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RESEARCH ARTICLE

PHENOMENON OF VICARIANCE IN THE ACANTHACEAE FAMILY IN CENTRAL AFRICA (DR CONGO, RWANDA AND BURUNDI)

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ABSTRACT

This study was aimed to analyze the cases of vicariance from Acanthaceae family using the phytogeographic systems of Robyns (1948) for Central Africa and White (1979, 1986) for tropical Africa. It covered 9181 samples (48 genus, 310 species) harvested in DR Congo, Rwanda and Burundi. A geographic information system was used to produce the potential distribution maps. The uniformity of sampling density was assessed by the Pielou evenness index. It was observed that some of the phytogeographic territories have been explored more than others. Consequently, maps reflecting the potential distribution, based on harvesting locations and environmental variables, were produced to better determine the ecological niches of the species and the cases of vicariance. Two types of vicariance have been determined at the genus and subspecies level. For the phytogeographic territories of Robyns, 27 ecological vicariance pairs and six pairs of geographic vicariance were identified at the genus level; at the level of the subspecies, six pairs of ecological vicariance and two pairs of geographic vicariance were observed. Concerning the phytogeographic territories of White, 43 pairs of ecological vicariance and seven pairs of geographic vicariance were observed at the genus level; five ecological vicariance pairs and a pair of geographic vicariance were identified at the subspecies level. This study also revealed two zones of speciation that were the refuge zones and, consequently, as areas of high biological diversity (hotspots). The observations mentioned above are not only important from a phytogeographic point of view (speciation zones), but also for conservation policies development.

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INTRODUCTION

The discovery of common factors of distribution to several species, the delineation of biogeographically diversified regions, the search for biogeographic boundaries and the study of abundance - distribution relationships have led to the emergence of theories and numerous models in biogeography (Mac Arthur and Wilson 1967, Levins 1969, Hanski 1982, Brown 1984), paleogeography, systematics and evolution studies (Croizat 1981, Wiley 1988, Szalay and Bock 1991, Wilson 1991). The determination of the distribution areas of the species is imperative in systematics and phytosociology. Firstly, at the systematic level, the determination of the plants is based on the characteristics of roots, stems, leaves, flowers and fruits (Mangenot 1973) as well as on its distribution area. Then, on the floristic and autoecological level, it is assumed that the area of a species is a characteristic of this species in the same way as its morphological characteristics (Ozenda 1982). Finally, from a synecological point of view, spatio-temporal factors are among of the individualization of plant communities bases (Habiyaremye 1997). Several studies of phytogeographic divisions based on physiognomic and endemic arguments have been carried out in Central Africa on several botanical families such as the Acanthaceae family. This family was largely harvested from 1888 to 2001 by about 427

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collectors in DR Congo, Rwanda and Burundi. Most of these samples are stored in the herbarium of the National Botanical Garden of Belgium (BR) where they have recently undergone a systematic review (Champluvier 1991, 1997, 1998). Previous analyzes of the spatial distribution of Acanthaceae in relation to the phytogeographic systems of Robyns (1948) and White (1979, 1986) have shown different distribution patterns (Koffi et al. 2007). Some species of this family have a wide spatial distribution, while others are subordinate to certain phytogeographic territories. The heterogeneity of the degree of exploration has been demonstrated by several researchers (Hepper 1979, Bürger 2001, Koffi 2005, Küper et al., 2006). The evolution of species and the replacement of one taxon by another can take place in time and space. This explains the reason why species that are very similar in their phylogeny may occupy similar or different areas: the species are then called vicariant. Several types of vicariances are distinguished according to the relations existing between the entities composing the vicarious couples: geographic vicariance (Rothmaler 1950, Contandriopoulos 1981, Rameau et al. 1989); Physiognomic vicariance (Contandriopoulos 1981); ecological vicariance (Vierhapper 1919, Rothmaler 1950, Rameau et al. 1989); edaphic vicariance (Rothmaler 1950); physiological vicariance (Vierhapper 1919, Polunin 1967, Contandriopoulos 1981); climatic vicariance (Gounot 1969); chorological vicariance (Kiriakoff 1965, Contandriopoulos 1981) and fossil vicariance (Bernardi 1986). The objective of this work was to study cases of Acanthaceae vicariance in Central Africa. A general floristic analysis was carried out in order to assess the degree of exploration from the sampling and then to examine the different cases of pairs of species that respond to the notion of vicariance in the Acanthaceae family harvested in Central Africa, through the phytogeographic territories defined by Robyns (1948) and White (1979, 40.1986) presented in Figure 1.

