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Niche conservatism of *Eulophia alta*, a trans-Atlantic orchid species

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Abstract

The genus *Eulophia* embraces over 230 species distributed through the tropical and subtropical Africa, Asia, Australia and the Americas. In Neotropics it is represented by a sole species – *E. alta*. The aim of the presented study was to evaluate the difference between ecological niches occupied by American and African populations of this species based on the ecological niche modeling. The similarity between the glacial and present niches occupied by *E. alta* was calculated and the factors limiting the species occurrence were identified. Areas of seasonal tropical forest, tropical savanna and woodland served as refugia for the studied species during last glacial maximum and they were more widespread in Neotropics than in Africa. No significant niche shift after last glacial maximum was observed. The distribution of *E. alta* in its whole range is restricted mainly by temperature seasonality. The differences in the niches occupied by African and Neotropical populations of *E. alta* suggest preglacial disjunction of the species range and independent adaptation of both groups. Despite the significant range disjunction of *E. alta* the species is characterized by relatively high degree of niche conservatism.

Keywords: ecological niche modeling; last glacial maximum; Orchidaceae; trans-Atlantic disjunction

Introduction

The trans-Atlantic range disjunction is observed within about 110 angiosperm genera [1]. Despite over 40 years of biogeographical studies [2–4] the understanding of timing, direction and pattern of long-distance dispersal across the Atlantic is still very limited. Little is known also about the niche variation of the taxa characterized by remarkable distribution gap.

The niche conservatism of numerous organisms was recently intensively studied using ecological niche modeling (ENM) methods [5–7], but so far this analysis was not apply to evaluate niche variation of species exhibiting trans-Atlantic disjunction. Based on the incoming research results it is difficult to formulate any explicit principle about the tendency of such species to retain characteristics of their fundamental niche over time. The degree of niche conservatism varies among groups of species (small-ranged and specialist [6]) and it is related to the evolutionary history of each taxon [8]. While some authors [9] considered evolutionary and biogeographic patterns of species diversity as completely separated processes, the concept of niche conservatism offers a bridge between them [10–13]. Studies on ecological niche variation are particularly important to recognize fundamental distribution factors and evolutionary models of species characterized by the disjunctive range. While in some taxa the geographical discontinuity resulted in adaptive [14,15], other adjusted evolutionary stable strategy [16].

The object of our study was *Eulophia alta* (L.) Fawc. & Rendle, a sole representative of the genus in Neotropics where its range extends from USA (Florida) south to Argentina. Except Americas *E. alta* occurs in the Africa, from Senegal to Zimbabwe and it is assumed that it originates in the Old World where high specific diversity of the genus is observed. However, no clear evidence of this hypothesis was presented so far. *Eulophia alta* is terrestrial, large plant producing a subglobose, subterranean corm and loosely many-flowered, racemose inflorescence. The species is found in open areas, along roadsides and on cleared land reverting to bush lower montane forest, usually in heavy, moisture-retentive soils. Populations of *E. alta* were found in lowland and premontane areas, at the altitudes up to 1500 m. The main flower visitors and most effective pollinators of this species are anthophorid bees. Six Hymenopteran and two Lepidopteran families were observed visiting the flowers [17].

The aim of this study was to evaluate the similarity of the niches occupied by African and Neotropical populations of *E. alta* using ENM tools. Because adaptation to local climatic conditions is a significant force driving morphological evolution and speciation, the availability of the suitable niches of the studied species during last glacial maximum (LGM; 26 500–19 000 years ago) was evaluated to estimate the possible postglacial niche shift and geographical range changes of *E. alta*. In the studies on Orchidaceae the ENM was applied so far mainly in the research on invasive species [18,19] and

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a sole analysis [20] concerned the potential distribution of orchid during last glacial maximum.

Material and methods

Localities and georeferencing

The database of *E. alta* localities was prepared based on the examination of herbarium specimens deposited in herbaria AMES, BM, BR, COL, HUA, K, MO, NY, P, UGDA, VALLE, W, and WAG. Herbaria acronyms are cited according to "Index Herbariorum" [21]. To enlarge the dataset, the information obtained from the electronic database of the Missouri Botanical Garden (available at http://www.tropicos.org) was included in the analysis.

