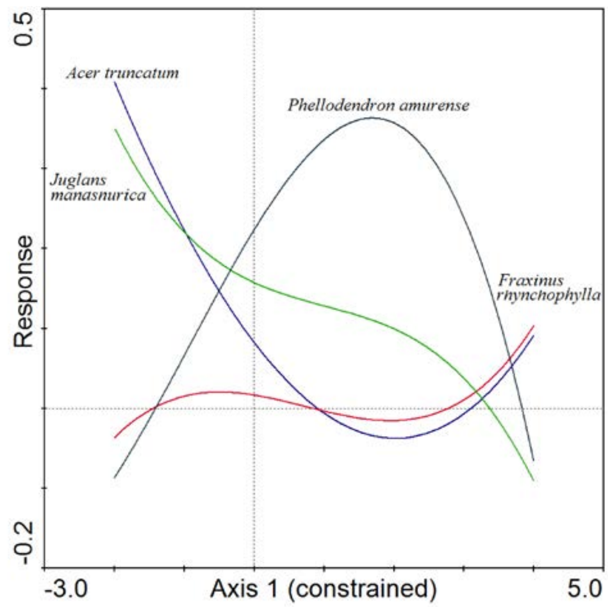

Fig. 4. Generalised linear model simulation curves of importance values for the four dominant tree species along a comprehensive gradient (the first CCA axis) in *Ph. amurense* communities in the Xiaolongmen Forest Park, Beijing, China.

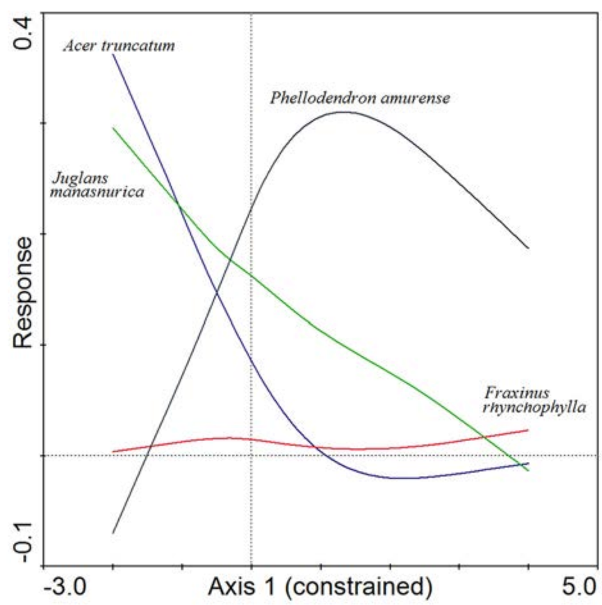

Fig. 5. Generalised additive model simulation curves of importance values for the four dominant tree species along a comprehensive gradient (the first CCA axis) in *Ph. amurense* communities in the Xiaolongmen Forest Park, Beijing, China.

