Acta Societatis Botanicorum Poloniae
Journal homepage: pbsociety.org.pl/journals/index.php/asbp
SHORT COMMUNICATION Received: 2013.02.21 Accepted: 2013.09.09 Published electronically: 2012.09.11 Acta Soc Bot Pol 82(3):225–230 DOI: 10.5586/asbp.2013.024

Glacial refugia and migration routes of the Neotropical genus *Trizeuxis* (Orchidaceae)

Marta Kolanowska*
Department of Plant Taxonomy and Nature Conservation, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland

Abstract

The morphology and anatomy of the monotypic genus *Trizeuxis* make this taxon almost impossible to recognize in fossil material and hereby difficult object of historical geographic studies. To estimate the distribution of potential refugia during the last glacial maximum and migration routes for *Trizeuxis* the ecological niche modeling was performed. The potential niche modeling was done using maximum entropy method implemented in Maxent application based on the species presence-only observations. As input data climatic variables and the digital elevation model were used. Two models of suitable glacial habitats distribution were prepared – for the studied species and for its host. The compiled map of the suitable habitats distribution of *T. falcata* and *P. guajava* during the last glacial maximum (LGM) indicate two possible refugia for the studied orchid genus. The first one was located in the Madre de Dios region and the other one in the Mosquito Coast. The models suggest the existence of two migration routes of *Trizeuxis* species. The results indicate that the ecological niche modeling (ENM) is a useful tool for analyzing not only the possible past distribution of the species, but may be also applied to determine the migration routes of the organisms not found in the fossil material.

Keywords: ecological niche modeling, habitats, last glacial maximum, Neotropics, phorophyte

Introduction

John Lindley described orchid genus *Trizeuxis* in 1821 [1] based on its conduplicate leaves, small, non-resupinate flowers arranged in the paniculate inflorescence with 3-lobed lip parallel to gynostemium and excavate stigma. In the same paper Lindley provided the description of *Trizeuxis falcata* L. In 1922 Schlechter described second species of the genus, *T. andina*, based on the specimen characterized by the lip difficult to expand with short and thick gynostemium [2], but those small differences observed in just one specimen cited by the author were recognized by taxonomists as an infraspecific variation of *T. falcata* [3].

The genus is a representative of oncidioid orchids, which classification is one of the most intractable group within Orchidaceae. The scientists do not agree about the taxonomic affinity of the genus. Based mostly on vegetative and floral characters Dressler and Dodson [4] classified *Trizeuxis* in the subtribe Oncidiinae Benth. within Epidendreae Lindley. Due to the similarity in the gynostemium structure, mainly the anther, pollinarium and rostellum morphology Szlachetko [5] placed *Trizeuxis* along with inter alia *Hybochilus* Schltr., *Leochilus* Knowl. & Westc. and *Sanderella* Kuntze in Leochilinae Szlach. within Oncidieae Pfitzer. The results of the molecular research [6] indicated the *Trizeuxis* and other oncidioid orchids should be embedded in Cymbidieae, however in this analysis, the generic topology of this taxon remains unsolved.

Despite the confusion about the tribal and subtribal classification of *Trizeuxis*, its generic separateness is not in doubt. The geographical range of this monotypic genus ranges from Costa Rica south to Peru and eastern Brazil (Fig. 1). Its flowers are one of the smallest within oncidioid orchids reaching just 2–3 mm in diameter. Plants grow usually as twig-epiphytes in humid areas between 200 and 1000 m a.s.l., often on *Psidium* L. (Myrtaceae) trees. The pollinators of this genus are trigonid bees [7] although also self-pollination has been reported [8].

The small plant size, the leaves with sclerenchyma present exclusively on the phloem side, the thin epidermal cells of the stem [9] and the capsule containing abundant dust-like seeds make *Trizeuxis* almost impossible to recognize in fossil material and hereby difficult object of historical geographic studies.

While recently the ecological niche modeling (ENM) technique was successfully used to estimate the glacial refugia of numerous organisms in various regions of the world [10–15], so far it was not applied in reconstruction of possible past distribution of any orchid species.