MATERIALS AND METHODS

Study area

This study covered the entire DR Congo, Rwanda and Burundi, designated here as "Central Africa". This territory is straddling the equatorial domain and the subequatorial domain. The equatorial domain is characterized by an average annual temperature varying between 25 and 27 ° C and by an average annual precipitation ranging from 2000 to 3000 mm with the absence of a dry season. The subequatorial domain is characterized by a significant variation of the climatic conditions, with one or sometimes two well-marked dry seasons. At the physiographic level, the landscape of the study area consists essentially of staggered plateaux, forming a kind of bead around the lower central basin (Sys 1960), at altitudes ranging from less than 200 m (littoral zone) to over 1500 m in the eastern mountains. In this area there are high plateaus rising steadily to the southeast and reach 1000 to 2000 m above sea level in the east, on the Rift valley edges (Van Chi Bonnardel 1973).In the volcanic massif of Virunga, the altitudes reach 4500 m; they even exceed 5000 m in the Ruwenzori massif. The vegetation of Central Africa is made up of forests and savannas. The Sudanese savannas that extend into the Guinean-Congolese / Sudanese transition zone occupy the northern part of the territory. In the central, area of the equatorial forest, there are gaps that mark the presence of the included savannas. In the southern part, savannah vegetation arrives in the Guinean-Congolese / Zambezian transition zone. In some places, dense dry forests (muhulu), clear forests (tropophile forests or miombo) and mangroves (Mayaux et al. 1999).