The georeferencing process followed Hijmans et al. [22] and only the localities, which could be precisely placed on the map were used in the study. The information about the latitude and longitude provided on the herbarium sheet labels were verified. If no geographic coordinates were indicated by the plant collector, they were assigned based on the data about the collection place. The Google Earth (v. 6.1.0.5001, Google Inc.) application was used to validate all gathered information.

In total 54 localities were included in the database (Fig. 1, Tab. 1), 8 African and 46 Neotropical, which is more than the minimum number of localities (>5) required by Maxent to obtain reliable predictions [23].

Fig. 1 Locations of *E. alta* used in the ecological niche modeling.

Maximum entropy analysis

The maximum entropy method implemented in Maxent version 3.3.2 [24–26] was used to create models of the distribution of the ecological niches of *E. alta*. Because Maxent is relatively robust against collinear variables [27,28], all available climatic factors (Tab. 2) in 2.5 arc-minutes developed by Hijmans et al. [29] as well as the altitudinal data were used as an input data. This was also justified by the insufficient data on habitat requirements of the studied species that could lead to premature exclusion of the correlated variables. The analogical bioclimatic data for the last glacial maximum period was mapped by Paleoclimate Modelling Intercomparison Project Phase II [30].

To assess high specificity of the modeling, the maximum iterations was set to 10 000 and convergence threshold to 0.00001. For each run 20% of the data were used to be set aside as test points [31]. The "random seed" option which provided random test partition and background subset for each run was applied. The run was performed as a bootstrap with 100 replicates, and the output was set to logistic. All operations on GIS data were carried out on ArcGis 9.3 (ESRI).

Niche similarity

The geographical overlap of the niches calculated based on two different datasets (African and Neotropical locations only) as well as the similarity of niches occupied by the populations from the New World and Africa were defined based on the test implemented in ENMTools application. The Schoener's D [32] and I [33] statistics were calculated. In Schoener's D statistic the local species density measures are compared with each other. "I" statistic is based on Hellinger distance and measures the ability of the model to estimate the true suitability of the habitat. Both metrics range from 0 (no similarity) to 1 (overlapping).

Results

Models evaluation

All repeated ecological niche models for the present time received high area under the curve (AUC) scores of 0.972–0.984 (Tab. 3) that indicate very high reliability of the analysis.

Bioclimatic limiting factors

The results of the niche modeling indicated three main bioclimatic variables limiting the distribution of suitable habitats for *E. alta*. The crucial factor is the temperature seasonality (bio4), which influenced significantly models of both African and Neotropical populations of the studies species. While the range of latter geographical group is also related with the amount of precipitation in the coldest quarter (bio19), the African plants are more dependent on the mean temperature of the coldest quarter (bio11). The estimates of relative contributions of the environmental variables to the Maxent model for both present time and LGM are presented in Tab. 4.

Potential glacial refugia

The model of habitats available in Neotropics during the LGM indicate few possible glacial refugia of *E. alta* (Fig. 2). In Mesoamerica the suitable niches were located in the Gulf of Honduras, Mosquitia lowlands, Mosquito Coast, Cordillera de Talamanca, the Darién Gap as well as in Jamaica. In South America the possible glacial refugia were located in the northern Andes, eastern pre-Andean highland and partially Amazon basin, Guiana Highlands as well as western Brazilian coast. The African refugia were much more limited and there were distributed in the northern Grain Coast and around the Gulf of Guinea. Less suitable habitats were located in the Zanzibar Archipelago and northern Madagascar. The areas determined for both, African and Neotropical populations,

Tab. 1 Localities of *Eulophia alta* used in ENM analysis.