In this paper ENM was applied to estimate the distribution of potential refugia during the last glacial maximum (26500 and 19000–20000 years ago [16]) and migration routes for *Trizeuxis*

* Email: martakolanowska@wp.pl
Handling Editor: Zygmunt Kącki

This is an Open Access digital version of the article distributed under the terms of the Creative Commons Attribution 3.0 License (creativecommons.org/licenses/by/3.0/), which permits redistribution, commercial and non-commercial, provided that the article is properly cited.

© The Author(s) 2013 Published by Polish Botanical Society

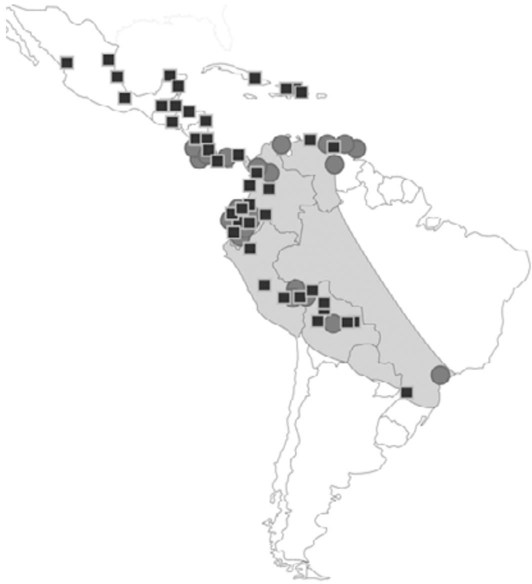

Fig. 1 Current geographical range of *T. falcata* and locations used in the modeling (*T. falcata* – circles; *P. guajava* – squares).

which is now one of the widest distributed Neotropical orchid. The estimation of the migration routes of *T. falcata* is based on the niche conservatism hypothesis [17]. The tendency of species and clades to retain their niches and related ecological traits over time was recently intensively studied by botanists and zoologists [18–20] and as suggested by Crisp et al. [21] species capacity to adapt to new biomes is limited. Based on the comparison of the current distribution of the studied species and the location of their possible glacial refugia, the most probable migration routes were determined.

Since the models created in MaxEnt are mapping the fundamental niche of the studied taxon, i.e. provide information about all regions characterized by the climatic conditions suitable for the analyzed species, the actual range of the species is most often narrower than suggested by the ENM. To restrict the actual distribution of the possible glacial refugia of *T. falcata* and hereby to precisely estimate its migration routes, the model was compared with the glacial localities of its host – *Psidium guajava* L. While no studies on the nature of the relationship between studied orchid and its phorophytes were conducted, *P. guajava* is referred as the main host of *T. falcata* [22] and it is often mentioned on the labels of herbarium specimens. Populations of *T. falcata* were reported also growing on *Citrus* L. and *Coffea* L., however those plants were not included in the presented study since they are not native for Neotropics and they could not serve as hosts for *T. falcata* during last glacial maximum (LGM).

Material and methods

The potential niche modeling was done using maximum entropy method implemented in Maxent version 3.3.2 [23–25] based on the species presence-only observations. The list of *T. falcata* and *P. guajava* localities was compiled based on the examination of the herbarium specimens stored in AMES, HUA, JAUM, MO and UGDA. Those data were complemented by the information from the electronic database of Missouri Botanical Garden (available at http://www.tropicos.org). Only the localities, which could be precisely placed on the map, were used in the ecological niche modeling. In total 36 *T. falcata* and 70 *P. guajava* locations were used (Tab. 1, Fig. 1), which is more than the minimum number of localities (>5) required to obtain reliable predictions in Maxent application [26].

Tab. 1 List of localities used in the modeling.