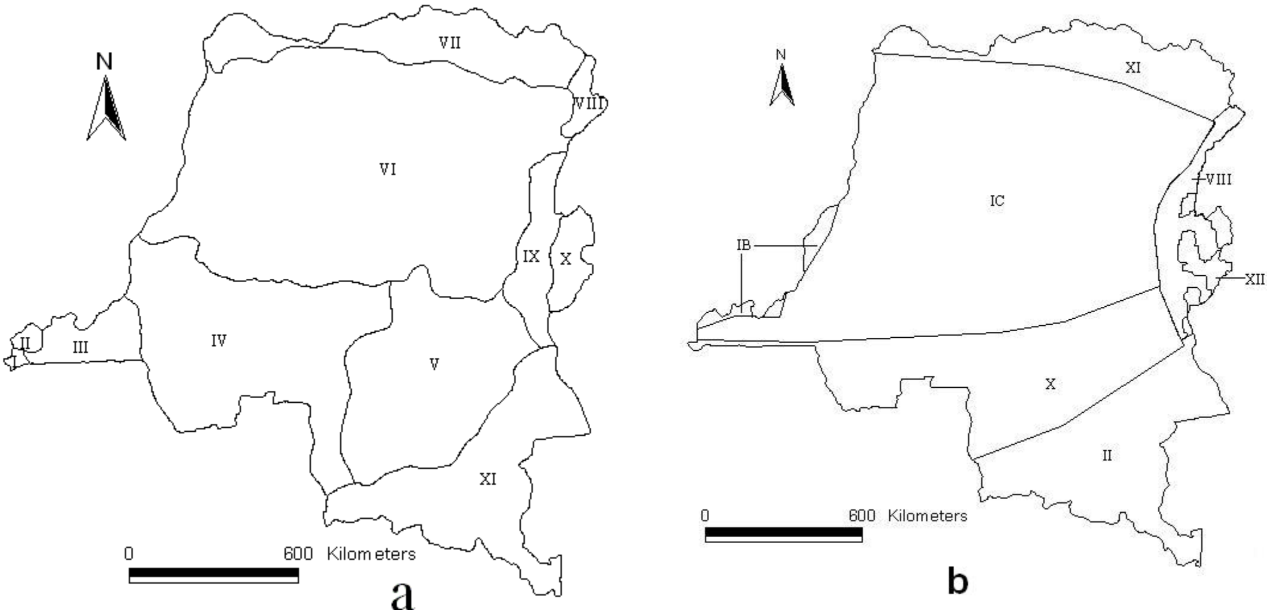

Figure 1. The two phytogeographic systems used in this study: (a) Robyns Phytogeographic Districts (1948). I: Coastal; II: Mayumbe; III: Bas-Congo; IV: Kasai; V: Bas-Katanga; VI: Central Forestry Officer; VII: Ubangi-Uele; VIII: Lac-Albert; IX: Lakes Edward and Kivu; X: Ruanda-Urundi; XI: Haut-Katanga; (b) White Phytogeographic entities (1979, 1986) covering DR Congo, Rwanda and Burundi (modified by Koffi 2008). I: regional center of Guinean-Congolese endemism (IB: lower Guinean sub-center, IC: Congolese sub-center); II: regional center of Zambezian endemism; VIII: regional center of Afromontane endemism; X: Guinean-Congolese / Zambezian regional transition zone; XI: Guineo-Congolese / Sudanese regional transition zone; XII: Regional mosaic of Lake Victoria. The features represent the boundaries of the phytogeographic territories

Floristic data

This study involved 9181 samples of Acanthaceae comprising 48 genus and 310 species harvested in 6362 localities. Ruderal species, aquatic, introduced and cultivated were excluded because their spatial distribution was determined by non-ecological factors. In this study, only species represented by more than ten samples (137 species and 38 genera) were selected for the analyses. The Directory of Bamps (1982) was used for harvesting localities. The material used for the vicariance cases mentioned in this work is in the appendix. The spatial distribution maps have been produced with QGIS software version 2.16.0 (http://www.qgis.org).

Degree of exploration

The territory was covered by 1.5 ° meshes numbered from 1 to 118 (Koffi 2005) within which the number of samples was determined. An interpolation was carried out to highlight the most explored areas and gaps. As well, the Pielou (1975) equality or regularity index was calculated through the meshes, according to the following formula:

$$E = -\frac{\sum_{i=1}^{n} p_i \log p_i}{\log n}$$

With *pi* = the proportion of the number of samples collected in each mesh and *n* = the number of meshes (*n* = 118). *n* varies between 0 (some meshes have been much more sampled than others) and 1 (perfect balance between the meshes).

Table 1. BIOCLIM environmental variables (http://www. worldclim.org/bioclim.htm) used to generate potential distribution maps

Bioclimatic variables	
bio _1	Annual Mean Temperature
bio _2	Mean Diurnal Range (Mean of monthly (max temp - min
bio _3	Isothermality (BIO2/BIO7) (* 100)
bio _4	Temperature Seasonality (standard deviation *100)
bio _5	Max Temperature of Warmest Month
bio _6	Min Temperature of Coldest Month
bio _7	Temperature Annual Range (BIO5-BIO6)
bio _8	Mean Temperature of Wettest Quarter
bio _9	Mean Temperature of Driest Quarter
bio _10	Mean Temperature of Warmest Quarter
bio _11	Mean Temperature of Coldest Quarter
bio _12	Annual Precipitation
bio _13	Precipitation of Wettest Month
bio _14	Precipitation of Driest Month
bio _15	Precipitation Seasonality (Coefficient of Variation)
bio _16	Precipitation of Wettest Quarter
bio _17	Precipitation of Driest Quarter
bio _18	Precipitation of Warmest Quarter
bio_19	Precipitation of Coldest Quarter

