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RESEARCH PAPER

A Topography-Based Model of the Vegetation Cover of the Lanzhinskie Mountains

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ABSTRACT

By means of the GAM technique it is possible to create detailed maps of the potential vegetation for regions that are difficult to access. This is particularly important for wide mountain areas of Northeast Asia, where such maps have never been created. High-resolution DEMs permit increased prediction accuracy and modeling of complex vegetation patterns. Most vegetation types in the area are controlled mainly by the moisture regime and by regimes of sediment transport and accumulation. The relatively small amounts of rainfall in the continental climate are distributed spatially by relief elements. This creates a wide range of soil moisture regimes: from very dry, with a prolonged period of moisture deficit, to wet, without moisture deficit during the growing season at all. Therefore, moisture appears to be a critical resource in this climatic region, and it is a main differentiating factor for the vegetation. The map of potential vegetation, obtained satisfactorily, reflects altitudinal zonation and inter-zonal patterns of vegetation distribution. The area occupied by some vegetation communities is overestimated, however, due mainly to insufficient DEM resolution.

Keywords:
vegetation cover, larch forest, generalized additive model, GAM, DEM, refugium

Омелько А.М., Крестов П.В., Яковлева А.Н. Модель растительного покрова Ланжинских гор на основе топографических переменных

Показана возможность создания подробных карт потенциальной растительности для труднодоступных регионов с помощью техники GAM. Это особенно важно для обширных горных районов Северо-Восточной Азии, для которых такие карты до сих пор отсутствуют. Высокое разрешение матрицы высот позволяет увеличить точность прогнозирования и моделирования сложно организованного растительного покрова. Большинство типов растительности в районе контролируется режимами увлажнения, а также склоновой аккумуляции и транспортировки материала. Относительно небольшое количество осадков в условиях континентального климата распределяется в пространстве по элементам рельефа. Это создает широкий диапазон режимов увлажнения почвы: от очень сухого, с длительным периодом дефицита влаги, до хорошо увлажненного без периода дефицита влаги в течение вегетационного сезона. Таким образом, влага в данном регионе представляется важнейшим ресурсом и служит основным дифференцирующим фактором для распределения типов растительности. Карта потенциальной растительности, удовлетворительно отражает закономерности высотной зональности и распределение азональных растительных комплексов. Площадь, занимаемая некоторыми типами растительных сообществ, слегка завышена из-за недостаточного разрешения DEM.

Ключевые слова:
растительный покров, лиственничные леса, генерализованная аддитивная модель, GAM, DEM, рефугиум

Relationships between vegetation and environmental factors, and their interdependence, are fundamental problems that provide an important component for the methodologies of many disciplines related to vegetation science. Changes in vegetation cover in relation to climatic changes, on the one hand, and in relation to ecological factors deriving from terrain characteristics, on the other hand, are of great interest at a large scale. Since the 1990s, research teams involved in studies of vegetation-environment relationships obtained a powerful tool for quantification in the form of generalized additive models (GAMs), a variant of semi-parametric regression models (Hastie & Tibshirani 1990).

Response curves in GAMs are estimated with smooth functions (usually cubic splines), allowing a wide range of response curves to be fit (Yee & Mitchell 1991). This is considered by some authors to be important progress, since species only rarely present bell-shaped or linear response curves along environmental gradients (Austin & Smith 1989, Austin 2002). Generalized additive models constitute powerful explanatory and predictive tools (Austin 1999, Overton et al. 2002), and many applications in the field of distribution modeling have been reported (Guisan et al. 2002, Lehman et al. 2002, Cawsey et al. 2002, Clarkson et al. 2004, Schimer & Lehmann 2004).

In mountain regions, topography appears to be an important determinant of various local conditions, including microclimate, soil properties, disturbance regimes and others (Brown 1994). Use of topographic variables derived from a digital elevation model (DEM), as a substitute for field-measured environmental variables, becomes a common practice in spatial modeling of mountain vegetation (Brown 1994, del Barrio et al. 1997, Hoersch et al. 2002, Dirnbock et al. 2003, Hörsch 2003, Van Niel et al. 2004). The advantage of using a DEM is its spatial continuity and availability at no cost for the entire world (Jarvis 2008), even though not always at the required spatial scale. Whenever direct climatic and other environmental measurements are available, such as climate-station data or data from vegetation surveys, DEMs can be used effectively for interpolation of these discrete measurements (Zimmerman & Kienast 1999, Dirnbrock et al. 2003, Krestov et al. 2008). In areas, where direct environmental data are not always available at local level, as for most of the territory of Northeast Asia, DEMs can serve as the only tool capable of generating the relative values for several ecologically relevant environmental variables.

The small Lanzhinskie Mountain massif, located on the northwestern side of the Sea of Okhotsk coast, was selected as a modeling area for this study. This area is characterized by the most contrasting climatic conditions on the Northeast Asian coast and has very high values of continentality (Krestov et al. 2008), as compared with other coastal areas. The vegetation of the region is represented by poorly known continuous *Larix cajanderi* forests that change, at higher elevation, to the thickets of *Pinus pumila* and, further up, to alpine tundra vegetation.

The combination of high climatic continentality and proximity to the seacoast affects the structure of the vegetation cover, changing considerably the zonal patterns that become complicated with many kinds of azonal vegetation. Thus, the vegetation of the Lanzhinskie Mts. is a complex system of zonal and azonal elements, the distribution of which is controlled by a unique combination of environmental factors. In addition to the climatic factors acting at regional level, there are important local factors.

This study aims to map the potential vegetation of the Lanzhinskie Mountains using statistical modeling of the relationship between different vegetation types and topographic variables; it also attempts to identify the main variables and related environmental factors that affect the current vegetation patterning.