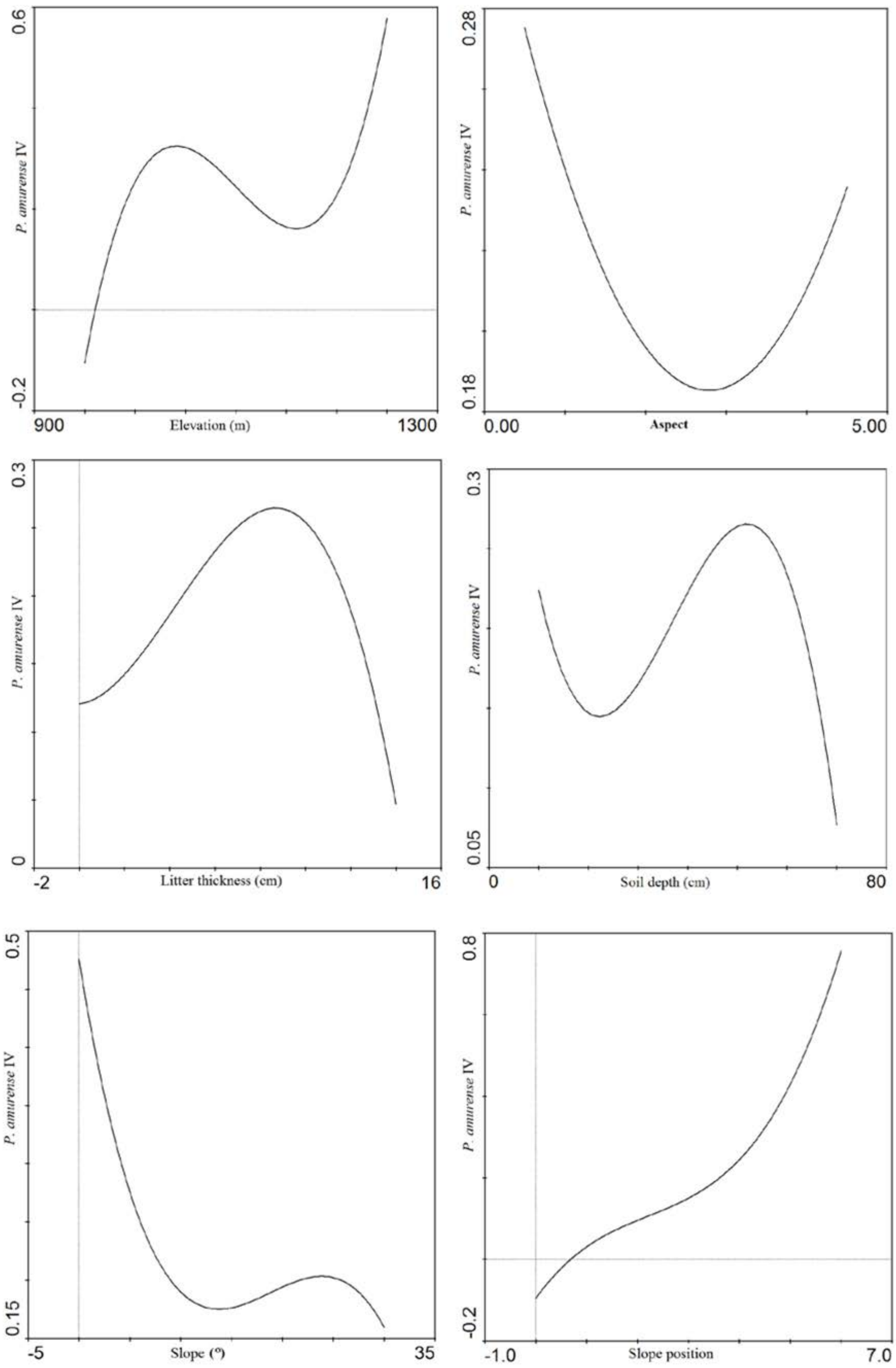

Fig. 6. Generalised linear model simulation curves of importance value of *Ph. amurense* along different environmental gradients in the Xiaolongmen Forest Park, Beijing, China.