Potential distribution

The Maximum Entropy (Maxent) approach, developed by Phillips et al. (2004), was used to produce maps of the potential distribution of species. The environmental variables were obtained on Worldclim (http://www.worldclim.org/) with a resolution of 2.5 arc-minutes on the ground (5 km compared to the equator) (Hijmans et *al*., 2005). They cover the period from 1950 to 2000. The variables are mean monthly precipitation, minimum and maximum temperature and 19 bioclimatic variables (BIOCLIM: http://www.worldclim.org/ bioclim.htm) (Table 1), which may have an influence on species potential distribution.

RESULTS

Floristic analysis and degree of exploration

The phytogeographic entities of White (1979, 1986) having the most abundant species were the regional center of Afromontane endemism, including the regional Mosaic of Lake Victoria and the regional center of Zambezian endemism center with 172 species (55.48%) and 156 species (50.32%). When the Lower Guinean sub-center and the Congolese sub-center are assembled, they give the regional center of Guinean-Congolese endemism, in which 142 species (45.81%) have been harvested. The Guinean-Congolese/Sudanese regional transition zone contains 75 species (24.19%). The most sampled meshes are: mesh 51 (1017 samples), mesh 112 (654 samples), mesh 40 (637 samples), mesh 33 (509 samples), mesh 30 (454 samples), mesh 83 (306 samples), mesh 39 (270 samples), mesh 37 (255 samples), mesh 50 (251 samples) and mesh 107 (238 samples) (Figure 2a). These meshes account for 48.95 % of total harvest. According to Robyns (1948), the densely explored mesh is located in the districts of Lakes Edouard and Kivu, Ruanda-Urundi, Upper Katanga (Figure 2b) or the regional center of Afromontane endemism including the regional Mosaic of the lake Victoria and the Zambezian regional center of endemism according to White (1979, 1986) (Figure 2c). Meanwhile, 33 meshes have between zero and ten samples and represent 2.48 % of the total harvest. These meshes are located, according to Robyns (1948), oin the districts of Kasai, Lower Katanga and south of the Central Forestry Zone corresponding to the Guinean-Congolese / Zambezian regional transition zone and south of the Congolese sub-center (White 1979, 1986).The value of the equitability index (E = 0.02), computed through the meshes, is very low; which proves that there are really more sampled meshes than others.

Spatial distribution of species

Analysis of distribution maps of all species showed different models of spatial distribution.While some species are submitted to phytogeographic territories (single or endemic species), many have been harvested in two or three phytogeographic territories (linkage species) and others have been collected in all the phytogeographic Districts of Robyns (1948) or phytogeographic entities of White (1979, 1986) (broadly distributed species).Table 2 shows the spatial distribution of some species with the phytogeographic entities of White (1979, 1986).

Vicariousness

In this study, two types of vicariance were observed at the genus level and within the subspecies, through the phytogeographic territories defined by Robyns (1948) and White (1979, 1986): ecological vicariance and geographic vicariance. Ecological vicariance applies to species or subspecies harvested in the same phytogeographic territories and geographic vicariance concerns species or subspecies harvested in separate phytogeographic territories.

