Aspects of Orchidaceae distribution in Costa Rica and northwestern South America: a study on similarity with emphasis on the Amazonian Region

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ABSTRACT - (Aspects of Orchidaceae distribution in Costa Rica and northwestern South America: a study on similarity with emphasis on the Amazonian Region). The purpose of this study was to compare the floristic composition of Orchidaceae among different areas of Costa Rica and northwestern South America, aiming to answer the following questions: 1) Is the variation in the species composition among the study areas better explained by physical features, geographical closeness, or potential endemism centers? 2) Does the floristic similarity decay with geographical distance? We selected 11 surveys conducted in South America and two in Central America (Costa Rica). Cluster analysis was conducted using the software MVSP. The result was a split pattern between Amazonian and non-Amazonian floristic compositions. The environmental conditions analyzed appear to be important factors in explaining the orchid composition of areas outside the Amazon basin. The Amazonian group is environmentally very uniform, but floristically very distinct, and no physical features were determinant of the internal segregation into two subgroups. Geographic closeness has no influence on the species composition of the areas, and historical factors may explain the pattern observed.

Keywords: Biogeography, Brazil, Colombia, Costa Rica, Neotropics, Venezuela

Introduction

Orchidaceae is one of the most diverse families of angiosperms with ca. 25,500 species (Dressler 2005) and 800 genera (Dressler 1993). Orchids are widely distributed (Christenson 2004), although their diversity center is in the tropics, especially in the Indo-Malayan region and Neotropics (Dressler 1993), in which we highlight Brazil, Colombia, Ecuador and Peru as the richest countries in Orchidaceae species (Dressler 1981). The family is also very well represented in the Brazilian Atlantic Forest (Stehmann et al. 2009) as well as in the Amazon Forest (Ribeiro 1999, Funk & Hollowell 2007).

The homogeneous seed wind-dispersal mechanism in the family, turn the dispersion process completely independent of animals, and it makes orchids a good case for distribution studies. The distribution patterns may be explained by ecological, geographical or historical factors (Trejo-Torres & Ackerman 2001),

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and it is not linked to animal distribution such as birds or mammals species.

Northwestern South America is characterized by a large diversity of ecosystems, among which are the Amazon forest, the Amazon Cerrado (Campinaras or Lavrados), the Tepui vegetation, the Páramos, the Chocó and the Llanos (Daly & Mitchell 2000). The Amazon Forest is the largest plant formation in the area, located in the Amazon river basin, and comprises mainly lowland forests (Ab’Sáber 2006). The large area of evergreen moist forest mistakenly suggests homogeneous vegetation. However, up to now it is known that it is a mosaic of ecosystems and includes several centers of endemism (Silva et al. 2005), with islands of open vegetation (Daly & Mitchell 2000).

Studies with vertebrates (Haffer & Prance 2001), butterflies (Hall & Harvey 2002), and woody plants (Prance 1982) have suggested the occurrence of distinct centers of endemism within the Amazon Forest. However, herbaceous and epiphytic species have never been used to test this biogeographic hypothesis.

Therefore, the present study was aimed at comparing the floristic composition of Orchidaceae among different areas of Costa Rica and northwestern South America in order to answer the questions: 1) Is the variation in the species composition among the studies areas better explained by physical features (elevation, precipitation, temperature, presence of rock outcrops and vegetation), geographical closeness, or potential endemism centers? 2) Does the floristic similarity decay with geographical distance?

Material and methods

Distribution data - Surveys already published or in press focused on Orchidaceae and conducted in the area of interest were selected for the analysis (table 1, figure 1). The main selection criterion was the accuracy of taxonomic identification of orchids. Consequently, we selected 11 areas from northwestern South America, and two from Central America (Costa Rica). This study avoided the inclusion of online data available from herbarium collections due to the usual problems with taxonomic identification. It often compromises wide studies in biogeography, conservation and phylogeny (Kury et al. 2006, Iganci & Morim 2012).

The number of available surveys included in our selection criteria is small, and there are significant differences between the sizes of the studied areas, these limitations make preliminary the conclusions of this study. We recognize that these factors could interfere in the analysis, however this study provides the first data about distribution of orchids in northwestern South America and Costa Rica by using current knowledge of the local flora. The increase in the number of areas could lead to more effective results regarding the floristic similarities between Central and South America.

Taxonomic Adjustments - In recent years profound taxonomic changes have been proposed for Orchidaceae, especially related to generic circumscription. Due to the different times of publication of the surveys selected for this study, they followed different taxonomic classifications. Thus, prior to performing any analysis, a careful updating of the names used for each survey selected was mandatory.