Species	Country	Latitude	Longitude	Collector(s)	Coll. number	Institution(s)
Trizeuxis falcata	Bolivia	−16.383	−63.458	Roberto Vásquez & J. Rivero	633	LPB
Trizeuxis falcata	Bolivia	−17.014	−64.833	Nur Ritter	3837	MO
Trizeuxis falcata	Colombia	6.867	−76.05	James L. Zarucchi, Julio C. Betancur B. & al.	5116	HUA, MO
Trizeuxis falcata	Colombia	5.883	−74.85	Álvaro Cogollo P.	4475	JAUM, MO
Trizeuxis falcata	Costa Rica	8.45	−84.817	Paul H. Allen	6736	SEL
Trizeuxis falcata	Costa Rica	10.09	−84.37	Alberto M. Brenes	10	AMES
Trizeuxis falcata	Costa Rica	9.99	−85.15	Carroll W. Dodge	7762	AMES
Trizeuxis falcata	Costa Rica	9.17	−83.42	Kathleen Utley	5940	DUKE
Trizeuxis falcata	Costa Rica	9.2	−83.44	Louis O. Williams	19263	US
Trizeuxis falcata	Costa Rica	8.95	−83.46	Paul H. Allen	5494	US
Trizeuxis falcata	Costa Rica	8.53	−83.3	G. Cufodontis	154	AMES
Trizeuxis falcata	Costa Rica	9.37	−83.69	Louis O. Williams & Terua P. Williams	24445	F
Trizeuxis falcata	Costa Rica	9.347	−83.658	Alexander F. Skutch	4231	MO
Trizeuxis falcata	Costa Rica	9.372	−83.653	Alexander F. Skutch	4806	MO, US
Trizeuxis falcata	Costa Rica	9.69	−84.36	Juan Francisco Morales	3860	CR, MO
Trizeuxis falcata	Ecuador	0.45	−79.54	Calaway H. Dodson, Carl A. Luer, Jane Luer, P. Morgan, H. Morgan, Janet Kuhn & A. Perry	10429	SEL
Trizeuxis falcata	Ecuador	−0.583	−79.367	Calaway H. Dodson	5181	MO, SEL
Trizeuxis falcata	Ecuador	−1.267	−79.7	Calaway H. Dodson & al.	8817	GUAY, MO, SEL
Trizeuxis falcata	Ecuador	−0.644	−77.792	Carl A. Luer & al.	467	SEL
Trizeuxis falcata	Ecuador	−1.067	−77.6	Carlos E. Cerón & Carlos Iguago	5630	MO, QCNE
Trizeuxis falcata	Ecuador	−0.644	−77.792	Carl A. Luer & R. Kent	512	SEL
Trizeuxis falcata	Ecuador	−0.067	−77.617	Walter A. Palacios	1711	MO
Trizeuxis falcata	Ecuador	−1.583	−77.333	Galo A. Tipaz, Severo Espinoza & César Gualinga	524	MO, QCNE