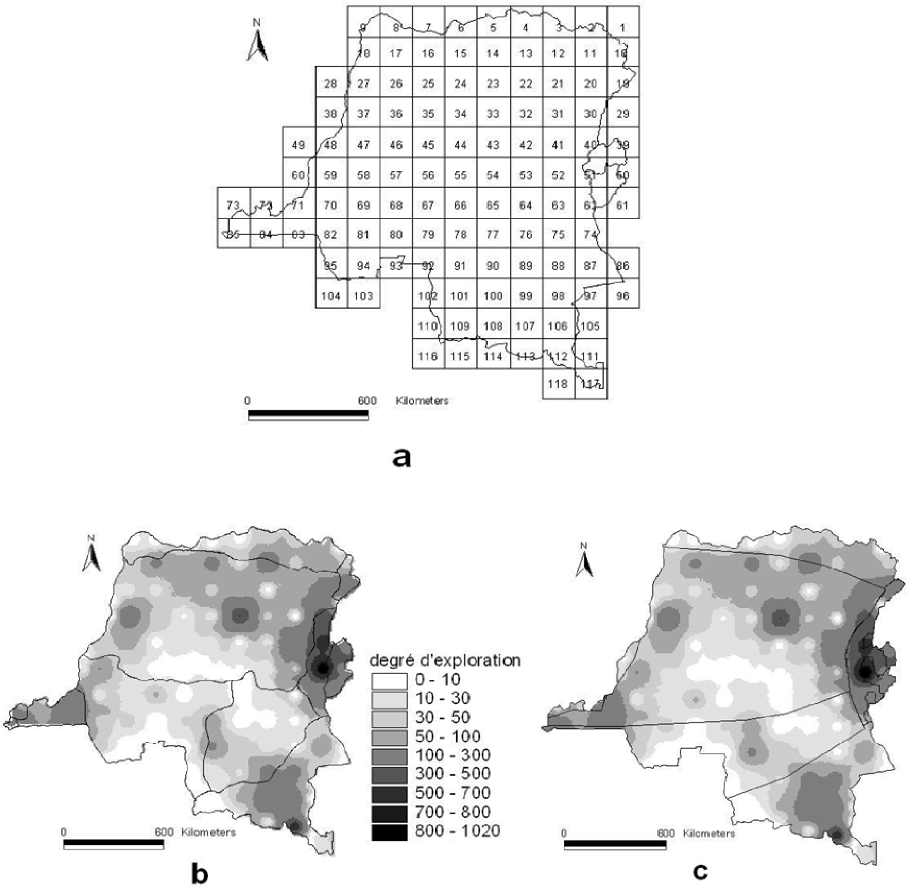

Figure 2. Degree of floristic exploration according to the Acanthaceae database: (a) Meshes numbered 1 to 118; (b) Phytogeographic Districts of Robyns (1948); (c) Phytogeographic Entities covering the DR Congo, Rwanda and Burundi (White 1979, 1986). For the names of the phytogeographic territories, see Figure 1

Table 2. Different types of spatial distribution of Acanthaceae according to thephytogeographic entities of White (1979, 1986) with the phytochories of the bindingspecies. For the names of the phytogeographic entities I to XII, see Figure 1

Distribution types	Examples
Species distributed in all the phytogeographic territories of the study area	*Asystasia gangetica* T.Anders. subsp. *micrantha* (Nees) Ensemu Kelbessa
	Brillantaisia owariensis P.Beauv.
	Hypoestes forskalei (Vahl.) Soland. ex Roem. & Schult.
	Nelsonia smithii Oerst.
	Phaulopsis imbricata (Forssk.) Swelt. subsp. *poggei* (Lindau) Manklow
	Rungia grandis T.Anders.
	Whitfieldia elongata (P.Beauv.) De Wild. & T.Dur.
Linkage species	*Acanthus latisepalus* C.B.Cl. (IB, IC, X, XII)
	Anisosepalum alboviolaceum (R.Ben.) E.Hossain (IC, X, XII)
	Anisotes macrophyllus (Lindau) Heine (IC, X, XI, XII)
	Barleria descampsii Lindau (II, X)
	Brillantaisia kirungae Lindau (IC, II, VIII, X, XII)
	Dicliptera wittei Mildbr. (IC, VIII, X, XI, XII)
	Justicia matammensis (Schwcinf.) Oliv. (IC, VIII, XI, XII)
	Justicia pynaertii De Wild. (IC, XII)
	Lankesteria elegans (P.Beauv.) T.Anders. (IB, IC, X, XI, XII)
	Monechma depauperatum (T.Aders.) C.B.Cl. (II, XI)
	Peristrophe paniculata (Forssk.) Brummit (IB, IC, II, VIII, X, XII)
	Thunbergia petersiana Lindau (II, VIII, XI, XII)
Zambezian species	*Asystasia zambiana* Brummit & Chisumpa
	Barleria velutina Champl.
	Blepharis katangensis De Wild.
	Hygrophila pilosa Burkill
Guinean-Congolese species	*Justicia alchorneeticola* Champl.
	Physacanthus batanganus (J. Braun & K.Schum.) Lindau
	Ruellia mayumbensis Champl.
	Thunbergia pynaertii De Wild.
	Whitfieldia laurentii (Lindau) C.B.Cl.
Afromontane species	*Blepharis cristata* S.Moore
	Dyschoriste clinopodioides Mildbr.
	Justicia anagalloides (Nees) T.Anders.
	Justicia exigua S.Moore
	Justicia nigrescens Champl.
	Monechma subsessile (Oliv.) C.B.Cl.
	Thunbergia mildbraediana Lebrun & Toussaint