Generally speaking, for this study, Pleurothallidinae are treated according to Pridgeon & Chase (2001); Gomesa R. Br. includes some species of Oncidium Sw. according to Chase et al. (2009); Maxillaria Ruiz & Pav. is segregated according to Blanco et al. (2007); Scaphyglottis Poepp. & Endl. is considered under Dressler et al.’s (2004) circumscription; and Trichocentrum Poepp. & Endl. is considered according to Braem (1993), Pupulin (1995) and Christenson (1999).

Synonyms and valid species names were standardized according to The Plant List database.

Study Areas - The areas chosen (13) are located in the Neotropics. Two of them are in Central America (Costa Rica), the others in South America. Three of the South American areas are outside the limits of the Amazon forest: the Chocó, on the Pacific coast of Colombia, and two areas near the Venezuelan Caribbean Coast (figure 1).

The Amazon Basin combines eight selected areas which are distributed in Brazil (seven) and French Guyana (one). Based upon the Centers of Endemism published by Silva et al. (2005), those areas can be placed in four of these centers - Inambari (IEC), Guyana (GEC), Xingú (XEC) and Belém (BEC).

The selected areas include a large variation in altitude, ranging from lowland forests (Ilha do Combu, 10 m mid-elev.) to highland forests (Chocó, 1,400 m mid-elev.). Furthermore, they include open vegetation such as Llanos in Venezuela, Campinaranas in Brazil, and also dense forest.

Data Analysis - A database of species consisting of a binary (presence × absence) matrix based on the thirteen surveys previously selected was built.
Table 1. Analysed areas, with country, geographical coordinates, number of orchid species, and reference.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Area name</th>
<th>Country</th>
<th>Geographic Coordinates</th>
<th>Species number</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACB</td>
<td>Estado do Acre</td>
<td>Brazil</td>
<td>10°07' S and 69°21' W</td>
<td>55</td>
<td>Christenson, 2008</td>
</tr>
<tr>
<td>AND</td>
<td>Serra das Andorinhas</td>
<td>Brazil</td>
<td>06°10' S and 48°35' W</td>
<td>69</td>
<td>Atzingen et al., 1996</td>
</tr>
<tr>
<td>CaRB</td>
<td>Serra de Carajás</td>
<td>Brazil</td>
<td>05°54' S and 48°25' W</td>
<td>98</td>
<td>Silveira et al., 1995</td>
</tr>
<tr>
<td>CAXB</td>
<td>Flona Caxiquanã</td>
<td>Brazil</td>
<td>01°42' S and 51°31' W</td>
<td>33</td>
<td>Koch et al., 2014</td>
</tr>
<tr>
<td>COB</td>
<td>Ilha do Combu</td>
<td>Brazil</td>
<td>01°25' S and 48°25' W</td>
<td>40</td>
<td>Cardoso et al., 1996</td>
</tr>
<tr>
<td>CHC</td>
<td>Departamento do Chocó</td>
<td>Colombia</td>
<td>05°29’ N and 77°10’ W</td>
<td>76</td>
<td>Gutiérrez &amp; Mosquera, 2006</td>
</tr>
<tr>
<td>CUV</td>
<td>Serrania de La Cuchila</td>
<td>Venezuela</td>
<td>10°07’ N and 63°33’ W</td>
<td>47</td>
<td>Leopardi, 2010</td>
</tr>
<tr>
<td>DUB</td>
<td>Reserva Ducke</td>
<td>Brazil</td>
<td>03°00’ S and 59°52’ W</td>
<td>68</td>
<td>Ribeiro, 1999</td>
</tr>
<tr>
<td>QUC</td>
<td>Parque Nacional Manuel</td>
<td>Costa Rica</td>
<td>9°21’ N and 84°06’ W</td>
<td>39</td>
<td>Pupulin 1998</td>
</tr>
<tr>
<td>SFG</td>
<td>Departamento de Saul</td>
<td>French Guyana</td>
<td>03°30’ N and 53°28’ W</td>
<td>122</td>
<td>Christenson, 1997</td>
</tr>
<tr>
<td>SUV</td>
<td>Estado do Sucre</td>
<td>Venezuela</td>
<td>10°38’ N and 63°02’ W</td>
<td>121</td>
<td>Leopardi &amp; Cumana, 2008</td>
</tr>
<tr>
<td>VIB</td>
<td>Parque Nacional do Viruá</td>
<td>Brazil</td>
<td>01°42’ N and 61°10’ W</td>
<td>65</td>
<td>Pessoa, 2013</td>
</tr>
</tbody>
</table>

The relationship among the biological variable richness and mid-elevation, average temperature, vegetation and precipitation of each study site was analyzed according to Generalized Linear Models (GLM) (McCulloch & Searle 2001) generated in the program Statistica 7.0 (StatSoft 2004). The GLMs test for a series of relationships between the dependent and independent variables and manage the data using link functions and exponential family (e.g., normal, Poisson or binomial) distributions (Baldwin and Bradfield 2007, Bolker et al. 2008).