© The Author(s) 2013 Published by Polish Botanical Society

Tab. 1 *(continued)*

Species	Country	Latitude	Longitude	Collector(s)	Coll. number	Institution(s)
Trizeuxis falcata	Ecuador	−4.065	−78.946	Calaway H. Dodson, Carl A. Luer, Jane Luer, P. Morgan, H. Morgan, A. Perry & Janet Kuhn	10543	SEL
Trizeuxis falcata	Panama	8.103	−80.982	Charles W. Powell	3526	AMES
Trizeuxis falcata	Peru	−13.217	−70.75	Percy Núñez V.	13945	MO
Trizeuxis falcata	Peru	−12.117	−70.967	Percy Núñez V.	6899	MO
Trizeuxis falcata	Peru	−12.54	−69.05	Percy Núñez V., C. Cárdenas, W. Duellman & B. Buchanan	10020	MO
Trizeuxis falcata	Peru	−12.54	−69.05	Percy Núñez V., C. Cárdenas, W. Duellman & B. Buchanan	9980	MO
Trizeuxis falcata	Venezuela	9.255	−60.95	Julian A. Steyermark, Ronald L. Liesner & Francisco Delascio C.	114952	MO
Trizeuxis falcata	Venezuela	10.083	−66.017	Gerrit Davidse & Angel C. González	13722	MO
Trizeuxis falcata	Venezuela	10.417	−63.1	Julian A. Steyermark, Ronald L. Liesner & Victor Carreño E.	121365	MO
Trizeuxis falcata	Venezuela	7	−64.917	Fernández	5198	MO
Trizeuxis falcata	Venezuela	9.817	−72.817	Gerrit Davidse, Angel C. González & R.A. León	18368	MO
Trizeuxis falcata	Ecuador	−2.646	−78.205	Mark Whitten, M. Mites, N. Williams, A. Embree, A. Hirtz, D. Cordier	1608	FLAS
Trizeuxis falcata	Colombia	−3.302	76.535	Kolanowska	101	UGDA
Psidium guajava	Argentina	−27.167	−54.333	Maria E. Múlgura de Romero, Sandra S. Aliscioni, Manuel J. Belgrano & M.A. Romero	3024	JUA, SI
Psidium guajava	Argentina	−27.267	−55.583	Osvaldo Morrone, Norma B. Deginani & Ana M. Cialdella	1095	MO, SI
Psidium guajava	Bolivia	−14.5	−66.617	José Balderrama	162	LPB, MO
Psidium guajava	Bolivia	−15.15	−67.517	David N. Smith, Valentín García & Edgar García	13935	MO
Psidium guajava	Bolivia	−16.167	−67.75	Otto Buchtien	3856	GH
Psidium guajava	Bolivia	−16.596	−61.866	R. Guillén V. & R.A. Medina	2605	MO, USZ
Psidium guajava	Bolivia	−16.667	−62.533	Mario Saldías P., James Johnson & Blas García	1202	MO
Psidium guajava	Caribbean	18.767	−68.783	Mejia	11109	MO
Psidium guajava	Caribbean	18.867	−70.717	Milcíades M. Mejía & Thomas A. Zanoni	7668	MO
Psidium guajava	Caribbean	20.267	−76.6	R. Dechamps, R. Carreras & M. Hendrickx	12393	MO
Psidium guajava	Colombia	3.551	−74.719	LLanos	1137	MO
Psidium guajava	Colombia	3.883	−77.167	Donald Faber-Langendoen & Enrique Rentería A.	931	MO
Psidium guajava	Colombia	6.25	−75.567	Ramiro Fonnegra G. & Francisco J. Roldán	4938	HUA, MO
Psidium guajava	Costa Rica	8.650	−83.436	Luis Acosta, Víctor H. Ramírez, Gerardo Soto & Geovanny Sancho	1289	MO
Psidium guajava	Costa Rica	9.77	−84.53	Quírico Jiménez M., Alwyn H. Gentry, Barry E. Hammel, Michael H. Grayum, Nelson Zamora V. & Curso de Botánica	1271	CR, MO
Psidium guajava	Costa Rica	9.975	−84.092	Sandy Salas	126	INB, MO
Psidium guajava	Costa Rica	10.044	−83.617	Juan Francisco Morales	11209	
Psidium guajava	Costa Rica	10.167	−84.474	Austin Smith	41145	MO
Psidium guajava	Costa Rica	10.198	−83.857	Luis Diego Vargas	3395	
Psidium guajava	Costa Rica	10.3	−84.8	William A. Haber	10046	CR
Psidium guajava	Costa Rica	10.33	−84.84	Ronaq Khan, M.C. Tebbs & A. Roy Vickery	1114	MO
Psidium guajava	Costa Rica	10.431	−84.004	Margaret K. Whitson	313	DUKE
Psidium guajava	Costa Rica	10.45	−83.78	Kelly Keefe	10	MO
Psidium guajava	Costa Rica	10.632	−85.426	Carroll W. Dodge & W.S. Thomas	6627	MO
Psidium guajava	Ecuador	0.067	−78.667	Carlos E. Cerón	12983	MO
Psidium guajava	Ecuador	−0.217	−76.433	Gabriela Moya & Nelson Miranda-Moyano	566	QCNE
Psidium guajava	Ecuador	−0.483	−78.983	Juan Carlos Valenzuela, W. Gallegos & J. Andino	353	QCNE
Psidium guajava	Ecuador	−0.374	−76.552	Diego Reyes & Lorena Carrillo	439	MO, QCNE
Psidium guajava	Ecuador	0.383	−78.1	S. Bibiana Cuamacás	10	MO
Psidium guajava	Ecuador	0.433	−77.867	Carlos E. Cerón	7031	MO
Psidium guajava	Ecuador	0.433	−77.983	Carlos E. Cerón & Mery Montesdeoca	12551	MO
Psidium guajava	Ecuador	0.433	−76.517	Diego Reyes & Lorena Carrillo	501	MO, QCNE
Psidium guajava	Ecuador	−0.495	−76.077	Diego Reyes & Lorena Carrillo	782	MO, QCNE
Psidium guajava	Ecuador	0.517	−78.2	Carlos E. Cerón	11343	MO
Psidium guajava	Ecuador	−0.624	−75.859	Lorena Carrillo & Diego Reyes	770	MO, QCNE
Psidium guajava	Ecuador	−0.663	−76.667	Diego Naranjo & Bolívar Freire	442	MO, QCNE
Psidium guajava	Ecuador	0.833	−78.133	Daniel Rubio & Carlos Quelal	1524	MO
Psidium guajava	Ecuador	−0.95	−77.917	Angela Herrera & W. Guerrero	148	QCNE
Psidium guajava	Ecuador	−1.033	−80.683	Miranda	40	MO, QCNE
Psidium guajava	Ecuador	1.117	−78.617	W. Scott Hoover, Lorentzen, R. A. & Gelpi, P.	4141	MO
Psidium guajava	Ecuador	−1.25	−80.633	Miranda	86	MO, QCNE