MATHERIAL AND METHODS

Study area

The Lanzhinskie Mts., a small system of ridges, are located on the Sea of Okhotsk coast, between two larger mountain systems, the Dzhugdzhurskii Mountains to the south and the Oymyakonsky Plateau to the north (59°19.3'–59°33.3'N and 143°18.7'–143°37.6'E). To the south, the Lanzhinskie Mts. descend to the Sea of Okhotsk, while on the west and east they are bounded by the Kuchtui and Bolshoi Marekan rivers flowing to the Sea of Okhotsk. The area of the Lanzhinskie Mts. is about 370 km^2. This is a relatively isolated mountain range, the closest mountain systems being about 30 km from the Lanzhinskie foothills. The maximum elevation of these mountains is 530 m (Mt. Njaura); average elevation is about 300 m (Fig. 1).

The climate of the region is characterized as subarctic (Vitvitskii 1961), with mean annual temperature of –5°C; Kira (1977) warmth index of 19.4°C and coldness index of –138.9°C; 36°C difference between the means of the coldest and warmest months (continentality); average annual precipitation of 364 mm; and precipitation of 116 mm in months with negative mean temperatures (Anonymous 1966-1971). The climate of the study area is characterized by the largest annual temperature range of any coastal area in the world (Nakamura et al. 2007, Krestov et al. 2008).

The high degree of continentality is connected with such physiologically important climatic characteristics as very low winter temperatures and shallow snow cover. These features of climate lead to severe soil freezing and, consequently, to the exclusion of plant species characteristic of suboceanic climate, which are common to regions where the soil is protected in winter by deep snow (Krestov 2004). Another consequence of the continental climate is relatively high summer temperatures and generally low precipitation, which leads to a moisture deficit during the growing season. Permafrost compensates substantially for the moisture deficit in northern Okhotia, but only a few plant root systems are adapted to water uptake at low temperatures.

The winter in this region lasts about seven months (latter half of October to latter half of May). Rather strong continental northwest winds are prevalent in winter and results in low winter temperatures. The mean daily temperature from December to February remains below –20°C. The coast of the Sea of Okhotsk is far from the tracks of winter cyclones, so this territory has low precipitation. Temperatures rise only slowly in spring. Only by latter May does the snow cover melt away. Favorable conditions for the vegetation begin two weeks later, when the danger of late frost is past. South and southeast winds from the Sea of Okhotsk are usual from May to August. During two months, July and August, daily temperatures exceed 10°C (but do not reach 15°C).

The vegetation of the region is represented by continuous *Larix cajanderi* forests that can be related to the continental sector of the middle boreal subzone (Krestov 2003, Nakamura et al. 2007). Altitudinal zonation is well expressed in the mountain systems. *Larix cajanderi* forests belonging to the order Ledo-Laricetalia cajanderi Ermakov et Alsynbayev 2004 occupy the lower vegetation belt, extending from sea level to 400–600 m above sea level (a.s.l.). Upwards, the forest vegetation changes to a belt of Siberian dwarf-pine thickets (Vaccinio-Pinetalia pumilae) and then to a belt of shrubby alpine tundra (Loiseleurio-Vaccinietea). Forest vegetation occupies about 24 % of the area studied, with the rest of the territory covered mainly by tundra and Siberian dwarf-pine thickets.

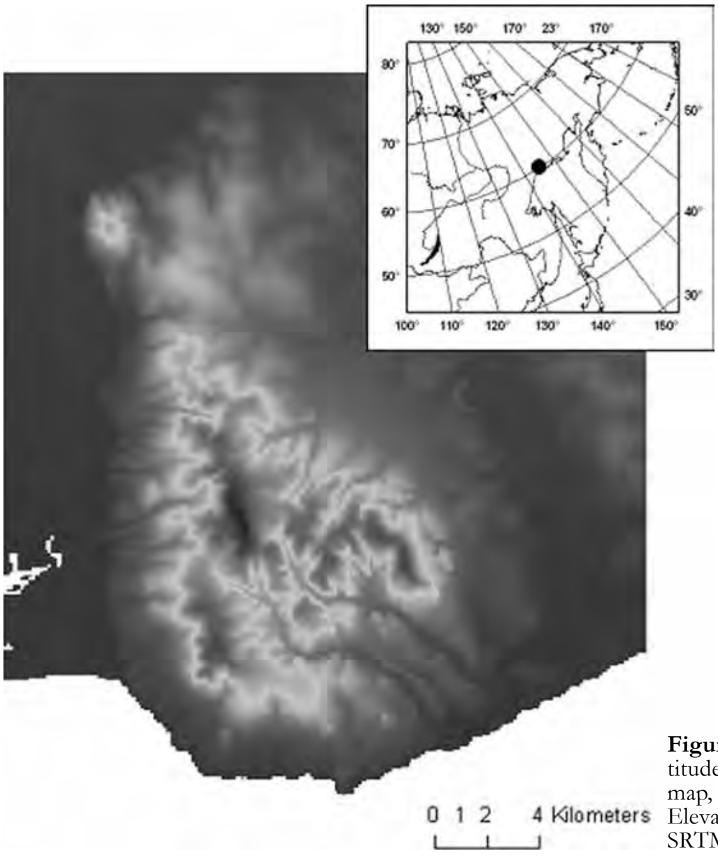

Figure 1 Location of the study area. Grey shading indicates altitude: higher altitudes represented by lighter shades on the main map, and darker shades on the inset map of Russian Far East. Elevation data used: inset, GTOPO30 (USGS, 2000); main map, SRTM (Jarvis 2008).

Zonal vegetation is considerably patterned with azonal vegetation complexes, most important of which are *Betula ermanii* forests in the forest belt; dry dwarf-pine thickets with lichens belonging to Loiseleurio-Vaccinietea in the subalpine dwarf-pine belt; and dry *Dryas punctata* and *Carex rupestris* tundra belonging to the class Carici-Kobresietea in the alpine tundra belt. Gentle slope tails and river valleys are covered by a unique dynamic tundra-forest complex, controlled by interrelations of permafrost and very intensive alluvial processes.

Data

Fieldwork during summer 2008 produced 152 full relevés covering a variety of vegetation types in the study area. In addition to phytosociological data, 239 plots in the main vegetation types were described more briefly for interpretation of satellite-derived imagery.