Response variables were transformed to improve the linearity and homogeneity of the variance, so that the GLMs could be applied based on a normal distribution in some situations. Thus, the values of the mid-elevation and precipitation variables were transformed into Log10 to obtain normality of the data and homogeneity of variances. In all cases, values of $p \leq 0.05$ were considered significant.

A cluster analysis was conducted to compare similarities in species composition among the study areas, quantified with the Jaccard index (Legendre & Legendre 1998) using UPGMA (Unweighted Pair-Group Method using Arithmetic Averages) as a clustering algorithm (Sneth & Sokal 1973) according to MVSP 3.1 (multivariate statistical package program) (Kovach 2000). This type of analysis is suitable for the presence-absence data available in this study, and the Jaccard index determines the proportion of species shared by a pair of sites in relation to the total number of species present in these sites.

The Jaccard indices and geographical distances among sites were evaluated through the application of a simple linear regression, performed by using the Statistica 7.0 (StatSoft 2004). The regression analysis was performed to test the hypothesis that species similarity decays with geographical distance since environmental conditions are always spatially auto-correlated, so that nearby sites tend to be more similar in their environmental conditions than distant sites (Legendre 1993).

In order to analyze the variation of species composition per area related to environmental variables (mid-elevation, average temperature, vegetation, precipitation and rock outcrop), we used the Canonical Correspondence Analysis (CCA), a multivariate technique that evaluates the patterns of co-variation among groups of species and a series of site variables (Ter Braak 1987). The CCA was conducted on species composition-environmental variables matrices using the software MVSP 3.1 (Kovach 2000).

Whenever necessary, the data were transformed to meet the assumptions of normality and heterogeneity of variances. Therefore, the values of the mid-elevation and precipitation variables were transformed into Log10 to obtain normality of the data and homogeneity of variances. In all cases, values of $p \leq 0.05$ were considered significant.

Results

From the total number of species (525) included in the analysis, 185 (35%) were shared by at least two
areas, and about 65% were restricted to a single area. Few species (14, about 2.7%) were widely distributed and found in at least half of the areas included in the present study.

The total complement of species belong to 153 genera, the most representative ones being *Epidendrum* L. (54 spp.), *Habenaria* Willd. (18 spp.), *Catasetum* Rich ex Kunth (14 spp.), and *Sobralia* Ruiz & Pav. (12 spp.). Nevertheless, 61 genera were represented by only one species.

Furthermore, *Campylocentrum micranthum* (Lindl.) Rolfe, *Dimerandra emarginata* (G. Mey.) Hoehne, *Epidendrum nocturnum* Jacq., *E. strobiliferum* Rchb.f. and *Rodriguezia lanceolata* Ruiz & Pav. were the most frequent species in the analyzed lists as they have been found in around 70% of the areas.

Based on the GLMs test, mid-elevation could explain the variation of richness ($F = 6.05$ and $p = 0.04$) (figure 2). Conversely, the independent variables average temperature ($F = 3.26$ and $p = 0.11$), vegetation ($F = 1.02$ and $p = 0.40$), and precipitation ($F = 1.51$ and $p = 0.25$) did not generate any significant effect on the richness values.

The cluster analysis results showed a split pattern between the Amazonian and extra-Amazonian orchid diversity composition (figures 3-4). The areas located in the Amazon Basin emerge together as a group with about 10% similarity basis, reaching a maximum of 38% between Serra de Carajás (CarB) and Serra das Andorinhas (AND) (both located in the State of Pará, Brazil).

Extra-Amazonian areas are arranged in three different groups. The first one consists of areas from Costa Rica, the second one is formed by a single area (Chocó, Colombia), and the third one combines Venezuelan areas.

The linear regression test (LRT) shows that the geographic closeness of the studied areas has no influence on the species composition arrangement ($R^2 = -0.06$ and $p = 0.56$).

According to the canonic correspondence analysis (CCA), the environmental physical features analyzed were partially determinant of the species composition variation among the studied areas. The analysis shows five significant axes, with cumulative percentage of explanation for 46.7% of the observed variation. It suggests that part of the variation in species composition found is actually affected by other factors which were not included in the present analysis.

Figure 5 shows the results from the two first axes (eigenvalues: Axis 1 = 0.73 and Axis 2 = 0.67; Canonic correlation: Axis 1 = 0.99 and Axis 2 = 0.98). In the first axis, the extra-Amazonian group formed by Chocó (CHC) (Colombia), Barra Honda (BHC) and Quepos (QUC) (both located in Costa Rica) shared similar species composition. This could be explained by shared physical attributes such as vegetation, temperature, precipitation and elevation. The Amazonian group and the Venezuelan areas are probably affected by the occurrence of rock outcrops. Moreover, the observation of Axis 2 shows that the distinction of the two cited groups is possibly related to the variation in elevation and precipitation.