© The Author(s) 2013 Published by Polish Botanical Society

Tab. 1 *(continued)*

Species	Country	Latitude	Longitude	Collector(s)	Coll. number	Institution(s)
Psidium guajava	Ecuador	−2.167	−78.2	Carlos E. Cerón	10513	MO
Psidium guajava	Ecuador	−2.4	−78.967	Carlos E. Cerón	17547	
Psidium guajava	Ecuador	−3.25	−79.6	Carlos E. Cerón	20363	MO
Psidium guajava	Ecuador	−13.667	−79.317	Carlos E. Cerón	13303	MO
Psidium guajava	El Salvador	−13.717	−89.25	R. Cruz	218	MO
Psidium guajava	El Salvador	13.717	−89.2	Paul C. Standley	19410	MO
Psidium guajava	El Salvador	13.814	−89.301	Alex K. Monro, Karen J. Sidwell, J. P. Dominguez & R. Díaz	2902	MO
Psidium guajava	Guatemala	15.471	−90.371	H. von Türckheim	II 987	MO
Psidium guajava	Guatemala	15.840	−91.212	Jorge Jiménez & Rony Rodas	432	MO, USCG
Psidium guajava	Honduras	15.769	−84.539	Cirilo H. Nelson & Mauro Hernández M.	923	MO
Psidium guajava	Honduras	15.772	−86.707	Héctor A. Martínez C.	191	MO
Psidium guajava	Honduras	15.798	−87.969	Carlos A. Cerrato B.	143	MO
Psidium guajava	Honduras	15.919	−85.938	Sandra Carolina Cerna	127	MO
Psidium guajava	Honduras	15.958	−85.908	Janice G. Saunders	292	MO
Psidium guajava	Mexico	17.75	−96.5	Ricardo López L.	72	MO
Psidium guajava	Mexico	19.43	−88.1	E. Ucán Ek	4039	MO
Psidium guajava	Mexico	20.163	−97.546	Thorsten Krömer	3020	MO
Psidium guajava	Mexico	20.3	−89.43	Guillermo Ibarra Manríquez & J.J. Flores M.	4072	MO
Psidium guajava	Mexico	22.267	−104.633	Pedro Tenorio L. & Gabriel Flores F.	16187	MO
Psidium guajava	Mexico	22.867	−99.117	Claudia González, L. Hernández & S. Rodríguez	s.n.	MO
Psidium guajava	Panama	8.333	−81.212	Gene A. Sullivan	270	MO
Psidium guajava	Panama	8.767	−82.433	Michael H. Nee	10644	MO
Psidium guajava	Panama	9.275	−79.314	Walter H. Lewis, Bruce MacBryde & R. Solís	2305	MO
Psidium guajava	Peru	−5.3	−78	Rodolfo Vásquez & al.	25958	MO
Psidium guajava	Peru	−10.673	−75.525	S. Vilca	516	AMAZ, HUT, MO, MOL, USM
Psidium guajava	Peru	−12.447	−72.501	Efrain Suclli	2489	CUZ, MO, USM
Psidium guajava	Peru	−12.583	−69.083	Alwyn H. Gentry	68965	MO
Psidium guajava	Peru	−12.965	−72.658	Jim Farfán, Yesenia Vizcardo & V. Chama	508	AMAZ, CUZ, HUT, MO, USM
Psidium guajava	Venezuela	10.833	−69.117	Ronald L. Liesner, Angel C. González & Robert C. Wingfield	7772	MO