A digital elevation model (DEM) produced by the Shuttle Radar Topography Mission (SRTM) (Jarvis 2008) and land images from the Landsat Enhanced Thematic Mapper (ETM) (from NASA's Global Ortho-Rectified Landsat Data Set, Tucker et al. 2004) were used for identification of vegetation spatial distributions. The DEM had a resolution of 90 m, and the Landsat-derived images had a resolution of 14.5 m (28.5 m for bands 1-5 and 7 and 14.5 m for panchromatic band 8). Both the Landsat images and DEM were geo-referenced by the supplier. The elevation values of the DEM were rounded to integers, resulting in 1-meter intervals (Jarvis 2008). The reported spatial accuracies of ortho-rectified data were < 50 m root-mean-square error for the Landsat data (Tucker et al. 2004), and < 9 m geolocation error and < 6 m height error for 90% of the SRTM DEM (Rodriguez et al. 2005).

Data processing

The relevés were classified as suggested by the Braun-Blanquet methodology (Mueller-Dombois & Ellenberg 1974), taking into account a number of conceptual approaches to the allocation of higher vegetation units in major published classifications of Northeast Asian boreal forests, made by Ermakov (2003, Ermakov & Alsynbayev 2004), Miyawaki (1980-1989) and Krestov (Krestov & Nakamura 2002, Krestov et al. 2009).

The number of field relevés was sufficient for vegetation classification but not for statistical models, because the relevé points did not cover the whole range of variation of the topographic variables. With the aid of 239 plots obtained for space-image interpretation, additional points for the main vegetation contours were obtained by deciphering the Landsat ETM+ images. As a result, for the statistical model, we used 1800 additional points from the main vegetation contours.

The DEM had some missing values over land and negative values over water bodies, and it contained terraces, probably caused by rounding of elevation values during preprocessing by the provider (Wood 2003). These "bad values" and terraces were removed by creating elevation isopleths from the DEM with steps of 5 m and subsequently creating a hydrologically correct DEM from these contour lines (Hutchinson 1989). The final DEM resolution was 30 m.

The DEM was used to create distribution maps for 18 environmental variables, which describe microclimate and other environmental conditions, created and transformed by relief (Table 1). For this purpose we used ILWIS software version 3.4 (Hengl et al. 2003). Environmental variables are of four types: morphometric (elevation, aspect, slope and so on); hydrological (compound topographic index, sediment transport index and stream power index); climatic (potential insolation and wind exposure); and, finally, generic landforms.

Maggini et al. (2006) showed that incorporating the general spatial trend and local autocorrelation in models allows significant improvement in model performance and stability. Much of the vegetation on the Lanzhinskie Mts., however, was affected by human activity (mainly repeated fires and logging). Thus, for this territory, we could not create the relevant maps of spatial trends and the local autocorrelations would not be included in models.

Statistical models

Statistical models were fit by generalized additive models (GAMs, Hastie & Tibshirani 1990). GAMs represent a further development of generalized linear models (Nelder & Wedderburn 1972), which represent a generalization of well known multiple regressions. The generalized linear model (GLM) differs from the multiple regression in two major aspects: first, the distribution of the dependent or response variable can be non-normal and does not have to be continuous (for example, binomial); second, the values of the dependent variable are predicted from a linear combination of predictor variables, which are “connected” to the dependent variable by a link function

$$g_i(\mu Y) = \beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n,$$

in which μY stands for the expected value of Y, X_1 through X_n represent the n values for the predictor variables, β_0 through β_n are the regression coefficients estimated by multiple regression, and g_i is called the link function. A generalization of the multiple regression model would be to maintain the additive nature of the model but to replace the simple terms of the linear equation $\beta_i X_i$ with $f_i(X_i)$, where f_i is a non-parametric function of the predictor X_i.

GAMs are very flexible and can provide an excellent fit in the case of non-linear relationships and significant noise in the predictor variables. It should be stressed, however, that because of this flexibility, one must be extra cautious not to over-fit the data, i.e. to apply an overly complex model to data so as to produce a good fit that likely will not stand up in subsequent validation studies. Another issue pertains to the interpretability of results obtained from GLMs vs. GAMs. Linear models are easily understood and summarized. GAMs are not easily interpreted, in particular when they involve complex non-linear effects of some or all of the predictor variables (and, of course, it is in those instances that generalized additive models may yield a better fit than generalized linear models).

For model fitting we used the GRASP version 3.3b package (Lehmann et al. 2002) for S-Plus 8.0 Student Edition (Insightful Corp., Seattle, WA, USA). The original GRASP was enhanced specifically for the purpose of Maggini et al. (2006), and it now incorporates new selection methods and the possibility of dealing with interactions among predictors as well as spatial autocorrelation (Lehmann et al. 2005). The

Table 1. Topographic Variables and Environmental Indices Used as Independent Variables in GAM

Variable	**Description**	**Calculation**	**Ecological meaning**
Morphometric			
Altitude	Altitude above sea level (m)	DEM	Temperature, moisture CO_2 pressure
Aspect	Aspect (degrees)		Solar radiation, wind, moisture
Slope	Slope (%)		Solar radiation, stability, erosion, moisture
East	Aspect east-wes (от 1 до -1)	sin(aspect)	Morning/afternoon solar radiation, moisture
North	Aspec north-south (от 1 до -1)	cos(aspect)	Summer/winter solar radiation
Dist	Distance to the seashore (m)		Moisture, wind
ProfC	Curvature in slope direction	-1 = concave, 1 = convex	Moisture, erosion/deposition
PlanC	Curvature perpendicular to slope	-1 = concave, 1 = convex	Solar radiation, moisture, erosion/deposition
Hydrological			
TWI (CTI)§	Compound topographic index	$\mathrm{Ln}(A_f / \tan \beta)$*	Moisture, water logging, cold-air ponding
STI†	Sediment transport index	$(A_f/22.13)^{0.6}(\sin \beta/0.0896)^{1.3}$*	Erosion potential
SPI†	Stream power index	$A_f \tan \beta$*	Erosion potential
Climatic			
Solin‡	Potential insolation (%)	Shaded relief**	Potential incoming solar radiation
WindS‡	South wind exposure (%)	Shaded relief**	Wind (summer), moisture
WindN‡	North wind exposure (%)	Shaded relief**	Wind (winter), moisture
Generic landforms			
glfChan	Channelness (0 to 1)	1 = channel	Moisture, temperature, erosion/deposition
glfPlane	Plainness (0 to 1)	1 = plain (terrace)	Moisture, erosion/deposition
glfRidge	Ridgeness (0 to 1)	1 = ridge	Moisture, erosion/deposition
glfSlope	Slopeness (0 to 1)	1 = slope	Moisture, temperature, erosion/deposition