Country	Latitude	Longitude	Collector and number	Institution
Angola	−9.553333333	16.3475	Mechow 344	W-R
Angola	9.132777778	14.77194444	Welwitsch 664	BM, K, W-R
Belize	16.99666667	−88.40694444	Percy H. Gentle 9262	MO
Belize	17.09944444	−88.32388889	William A. Schipp S-171	AMES, MO
Belize	−17.74166667	−63.2	Michael H. Nee 48842	NY
Bolivia	−14.75055556	−61.14361111	A. Carrión, M. Castro & V. Ayala 503	MO
Bolivia	−17.65	−63.16666667	Nur Ritter 2782	MO
Bolivia	−14.75055556	−61.14361111	A.M. Carrión, M. Castro & V. Ayala 503	MO, USZ
Cameroon	3.8	10.11666667	Sanford 5177	K
Cameroon	4.966666667	8.85	Thomas 2316	K, P, MO
Cameroon	18.83333333	−69.56666667	Thomas A. Zanoni & Milcíades M. Mejía 16316	MO
Caribbean	18.15	−77.23333333	Alwyn H. Gentry & Valerie Kapos 28306	MO
Caribbean	6.666666667	−74.86666667	Ricardo Callejas, Julio C. Betancur B. & Omar D. Escobar 9020	HUA
Central African Republic	6.394444444	21.59888889	Le Testu 4779	BM, K
Colombia	3.840277778	−76.89777778	Kolanowska 233	UGDA
Colombia	3.881111111	−76.33888889	Paz 1476	VALLE
Colombia	26.01386	−72.76	D. Cárdenas & R. López 6632	COL
Colombia	8.73	−83.4	Álvaro Fernández 401	CR
Costa Rica	8.74	−83.56	Gerardo Herrera Ch. 4558	CR
Costa Rica	−2.883333333	−78.35	B. Løjtnant & Ulf Molau 14510	AAU
Ecuador	−0.466666667	−76.91666667	L. Broder, Holm-Nielsen, Jaramillo J. & Coello F. 19607	MO
Ecuador	−0.466666667	−76.91666667	L.B. Holm-Nielsen & et al. 19607	AAU, MO
Ecuador	0.033333333	−77.38333333	Benjamin Øllgaard 99651	AAU
Ecuador	15.50833333	−87.45	John M. MacDougal, Paul R. House & Ramón Zúñiga 3276	MO
Gabon	0.408055556	9.4475	Le Testu 8669	BM
Guinea	10.62722222	−9.713611111	Adam 12539	K
Guyana	3.35	−59.56666667	Jansen-Jacobs, ter Welle, Gorts-van Rijn & Ek 670	K
Honduras	19.13944444	−89.32944444	Esteban M. Martínez S., Demetrio Alvarez M. & Santiago Ramírez A. 28639	MO
Ivory Coast	4.95	−6.066666667	de Wilde 358	K, WAG
Mexico	17.35	−100.4	Otto Nagel 2045	MO
Mexico	12.01666667	−85.15	Alfonso H. Heller s.n.	MO database
Nicaragua	9.168611111	−79.85194444	Thomas B. Croat 7788	MO
Panama	9.168611111	−79.85194444	Thomas B. Croat 12809	MO
Panama	9.169444444	−79.85416667	Thomas B. Croat 4391	MO
Panama	8.6	−80.13333333	Paul H. Allen 1988	MO
Panama	7.75	−77.66666667	Gordon McPherson 15038	MO
Panama	7.73	−80.87361111	Barry E. Hammel 4243	MO
Panama	9.100555556	−79.27777778	James A. Duke 5930	MO
Panama	9.266666667	−78.95	H.W. Churchill 3814	MO
Panama	9.266666667	−78.95	H.W. Churchill 3815	MO
Panama	8.875277778	−79.78777778	Paul H. Allen 2080	MO
Panama	9.365555556	−78.95	Gordon McPherson 11863	MO
Panama	9.3	−78.975	Greg C. de Nevers & Heraclio Herrera 4353	MO
Panama	−26.07611111	−56.85	Elsa M. Zardini 12678	MO, PY
Paraguay	−5.118888889	−78.32083333	Philip J. Barbour 4356	MO
Peru	−10.75	−74.38333333	D.N. Smith 6875	MO
Peru	−4.568055556	−78.19805556	Rodolfo Vásquez & et al. 24292	MO
Peru	−3.8	−73.41666667	Rodolfo Vásquez & Nestor Jaramillo 4953	MO
Peru	−3.746944444	−73.40861111	Rodolfo Vásquez & Rocío Rojas 22731	MO
Peru	−5.083333333	−73.83333333	Rodolfo Vásquez & Nestor Jaramillo 4804	MO
Peru	−11.91666667	−77.3	Percy Núñez V., J. Terborgh & et al. 14246	MO
Peru	−10.75	−74.38333333	David N. Smith 6875	MO
Peru	−5.866666667	−77.21666667	David N. Smith 5963	MO
Peru	−8.75	−75.08333333	David N. Smith & et al. 1187	MO

Tab. 2 Variables used in the modeling.