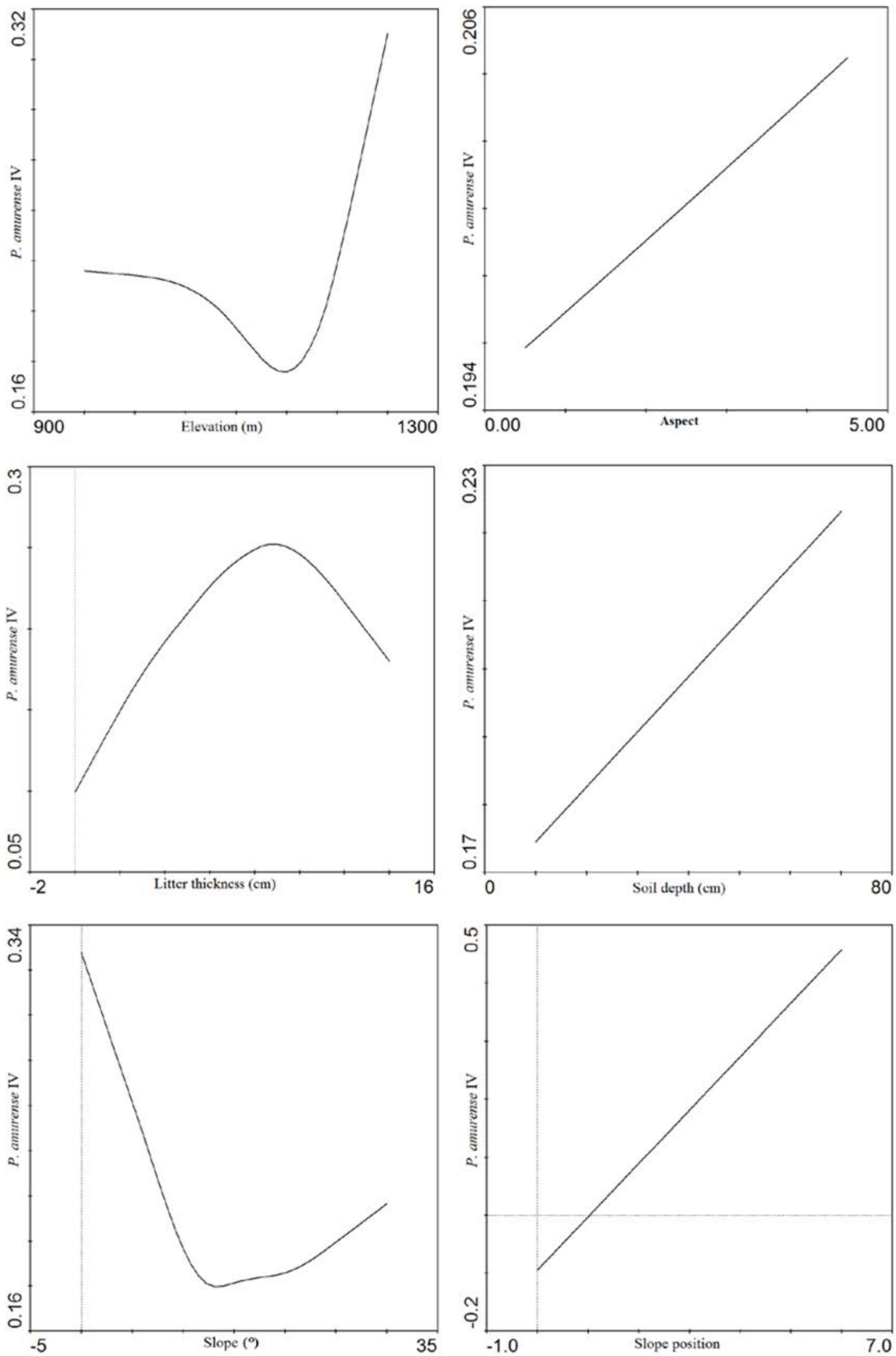

Fig. 7. Generalised additive model simulation curves of importance value of *Ph. amurense* along different environmental gradients in the Xiaolongmen Forest Park, Beijing, China.

tween these species in their communities (ter Braak & Smilauer 2012). *Phellodendron amurense* was absolutely the most dominant species, with a strong response curve to the comprehensive environmental gradient, and it played a constructive role in the community (Zhang *et al*. 2009). The other three species were co-dominant, and their abundances decreased with increase in the abundance of *Ph. amurense* (Fig. 2). These relations were good for stability and development of the forest community (Zhang *et al*. 2016; Song *et al*. 2017). For conservation of *Ph. amurense* communities, protection for these co-dominant species is also important.

This study proves that it is right to use the ordination axis as a comprehensive environmental gradient in species-environment analysis (Roberts 2008; Zhang *et al*. 2017). Combining the comprehensive gradient for all variables with a single gradient for each factor makes it easier to interpret the interactions of species, communities, and the environment.

CONCLUSION

The generalised linear model and generalised additive model were effective and useful methods in studying species-environment relations in communities of an endangered medicinal plant species, and they should be applied more often in future studies. The Gaussian (normal) model performed better than the Poisson and gamma models in modelling the species response to environmental gradients. *Phellodendron amurense* was absolutely the most dominant tree species, and it was found to play a significant role in community structure and composition. Environmental conditions in the Xiaolongmen Forest Park were shown to be suitable for this species and its community. Elevation, aspect, slope position, litter thickness, soil depth, etc., were important for its growth and development. Planting saplings of *Ph. amurense* on hills in places with lower slope position and medium soil depth can be suggested as a way to restore this species. The conservation of conditions needed for the community's survival and protection of the environment are also important.

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REZIME

Modelovanje bogatstva ugrožene lekovite vrste *Phellodendron amurense*: generalizovani linearni model ili generalizovani aditivni model

Naiqi Song i Jintun Zhang

Istraživanje odnosa lekovitih vrsta i njihove sredine je važno u ekologiji biljaka i u zaštiti lekovitih vrsta. Generalizovani linearni model i generalizovani aditivni model su korišćeni da opišu odgovor vrste na sredinski gradijent kod zajednica *Phellodendron amurense* (ugrožene lekovite vrste) u Xiaolongmen park-šumi, Peking, Kina. Podaci o bogatstvu vrste i sredinskim varijablama su istraživani na osnovu 25 površina 10 m × 10 m. Rezultati pokazuju da su i generalizovani linearni model i generalizovani aditivni model efikasni u opisivanju odnosa vrsta-sredina. Gausov model je pogodniji u modelovanju odgovora vrste na sredinski gradijent. *Phellodendron amurense* je apsolutno dominanta vrsta u zajednici. Sve dominantne vrste pokazuju harmonični odnos u zajednici. Distribucija i bogatstvo *Ph. amurense* su značajno korelisani sa nadmorskom visinom, nagibom, ekspozicijom, debljinom prostirke, itd. Sve ovo treba uzeti u obzir pri zaštiti istraživane vrste i njenih zajednica.

Ključne reči: odgovor vrste, generalizovani linearni model, generalizovani aditivni model, *Phellodendron amurens*, zaštita.