*A_f – specific catchment area draining trough the point, β – representative local slope angle.
**Shary et al. (2002), §Schmidt & Persson (2003), †Moore *et al.* (1993), ‡Hengl *et al.* (2003).

response variables were vegetation types that were defined as binary variables. The presence of a given vegetation community in a plot automatically precludes the occurrence of other communities. A binomial probability distribution was selected for the response, and the link function was designed as a logit function, so the GAM equations looks like the following:

$$\ln(p/(1\text{-}p)) = \Sigma f_i(X_i),$$

where p is the occurrence probability of a vegetation community of a certain type, the left side of the equation is the logit link, and the right side is the linear predictor. Four degrees of freedom were given to each smoothed environmental predictor.

The models and predictors were evaluated as follows: (1) statistical evaluation using the area under the curve of the receiver characteristic plot (ROC AUC, Fielding & Bell 1997) on the training data set (resubstitution); (2) a five-fold cross-validated ROC (cvROC AUC); (3) the percentage of explained deviation (D^2, Guisan et al. 2002); and (4) a Spearman rank correlation/cross-validated correlation (r_s, cv. r_s).

RESULTS

The vegetation of the Lanzhinskie Mts. was classified into 15 vegetation units, of which 7 units were orders that could be shown on the map in their own contours and 7 were composed into two complex contours.

The fewest points were observed for the communities of stone birch (*Betula ermanii*) forests (prevalence 2.2 %). This is because, in the study area, stone-birch forests occupy only small separated territories with total area up to only 100 square meters. These areas extend along narrow valleys or small ridges on slopes. Such areas are difficult to recognize on the Landsat images, and so the statistical model for stone-birth forests is based mainly on field observations. Thus we obtained 9 main vegetation types that could be mapped (Table 2).

All vegetation types were modeled successfully (Table 3). ROC AUC values ranged from 0.88 (LAR and PPM) to 0.99 (DDT). According to the classification of Swets (1988) (0.5-0.7: poor discrimination ability, 0.7-0.9: reasonable discrimination, 0.9-1.0: very good discrimination), values obtained in this study show reasonable to very good discrimination ability. Moreover, all models are stable and the five-fold cross-validation decreases the ROC AUC values by less than 0.02. The best ROC AUC and D^2 values were obtained for vegetation types ALT (N = 180), DDT (N = 127), VAL (N = 157), and SBF (N = 60). Lesser values were obtained for SCT, LTD and PPL. The least accurate models were obtained for types LAR and PPM.

The contributions by the different variables are shown in the Table 4. The CROSS selection method retained almost all the environmental variables except the generic landforms. The contribution of some variables, for example "Aspect" or "North", however, was less than 1 percent, and, on the whole, the models obtained do look a bit "noisy". We have tried to clear the models and have omitted some variables, the total contribution of which was less than 5% (variables marked with "+" in Table 4). We removed from two to six variables from each model. This resulted in little decrease of the D^2 values (4% on average), but the ROC AUC and cvROC AUC values changed by less than one percent. In some cases, removing variables increased model stability. The size of all models decreased significantly (by 15–36 %).

Figure 2 shows the overall contribution of four variable groups to the prediction of different vegetation types. The

Table 2. Main Vegetation Types of Lanzhinskie Mountains and the Percentage of the Point Number in Input Data

Vegetation type	Code	N	Prevalence (%)
Riparian complex of forests, shrubs, meadows, sedge bogs and sedge-cottongrass tundras	VAL	157	5.8
Stonebirch (*Betula ermanii*) forests with dwarf alder (*Alnus fruticosa*) thickets (Betulo-Ranunculetea)	SBF	60	2.2
Larch forests with *Carex globularis* and *Ledum palustre* in the understory (Ledo palustris-Laricetalia cajanderi)	LAR	587	21.5
Sedge-cottongrass tundra	SCT	442	16.2
Complex of larch forests and shrubby tundras on sites with dynamic permafrost	LTD	266	9.8
Siberian dwarfpine (*Pinus pumila*) thickets with lichens (Loiseleurio-Vaccinietea)	PPL	445	16.3
Siberian dwarfpine (*Pinus pumila*) thickets with green mosses (Vaccinio-Pinetalia pumilae)	PPM	461	16.9
Dry Dryas tundra (Carici-Kobresietea)	DDT	127	4.7
Shrubby alpine tundra (Loiseleurio-Vaccinietea)	ALT	180	6.6

Table 3. Explained Deviance (D^2), Degrees of Freedom Used (*DfU*), Receiver Operating Characteristic (*ROC*), Cross-Validated *ROC* (*cvROC*), Spearmen Correlation (*COR*), Cross-Validated *COR* (*cvCOR*) for Selected Models

Test	ALT	DDT	VAL	SBF	LAR	SCT	LTD	PPL	PPM
D^2	0.81	0.97	0.71	0.79	0.48	0.62	0.58	0.51	0.49
DfU	36.16	44.08	28.49	40.56	36.41	36.37	36.18	40.26	44.31
ROC	0.98	0.99	0.97	0.98	0.88	0.95	0.94	0.93	0.88
cvROC	0.97	0.99	0.95	0.97	0.87	0.94	0.92	0.92	0.87
COR	0.69	0.94	0.58	0.49	0.57	0.66	0.55	0.62	0.52
cvCOR	0.68	0.91	0.57	0.45	0.55	0.64	0.53	0.60	0.50