As input data 19 climatic variables in 2.5 arc minutes (±21.62 km^2 at the equator) developed by Hijmans et al. [27] as well as the digital elevation model were used (Tab. 2). The bioclimatic data for the LGM were developed and mapped by Paleoclimate Modeling Intercomparison Project Phase II [28] based on an atmosphere-ocean coupled general circulation model (AOGCM). To assess maximum specificity of the modeling, the maximum iterations was set to 10000 and convergence threshold to 0.00001, therefore forcing the program not to finish before threshold was reached. For each run 20% of the data were used to be set-aside as test points [29]. 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).

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

Results

The potential glacial range of *Trizeuxis*

The most suitable *Trizeuxis* habitats in Central America included Sierra Madre de Chiapas, the Caribbean Mosquito Coast and the coast of Gulf of Nicoya. The potential South American localities of *T. falcata* were distributed on both sides

© The Author(s) 2013 Published by Polish Botanical Society

of the Andes and it included the lower west-Andean region in Ecuador, as well as Colombian eastern slopes of the Eastern Cordillera. The southernmost suitable niches were located on the east of the Andean range in southern Peru (Fig. 2).

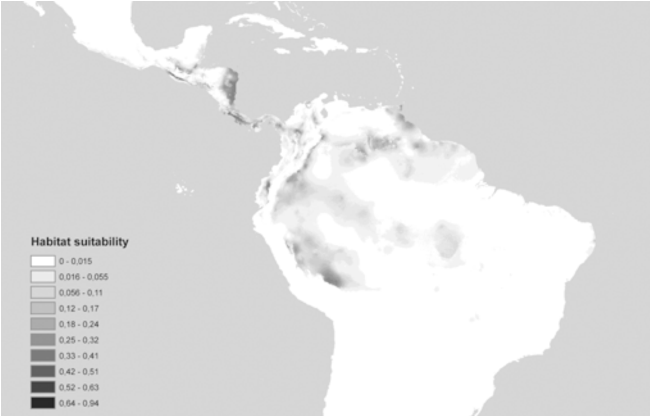

Fig. 2 Distribution of the suitable habitats of *T. falcata* during the LGM.

Glacial refugia

The compiled map of the suitable habitats distribution of *T. falcata* and *P. guajava* during the LGM indicate just two regions, which could be the possible refugia for the studied orchid genus (Fig. 3). The first one was located in the Madre de Dios region in southeastern Peru corresponded to the temperate semi-desert (sparse shrubland or grassland) characterized by the low vegetation cover (less than 2% above 80 cm off the ground and 4–25% total above ground [30].

Fig. 3 Compiled map of potential glacial refugia of *T. falcata* (black) and *P. guajava* (gray). The marked regions correspond to the habitats with over 0.5 suitability for the studied taxa.

The second probable refugium was located in the Mosquito Coast lowlands corresponded to the tropical savanna and woodland characterized by 60–20% cover of vegetation during the LGM [30].

Possible migration routes

The determined glacial refugia of *T. falcata* suggest the existence of two possible migration routes of this species. From the Mosquito Coast *Trizeuxis* could reach the northern South America and Eastern Venezuela as well as migrated south along the coast to Peru. Peruvian region of Madre de Dios was probably the origin of populations currently found along the western Andean slope as well as the southernmost population from Santa Catarina (Fig. 4).

Fig. 4 Possible migration routes of *T. falcata*.

Discussion and conclusion

The presented study indicate that the ecological niche modeling is a useful tool for analyzing not only the possible past distribution of the species [13], but may be also applied to estimate the migration routes of the organisms which are not found in the fossil material.

The only unresolved glacial refugium of *T. falcata* was indicated by modeling as located in the lowland areas of Suriname and Atlantic coast of Venezuela. While both the orchid and its host currently occur in this area, no suitable habitats of *P. guajava* were located in this region according to the conducted analysis. Possibly due to the lack of the main phorophyte of *T. falcata* in this region, the orchid was forced to adapt to different host, however this situation can be only speculated.