Code	Variable
bio1	Annual mean temperature
bio2	Mean diurnal range = mean of monthly (max temp − min temp)
bio3	Isothermality (bio2/bio7) × 100
bio4	Temperature seasonality (standard deviation × 100)
bio5	Max temperature of warmest month
bio6	Min temperature of coldest month
bio7	Temperature annual range (bio5 – bio6)
bio8	Mean temperature of wettest quarter
bio9	Mean temperature of driest quarter
bio10	Mean temperature of warmest quarter
bio11	Mean temperature of coldest quarter
bio12	Annual precipitation
bio13	Precipitation of wettest month
bio14	Precipitation of driest month
bio15	Precipitation seasonality (coefficient of variation)
bio16	Precipitation of wettest quarter
bio17	Precipitation of driest quarter
bio18	Precipitation of warmest quarter
bio19	Precipitation of coldest quarter
Alt	Altitude

Tab. 3 The AUC scores for each model created during the study with information on standard deviation values (*SD*).

	All locations	African locations only	Neotropical locations only
Present time	0.974 (*SD* = 0.005)	0.972 (*SD* = 0.012)	0.984 (*SD* = 0.004)
LGM	0.979 (*SD* = 0.005)	0.973 (*SD* = 0.012)	0.982 (*SD* = 0.005)

were covered during LGM with seasonal tropical forest as well as with tropical savanna and woodland [34].

Current potential range

The combined model (95% confidence level summary grids, Fig. 3a–c) of suitable habitats created using all available location data shows the general decreasing of the available niches in Neotropics and increasing of the African ones in comparison with the analogical models for LGM. In South America the highest concentration of proper niches is observed near the estuaries of Orinoco and Amazon rivers as well as in Cachimbo and dos Gradaús mountains. Less suitable areas are located in the lowland between Andes and Amazon basin. The African niches seem extended within the tropical Africa to east, but their general distribution did not change.

Niches overlap and identity

The calculated statistics confirm the geographical differences in the distribution of the suitable niches for African and Neotropical populations of *E. alta* ($D = 0.319$; $I = 0.587$), however the niche identity test indicate moderate similarity between the preferred habitats [$D = 0.657$ ($SD = 0.0609$); $I = 0.883$ ($SD = 0.036$)]. The overlap of models created for LGM and present time created based all known locations of *E. alta* gave results of $D = 0.800$ and $I = 0.947$.

Discussion

Ecological niches distribution vs. current range

The known geographical range of *E. alta* corresponds to the distribution of its suitable niches estimated in ENM analysis. The only areas where there are no proper niches for the studied species, according to the ecological model, and where the specimens of the studied orchid were found, are southern Florida and northern Cuba. The first region is significantly affected by non-native plants, which are naturalized from the horticultures, and it can be hypothesized that the ornamental usage of *E. alta* is the source of its North American populations [35]. The most probable reason of the occurrence of this orchid in Cuba is the migration of *E. alta* from other Caribbean islands. As it was shown in the previous studies the invasive populations may shift their niches to invade new areas [18,36]. As the Neotropical populations of *E. alta* often grow in disturbed, open areas, such as roadsides, their ecological amplitude is rather wide and it was confirmed in the ENM analysis. Hereby the chances of the North American populations to survive in habitats

Tab. 4 Relative contributions of the environmental variables to the Maxent models.

	African locations only		Neotropical locations only	
Present time	bio11 (46.5%)	bio4 (32.6%)	bio4 (35.5%)	bio19 (14%)
LGM	bio4 (36.9%)	bio11 (36.1%)	bio4 (35.5%)	bio19 (14.7%)

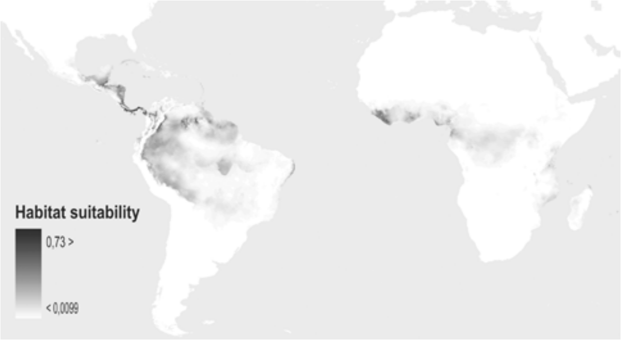

Fig. 2 The Maxent projections of suitable habitats of *E. alta* onto climatic conditions of LGM derived from Paleoclimate Modelling Intercomparison Project Phase II.

less suitable for the studied orchid are high. Unfortunately, the number of the known locations of *E. alta* in this region is not sufficient to conduct reliable analysis of their ecology and to verify the possible niche shift of those populations.