Table 4. Contribution in Percentage of the Predictors Within Selected Models (Model Contribution in GRASP)

Variable	ALT	DDT	VAL	SBF	LAR	SCT	LTD	PPL	PPM
Morphometric									
Aspect	+*	+	-**	+	+	+	+	+	+
Dist	+	0.39	-	-	-	+	+	0.08	0.06
East	+	+	-	0.03	+	+	+	+	0.02
ProfC	0.08	0.05	0.12	0.08	0.11	0.05	0.03	0.06	0.04
PlanC	+	-	-	+	-	-	+	+	-
Height	0.05	0.05	0.13	0.08	0.19	+	+	0.08	0.07
North	+	0.04	-	+	+	+	+	+	+
Slope	0.28	0.06	0.09	0.06	0.23	0.01	0.17	0.08	0.24
Hydrological									
SPI	0.24	0.03	0.27	0.12	0.07	0.55	0.24	0.18	0.18
STI	0.09	0.06	0.22	0.03	0.04	0.11	0.22	0.11	0.07
TWI	0.06	0.13	0.04	0.00	0.03	0.01	0.03	0.14	0.09
Climatic									
Solin	0.11	+	0.13	0.28	0.17	0.07	0.09	0.17	0.10
WindS	0.02	0.02	-	0.08	0.04	0.09	0.14	0.06	0.06
WindN	0.08	0.12	-	0.10	0.11	0.10	0.07	0.05	0.07
Generic landforms									
glfChan	-	-	+	-	-	-	-	-	-
glfPlain	-	-	-	-	-	-	-	-	-
glfRidg	-	-	-	-	-	-	-	-	-
glfSlope	+	0.05	+	-	+	0.01	0.01	-	+

* : predictor proposed in selection procedure but not retained in the model
** : predictor not proposed in the selection procedure

distribution of most vegetation types was predicted by morphometric variables and hydrological indices. If the vegetation type is controlled mainly by moisture regime and sediment transportation/accumulation regime (valley forests, tundra, dynamic complex), then the hydrological indices have a maximum "weight" in the model. For other vegetation types, such as larch forests and dwarf pine thickets, the influence of three groups of variables is about the same. The only exception was dry *Dryas* tundras, which are correlated mainly with distance from the sea.

In general, the models include three of the four groups of topographic variables. By their contributions to the models they can be ordered from hydrological variables (TWI, SPI, STI) (highest contribution), through morphometric variables (ProfC, Slope), to climatic variables (Solin, WindN, WindS) (lesser contribution).

Figure 3 shows the spatial predictions for vegetation types of the Lanzhinskie Mts. Analyzing the maps and comparing them with the Landsat images, we came to the conclusion that the models obtained can be divided into two groups: models predicting the real distribution of vegetation types and models predicting the occurrence of a vegetation type within some wider area. In fact, the actual vegetation distribution range lies within predicted but much smaller in size. The second group includes models for stone-birch forests (SBF in Fig. 3), shrubby alpine tundra (ALT) and riparian forest-meadow complexes (VAL). Figure 4 shows a comparison between the actual and predicted distribution of the shrubby alpine tundra (ALT).

We mapped the potential vegetation of the Lanzhinskie Mts. (Fig. 5) based on the spatial predictions, assigning to the each pixel the vegetation type that had the highest probability of occurrence there.

The riparian forest-meadow vegetation complex occupies the wide valleys, which are characterized by low values of SPI and STI indices and by high insolation levels (Solin). Lower parts of gentle slopes and slope tails are covered by the sedge-cotton-grass tundras and by the dynamic forest-tundra complex. Prediction models for these types include almost the same set of environmental variables, with similar contributions. These types occur on

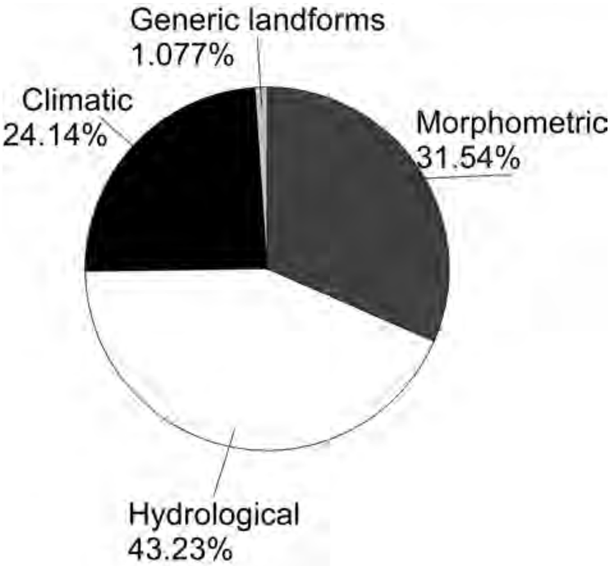

Figure 2 Contribution of four variable groups for different vegetation types (linear predictor scale in GRASP).