So far no studies regarding glacial refugia of Neotropical orchid species have been conducted, mainly due to the lack of the fossil remains, which is the result of their anatomical structure and ecology. Most of the Orchidaceae representatives occur in the tropical, humid and warm areas characterized by the rapid decomposition of the dead matter. Moreover, the structure of the tiny, dust-like seeds produced by orchids as a lack of a well-defined endosperm, more or less transparent, papery seed coat than loosely surrounds the small, undifferentiated embryo [31,32] make this plant group undetectable in the palynological procedures.

While the ENM was successively applied to reconstruction of the glacial refugia of numerous plant species, the result of those analyses should be interpreted with caution because the models show only the distribution of the fundamental climatic niches of the studied taxa and the realized niche is usually modified by the ecological interactions with other organisms.

The presented study, apart from the determination of the distribution of the suitable habitats of *T. falcata* during the LGM, indicate the importance of the comprehensive data selection in studies based on presence-only observations, especially information about the factors limiting the occurrence of the studied taxon (e.g. host or competitive organisms, pollinators).

Acknowledgments

The curators and staff of the cited herbaria are thanked for their kind hospitality and assistance during visits. I am grateful to Professor Dariusz Szlachetko for his valuable comments on the manuscript. The paper is a part of the project supported with the Ministry of Science and Higher Education grant (N N304 043939).