African vs. Neotropical niches

The differences between niches occupied by African and Neotropical populations of *E. alta* suggest preglacial disjunction of its range and gradual, independent adaptation of both groups to slightly different climatic conditions. This timing is indicated by the consistency of the glacial refugia of this orchid in Africa and Neotropics with its current distribution that confirm the postglacial migration of this orchids on different continents from the refugia defined in the ENM analysis. Nevertheless, the occurrence of adaptation processes requires confirmation in the genetic studies. Apparently the climate changes during LGM were more harmful for African populations and while *E. alta* is now common in Neotropics, its African potential range declined.

Niche conservatism

While numerous species shift their niches in response to warming climate after the last glacial maximum [37–39], the habitats suitable for *E. alta* seem to be rather stable as indicated by the niche overlap test for LGM and present time. Considering also the relative similarity of the suitable niches and limiting factors for *E. alta* populations from different continents the phylogenetic niche conservatism theory seems to be applicable to the evolution history or this species. Despite the significant geographical disjunction of *E. alta* a high degree of its fundamental niche conservatism was found. This is also implied by the morphological uniformity of species representatives that suggest lack of substantial, abrupt adaptation to distinct habitat conditions.

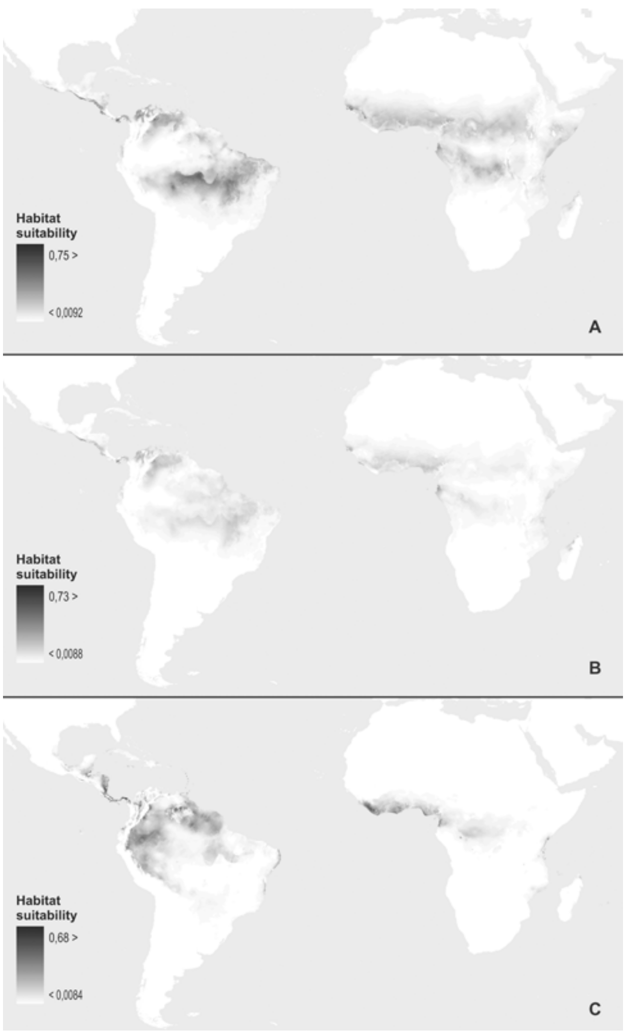

Fig. 3 The Maxent projections of suitable habitats of *E. alta* based on all localities (**a**), African localities only (**b**), Neotropical localities only (**c**).

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Authors' contributions

The following declarations about authors' contributions to the research have been made: research designing, conducting experiments, writing the manuscript (except "Introduction" section), appendices and figures preparation: MK; location database preparation, herbarium specimens examination, taxonomic information on the study object, writing the manuscript ("Introduction" section): DLS.

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