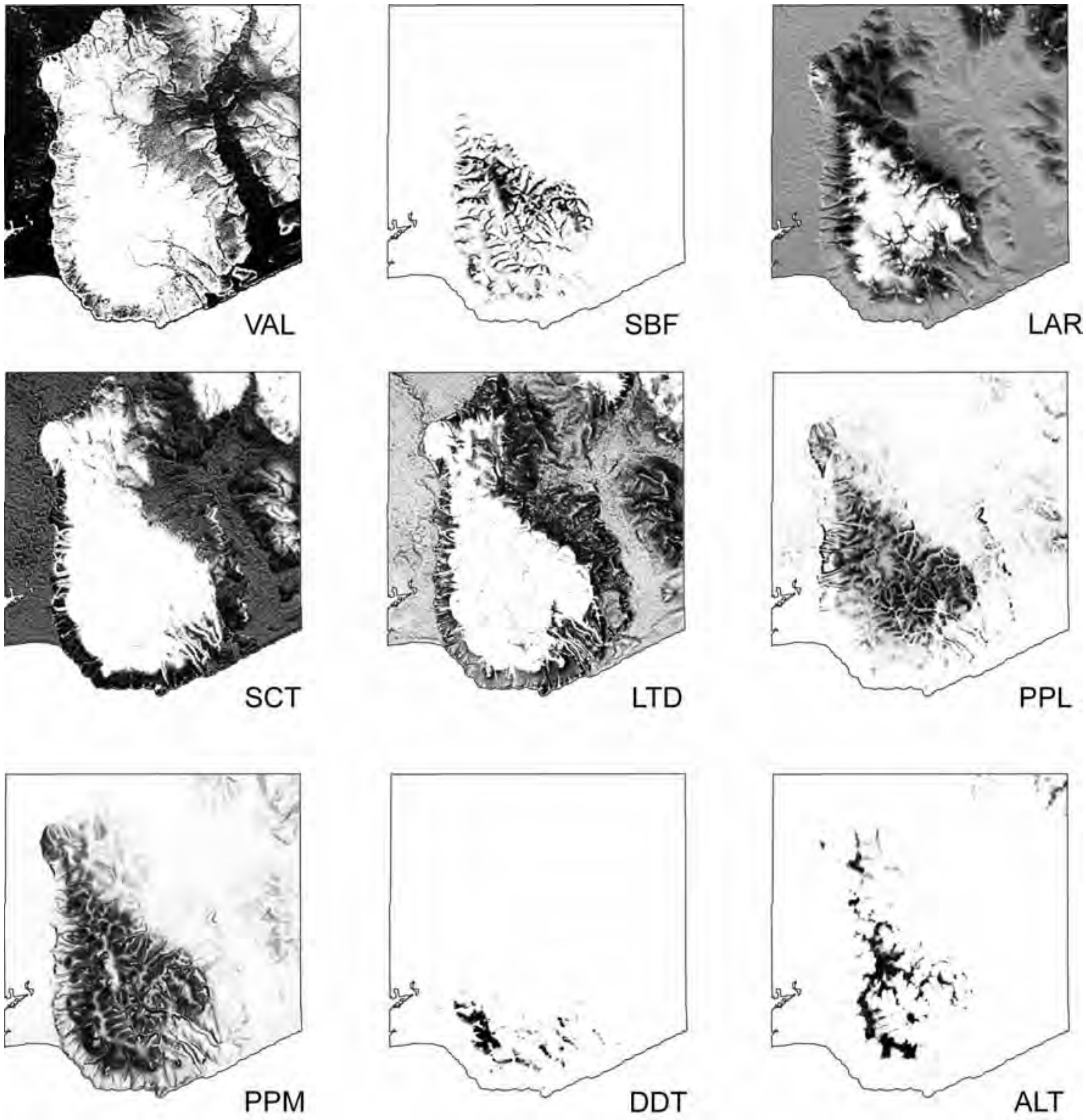

Figure 3 Spatial predictions for vegetation types of Lanzhinskie Mountains obtained using the selected models. Black shading indicates higher probability of occurrence. Legend: see table 2.

sites with relatively low values of the STI and SPI indices, not affected by wind (WindN, WindS), and with profile curvature (ProfC) values of almost zero. Therefore, there is no sharp boundary between these vegetation types (in fact the boundary is indented), and sometimes they form patterns caused by undulating slopes (Slope, glfSlope). Flat slopes are occupied by the dynamic forest-tundra complex, while wide level tops are more suitable for tundra.

On higher elevations, the dynamic forest-tundra complex changes to larch forest, which forms an altitudinal belt at mid-slope and occupies flat (ProfC values near zero), relatively flat gentle (slope value of 0-25%) and moderately insolated (Solin) slopes. In addition, larch forests may occur on sites characterized by negative values of 'ProfC' (i.e. in wide valleys) but are totally lacking on ridges (positive values of ProfC).

The mossy Siberian dwarf-pine thickets (of order Vaccinio-Pinetalia) occupy the upper parts of mountain slopes and wide saddles, which are characterized by high insolation (Solin), relatively higher moisture (TWI) and low values of SPI and STI. The lichen-rich dwarf-pine thickets (of order Loiseleurio-Vaccinietea) occupy steeper slopes and ridges.

Wide, flat mountain tops, characterized by small profile curvature (ProfC), near zero slope (Slope) and small values of the SPI and STI, appeared to be suitable for the shrubby alpine tundra of the order Loiseleurio-Vaccinietea. The model, however, overestimated the area for this type. The dry *Dryas* tundras (Carici-Kobresietea) occur on the upper parts of slopes, facing the sea (WindN, Dist).

Stone-birch forests (*Betula ermanii*) occur along narrow valleys (ProfC) and occupy moderately steep slopes (Slope) with high insolation (Solin).

Therefore, the map of potential vegetation reflects the altitudinal zonation and inter-zonal patterns of vegetation distribution satisfactorily. It should be noted, however, that contours of the actual vegetation may differ significantly from those predicted. For example, larch forests on the prediction map are shown only in the areas with highest

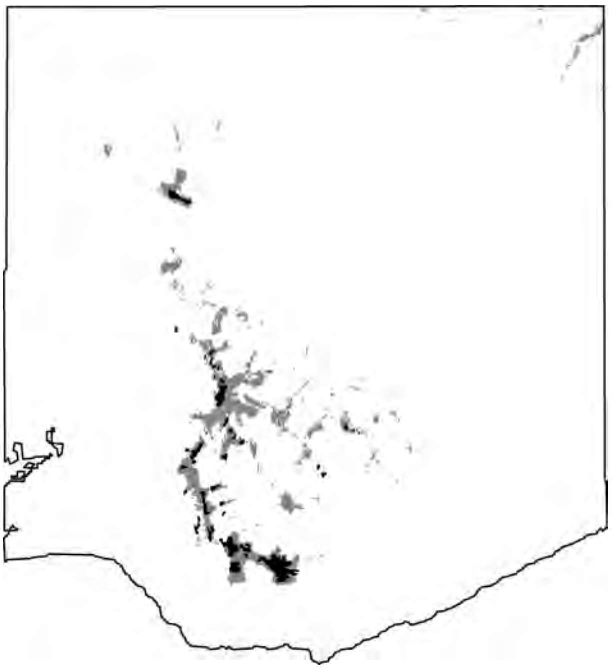

Figure 4 Comparison of spatial prediction (grey areas) and real distribution (black areas) of alpine tundra (ALT).