© The Author(s) 2013 Published by Polish Botanical Society

References

1. Lindley J. *Trizeuxis falcata*. Collect Bot. 1821;1:t.2.
2. Schlechter R. Orchideenfloren der Suedamerikanischen Kordillerenstaaten, V. Bolivia. Feddes Repert Beih. 1922;10:52.
3. Schweinfurth C. Orchidaceae, Orchids of Peru. Fieldiana Bot. 1960;30(3):784–785.
4. Dressler RL, Dodson CH. Classification and phylogeny in the Orchidaceae. Ann Mo Bot Gard. 1960;47:25–68.
5. Szlachetko DL. Systema Orchidalium. Fragm Flor Geobot. 1995;3 suppl:1–152.
6. Neubig KM, Whitten WM, Williams NH, Blanco MA, Endara L, Burleigh JG, et al. Generic recircumscriptions of Oncidiinae (Orchidaceae: Cymbidieae) based on maximum likelihood analysis of combined DNA datasets. Bot J Linn Soc. 2012;168(2):117–146. http://dx.doi.org/10.1111/j.1095-8339.2011.01194.x
7. Dodson CH, Dodson PM. *Trizeuxis falcata*. In: Dodson CH, editor. Orchids of Ecuador. Sarasota: The Marie Selby Botanical Gardens; 1980. p. 350. [vol 1(4)].
8. Van der Cingel NA. An atlas of Orchid pollination: America, Africa, Asia and Australia. Rotterdam: A.A. Balkema Publishers; 2001.
9. Stern WL, Carlsward BS. Comparative vegetative anatomy and systematics of the Oncidiinae (Maxillarieae, Orchidaceae). Bot J Linn Soc. 2006;152(1):91–107. http://dx.doi.org/10.1111/j.1095-8339.2006.00548.x
10. Carstens BC, Richards CL. Integrating coalescent and ecological niche modeling in comparative phylogeography. Evolution. 2007;61(6):1439–1454. http://dx.doi.org/10.1111/j.1558-5646.2007.00117.x
11. Marske KA, Leschen RAB, Buckley TR. Reconciling phylogeography and ecological niche models for New Zealand beetles: looking beyond glacial refugia. Mol Phylogenet Evol. 2011;59(1):89–102. http://dx.doi.org/10.1016/j.ympev.2011.01.005
12. Peterson AT, Nyári AS. Ecological niche conservatism and Pleistocene refugia in the Thrush-like Mourner, *Schiffornis* sp., in the neotropics. Evolution. 2008;62(1):173–183. http://dx.doi.org/10.1111/j.1558-5646.2007.00258.x
13. Waltari E, Hijmans RJ, Peterson AT, Nyári AS, Perkins SL, Guralnick RP. Locating pleistocene refugia: comparing phylogeographic and ecological niche model predictions. PLoS ONE. 2007;2(6):e563. http://dx.doi.org/10.1371/journal.pone.0000563
14. Provan J, Bennett KD. Phylogeographic insights into cryptic glacial refugia. Trends Ecol Evol. 2008;23(10):564–571. http://dx.doi.org/10.1016/j.tree.2008.06.010
15. Svenning JC, Normand S, Kageyama M. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. J Ecol. 2008;96(6):1117–1127. http://dx.doi.org/10.1111/j.1365-2745.2008.01422.x
16. Clark PU, Dyke AS, Shakun JD, Carlson AE, Clark J, Wohlfarth B, et al. The last glacial maximum. Science. 2009;325(5941):710–714. http://dx.doi.org/10.1126/science.1172873
17. Harvey PH, Pagel MD. The comparative method in evolutionary biology. Oxford: Oxford University Press; 1991.
18. Prinzing A, Durka W, Klotz S, Brandl R. The niche of higher plants: evidence for phylogenetic conservatism. Proc Biol Sci. 2001;268(1483):2383–2389. http://dx.doi.org/10.1098/rspb.2001.1801
19. Cooper N, Freckleton RP, Jetz W. Phylogenetic conservatism of environmental niches in mammals. Proc Biol Sci. 2011;278(1716):2384–2391. http://dx.doi.org/10.1098/rspb.2010.2207
20. Lavergne S, Evans MEK, Burfield IJ, Jiguet F, Thuiller W. Are species' responses to global change predicted by past niche evolution? Phil Trans R Soc Lond B. 2013;368(1610):20120091. http://dx.doi.org/10.1098/rstb.2012.0091
21. Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, McGlone MS, et al. Phylogenetic biome conservatism on a global scale. Nature. 2009;458(7239):754–756. http://dx.doi.org/10.1038/nature07764
22. Pridgeon AM, Cribb P, Chase MW, Rasmussen FN. Genera Orchidacearum. Volume 4: Epidendroideae. Oxford: Oxford University Press; 2005.
23. Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. A statistical explanation of MaxEnt for ecologists. Divers Distrib. 2011;17(1):43–57. http://dx.doi.org/10.1111/j.1472-4642.2010.00725.x
24. Phillips SJ, Dudík M, Schapire RE. A maximum entropy approach to species distribution modeling. In: Proceedings of the twenty-first international conference on Machine learning. New York NY: ACM; 2004. p. 655–662.
25. Phillips SJ, Anderson RP, Schapire RE. Maximum entropy modeling of species geographic distributions. Ecol Model. 2006;190(3–4):231–259. http://dx.doi.org/10.1016/j.ecolmodel.2005.03.026
26. Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr. 2007;34(1):102–117. http://dx.doi.org/10.1111/j.1365-2699.2006.01594.x
27. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int J Clim. 2005;25(15):1965–1978. http://dx.doi.org/10.1002/joc.1276
28. Braconnot P, Otto-Bliesner B, Harrison S, Joussaume S, Peterchmitt JY, Abe-Ouchi A, et al. Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum. Part 1: experiments and large-scale features. Clim. 2007;3(2):261–277. http://dx.doi.org/10.5194/cp-3-261-2007
29. Urbina-Cardona JN, Loyola RD. Applying niche-based models to predict endangered-hylid potential distributions: are neotropical protected areas effective enough. Trop Conserv Sci. 2008;1(4):417–445.
30. Olson JS, Watts JA, Allison LJ, United States Dept of Energy Office of Basic Energy Sciences Carbon Dioxide Research Division, Oak Ridge National Laboratory, Union Carbide Corporation, et al. Carbon in live vegetation of major world ecosystems. Washington DC: U.S. Department of Energy; 1983.
31. Arditti J. Fundamentals of orchid biology. New York NY: Wiley; 1992.
32. Yam TW, Yeung EC, Ye XL, Arditti J. Orchid embryos. In: Kull T, Arditti J, editors. Orchid biology VIII – reviews and perspectives. Dordrecht: Kluwer Academic Publishers; 2002. p. 287–385.

© The Author(s) 2013 Published by Polish Botanical Society