**Discussion**

The present study showed that the South American areas studied are related concerning the species composition of orchids. It contradicts previous theories by Cracraft & Prum (1988), Amorim & Pires (1996), Morrone (2004, 2006) and Quijano-Abril et al. (2006) who pointed out the close relationship between the species composition of the Chocó (CHC) (Colombia) and continental Central America (Darién province). The Andean uplift could be the main reason to segregate the northern South America lowland forest, whereas Pacific areas such as the Chocó remain in contact with the Central America and the Caribbean.

The wind-dispersal mechanism of the Orchidaceae diaspora would provide the possibility of long-distance dispersal (Gentry & Dodson 1987). Cross-Andean dispersal has been also observed in Euglossini bees (Dick et al. 2004), a group of insects strictly related to orchid pollination (Van der Pijl & Dodson 1966). Both factors could explain the disjunct pattern (Chocó-Amazon) found in our analysis.

The two areas of the Venezuelan Caribbean Coast included in this study represent a distinct bio-geographic province called the Coastal Cordillera by Daly & Michell (2000) or Venezuelan Coast by Morrone (2006). They emerge as an independent group, but related with the Amazon cluster. Both areas, based on Pennington et al. (2000), share a distinct physiognomy from the Amazon, as coastal vegetation, highland humid forest and seasonal forests. The CCA also showed that rock outcrops (axis 2) would be the main physical feature to distinguish them from the Amazon portion. Trejo-Torres & Ackerman (2001) also suggested a close floristic relationship among the Venezuelan coast and Caribbean areas (Lesser Antilles). It helps to understand the position of the group in the cluster.

The dry Llanos vegetation between the Venezuelan coast and the wet Amazon forest (Pennington et al. 2000) could represent an ecological barrier to dispersal for several species. However, it seems to be less effective than the Andes, since the Venezuelan areas used in this study emerge as a sister group of the Amazon areas with around 5% similarity.

The Amazonian area group shares similar environmental conditions as shown by the CCA analysis, with no physical variables to explain the two subgroups formed in the cluster analysis (figures 3, 4).

The first subgroup includes the two areas in the Inambari Center of Endemism [Reserva Ducke (DUB) and Acre, (ACB) and Saül (SFG) (French Guyana), which is part of the Guyana Center of Endemism (GEC). Although the two Inambari areas have a large geographical distance (LRT: geographical closeness is not relevant), the huge similarity found in the composition of orchid diversity may be explained by historical factors [Endemism Center, according Silva et al. (2005)]. Nonetheless, there is no clear explanation available from the methods used to explain the occurrence of Saül (SFG) in this group. Even so, a similar distribution pattern between areas located in the Center of Endemism of Inambari and Guyana was found for some species of frogs (Garda & Cannatella 2007).

The other Amazon subgroup is formed by two areas included in the Center of Endemism Guyana (CEG) [Viruá (VIB) and Caxiuanã (CaxB)] and three areas in the Center of Endemism Xingi (CEX) [Ilha do Combu (COB), Serra de Carajás (CARB) and Serra das Andorinhas (AND)], some of them located on the border of the Center of Endemism Belém (CEB).

The analysis corroborates in part with the biogeographic hypothesis presented by Cracraft & Prum (1988) and Amorim (2001) for the Amazon Basin, in which such authors proposed historical relationships among the three Centers of Endemism (GEC, XEC and BEC) based on cladistic biogeography. However, Viruá (VIB) and Caxiuanã (CaxB), despite belonging to the same Center of Endemism as assumed by Silva et al. (2005), do not emerge together. This
Conclusions

The analysis of the study areas showed the scarce knowledge we have regarding the orchid floristic composition in the western and central-eastern Amazon. We encourage further taxonomic studies in these regions.

The environmental conditions analyzed appear to be important factors to explain the orchid composition of areas outside the Amazon basin. Mid-elevation, precipitation, vegetation and average temperature distinguish the Costa Rican areas and the Chocó (Colombia), whereas the presence of rock outcrops distinguishes the Venezuelan areas.

The Amazonian group is environmentally very uniform, and no physical features were determinant of the internal segregation into two subgroups. Historical factors, which are the theory basis of the Endemism Centers, may explain the pattern shown.

Geographic closeness has no influence on the species composition arrangement for the areas studied. It could be explained by the large number of endemic species in the family, and the low percentage (2.7%) of widely distributed species. Based on the analysis overview, the pattern observed is similar to several other studies with invertebrates, vertebrates and plants.

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Literature cited