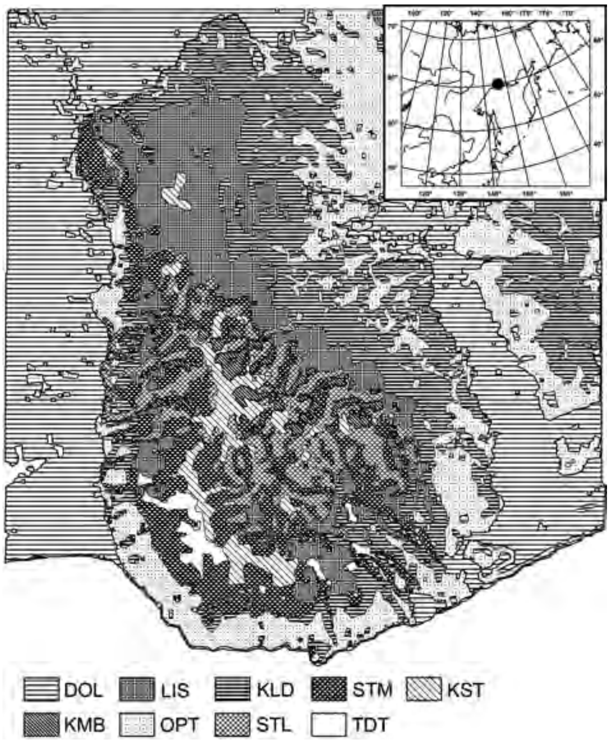

Figure 5 Map of the potential vegetation of Lanzhinskie Mountains based on spatial prediction of vegetation types. Legend: see table 2.

occurrence probability. One can assume that territory with occurrence probability of 50 % of the maximum values for these areas is also suitable enough for larch forests. If such territory is added, then the area of the larch forests is increased by 3 times (Fig. 6). The relative areas for different vegetation types, for 50 % probability, will be increased by about 2-2.5 times.

Comparing the actual and predicted occurrences of the larch forests shows that only 54% of all data points fall in the area with 100 % probability of larch-forest occurrence. Decreasing the probability threshold to 50 % increases this value to 84 %, which can be considered a much better result (Fig. 6). The same trend is characteristic for the other vegetation types (Fig. 7). The best prediction results, when 90 % of data points fall in the area with 100 % probability, were obtained for the dry *Dryas* tundra and the sedge-cottongrass tundra. This result could be expected for the dry *Dryas* tundra because it occurs within a narrow range of environmental conditions. For the other vegetation types, about 75 % of data points fall in the area with 100 % probability, and about 90 % of points fall in the area with 50 % probability.

DISCUSSION

Maggini et al. (2006) suggested five selection methods that can be used in the GRASP module: cross-selection, BRUTO, *F* test, AIC and BIC. The cross-selection method showed the best results in terms of model stability. Cross-selection in this study showed certain limitations when the total contribution by a particular variable to the model is too low (< 5% in linear predictor scale). Removing such variables does not decrease model stability significantly but, at the same time, does reduce model size dramatically. In order to achieve the best results for each new territory, it is probably necessary to test several methods of selection and choose the best one.

In this study, the distribution of 9 vegetation communities of the Lanzhynskie Mts. was modeled successfully using topographic predictors. Analysis of the model of potential vegetation allows us to address several points: 1) the relationships between environmental characteristics and plant communities; 2) relations of zonal and azonal vegetation complexes and the problem of modern refugia (Krestov et al. 2009); and 3) model limitations.

Relationships between environmental characteristics and plant communities

This study showed that most vegetation types in the area are controlled mainly by moisture regime (variables TWI, ProfC, Slope) and regimes of sediment transport and accumulation (SPI, STI, Slope). The relatively scant rainfall in the continental climate is distributed spatially by the relief elements. This creates a wide range of soil moisture regimes: from very dry, with a prolonged period of moisture deficit; to wet, with no moisture deficit during the growing season at all. Therefore, moisture appears to be a critical resource in this climatic region, and it is one of the differentiating factors for the vegetation. Sediment transport and accumulation controls the moisture content of the substrate and also regulates evapotranspiration. The vegetation on poorly drained, well aerated substrates on upper mountain slopes experiences significant moisture deficit, regardless of how much water comes with the rainfall. Also, sediment transport and accumulation depend on subsurface permafrost processes. Therefore, the distribution of vegetation communities is associated with ground-freezing processes, indirectly expressed by sediment transport.

Altitude above sea level restricts vegetation types to certain temperature ranges and regimes, which depend also on potential solar radiation. This mostly affects the stone-birch forests, as they are moisture-dependent ecosystems and occur only on the warmest sites in the area and in humid habitats sheltered from winter wind and frost. These conditions are found on south-facing, well insolated narrow valleys, where there is an accumulation of moisture and where deep snow protects the soil from severe frost in winter.

The intensity of solar radiation affects nearly all vegetation types of the Lanzhynskye Mts., although dense fog comes from the sea and may mediate solar intensity during the whole summer. The variables expressing generic landforms contributed only 1-5 % to the explanation of vegetation distribution in this area. This contrasts with the results of Yakovleva (2002, 2003), who found much greater contribution of geomorphological variables in a model of local vegetation cover in the temperate conifer-broadleaved deciduous forest zone of Eastern Asia. Such disagreement can be explained by the much stronger relationships between geomorphological characteristics and temperature regime, especially temperature inversions, within more temperate zones (Wardle 1985, Sarmiento 1986).

Thus, the vegetation pattern of the Lanzhynskye Mts. depends essentially on the moisture regime and the characteristics of sediment transport and accumulation. The only exception to this rule is the dry *Dryas* tundra, the distribution of which depends mostly on distance from the seashore (variable Dist) and wind regimes (variable WindN). Strong northern wind on the coast affects regimes of snow accumulation, drift and melting, and a ground-frost regime that leads to formation of a rubbly substrate, which is suitable for this vegetation type. In addition, fog often covers the sea-facing slopes and is a significant factor compensating for water deficit on the easily drained and aerated substrates.

Relations of zonal and azonal vegetation complexes and modern refugia

As several phytogeographical studies in Asia have shown (Qian et al. 2003, Krestov et al. 2009, 2010), much biodiversity is not related to zonal ecosystems (as defined in Pojar et al. 1987), which occupy extensive territories, but rather is concentrated on local sites characterized by certain local geomorphological, geochemical or climatic anomalies. The biota of such areas, as a rule, differs significantly from the regional (background) biota and may be characterized by high levels of endemism. This study allowed us to conclude that communities of *Betula ermanii* and *Alnus fruticosa*, dry *Dryas* tundras, and forest fragments of the riparian vegetation complex are strongly connected to azonal habitats, which are able to compensate for the regional deficit of several environmental resources, especially moisture and heat. The species compositions of these communities contrast with those of the zonal vegetation due to the presence of many endemic species and elements occurring here in certain isolation from their main areas of distribution.

Model limitations

Overall, the best results were obtained for communities that were rare in the samples. This was reported previously by Franklin (1998) for shrub species, by Guisan & Hofer (2003) and by Maggini et al. (2006). Reasons for this are probably related to their restricted niche breadth along particular environmental gradients, which are easier to capture in a model than are the wider niches of widespread species (Maggini et al. 2006).

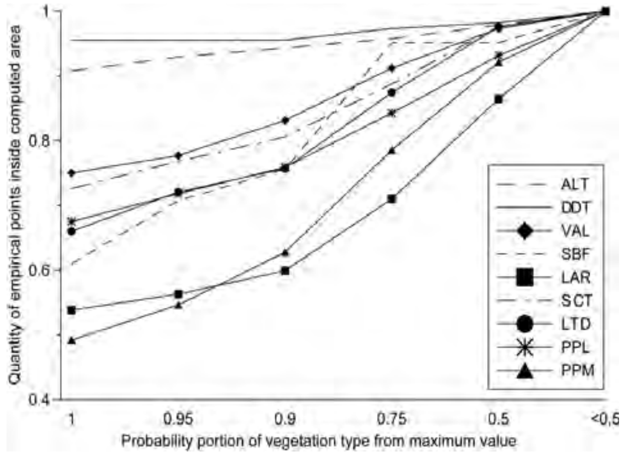

Figure 6 Growth of larch forest territory after addition of areas with 50 % probability of occurrence. (50 % from maximum value for each point). Darker areas – 100 % probability (100 % from maximum but not equals probability = 1), lighter areas – 50 % probability; b) empirical data points fall in areas of 100 % probability of occurrence (circles), 50 % probability (crosses) and outside these areas (triangles).

Our model overestimates the distribution areas for three vegetation types, namely VAL, SBF and ALT. The area of *Betula ermanii* forests is overestimated because of insufficient resolution of the DEM raster (90 m). As mentioned above, *Betula ermanii* forests occupy relatively small territories, most of which may fit into 1-2 raster pixels, which is not enough for localization of suitable environmental conditions. On the contrary, the shrubby tundras occupy larger areas, which can easily be recognized on the Landsat images. The tundra plants, however, are very sensitive even to minor changes in ecological regimes and occupy small depressions in the overall relief, making their detection again difficult at the present DEM resolution.

In the field and on the Landsat images, the riparian forest-meadow complex was registered in valleys only near rivers beds. The model, however, predicts occurrence of

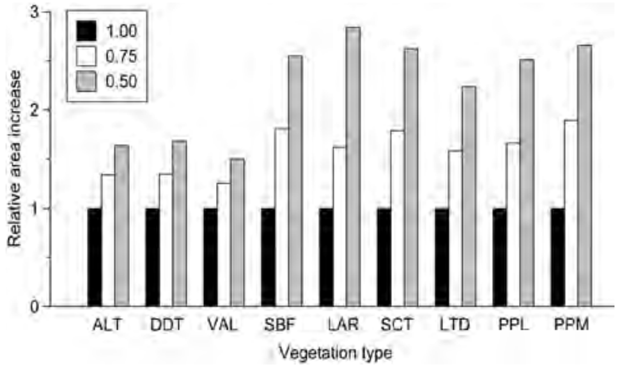

Figure 7 Number of the empirical data points fall in areas, which are occupied by communities of different vegetation types. Probability of occurrence varies from 100 % to 50 % from maximum value.

this complex with a high probability over the whole extent of the valleys. This cannot be considered a prediction error. Rivers drift continuously within broad valleys, smoothing the relief and leading to similar values of hydrological indices along the whole valley. Thus, in order to refine the position of riparian communities, additional variables such as distance from an actual riverbed may be required.

The map of the potential vegetation obtained in this study reflects the main patterns of vegetation distribution. About 35% of the empirical data points, however, appear outside the contours of the respective vegetation types. There are three possible reasons for this phenomenon.

First, the actual vegetation can be very fragmented into fine mosaics, but the 90m DEM with pixel areas of 8100 m^2 is not capable of showing the finer-scale variation. This is most significant for shrubby tundra, *Betula ermanii* forests, sedge-cottongrass tundras and dynamic vegetation complexes. In these cases, increasing the DEM raster resolution will probably improve the prognostic ability of the models.

Second, it is possible that several transitional gradients exist and that vegetation along these gradients may be classified into one of several types with similar probabilities. In this study such a gradient is indicated only between the larch forests and Siberian dwarf-pine thickets, with a gradual elevation increase. For other vegetation types, such gradients are poorly expressed, but such situations are rather usual for northern territories. For instance, the width of the boundary between larch forests and sedge-cottongrass tundra is less than one pixel of the Landsat image (14.5 m).

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