Vicariance at the genus level through the phytogeographic territories Robyns (1948)

Concerning the phytogeographic territories defined by Robyns (1948) and at the genus level, 27 couples with cases of ecological vicariance and six couples with cases of geographic vicariance were observed.

Ecological vicariance

An example of ecological vicariance is presented here, through the phytogeographic territories defined by Robyns (1948), within the genus *Blepharis* Juss, with the couple *B. katangensis* De Wild and *B. menocotyl* Milne-Redh. (Figure 3a and 3b). In fact, both species were harvested in District XI. Harvesting was carried out in the same environments (light forest, savanna, forest fallow, *miombo*, marsh, swamp, *muhulu, dembo*) at altitudes between 920 and 1410 m. The potential distribution map shows a likelihood of occurrence in districts I, II and III. The environmental variables that determine the potential spatial distribution according to Maxent are bio_3 (Isothermality) for *B. katangensis* and bio_7 (Temperature Annual Range) for *B. menocotyl*. These two species were harvested in the same environments and are circumscribed in the same phytogeographic territories. Thus, they present a case of ecological vicariance.

Geographic vicariance

An example of a case of geographic vicariance, through the phytogeographic territories defined by Robyns (1948), within the genus *Pseuderanthemum* Radlk. is presented by the pair *P. ludovicianum* (Büttn.) Lindau and *P. lindavianum* De Wild. & T.Dur. (Figure 3c and 3d). In fact, *P. ludovicianum* was collected in almost all the phytogeographic districts of Robyns (1948) except in districts I, II, X and XI. Harvesting was carried out in rain forest, forest galleries, secondary forests, transition forests, creek banks, mountain forests, palm groves, swamp forests, crops, in marshes, in riparian forests, at altitudes between 470 and 2100 m. The potential distribution map shows a maximum likelihood of occurrence in district X. The most significant environmental variable for the potential spatial distribution of this species, according to Maxent, is bio_19 (the precipitation of the coldest quarter). Conversely, *P. lindavianum* has a very restricted distribution. It was harvested only in District I and II. Harvesting was carried out in rainforest, savannah, lakeshore, forest fallow, secondary forest and ravine. The potential spatial distribution map shows that this species may be present in District XI. The environmental variable that has a significant influence on the potential distribution of this species, according to Maxent, is altitude. These two species have similar habitats, but are present in different territories, so they show a case of geographic vicariance.

Vicariance at subspecies level through the phytogeographic territories Robyns (1948)

For the phytogeographic territories defined by Robyns (1948) and at species level, six couples with cases of ecological vicariance and two couples of cases of geographic vicariance were observed.

Ecological vicariance

An example of ecological vicariance, through the phytogeographic territories defined by Robyns (1948), is presented by the couple *Thunbergia hockii* De Wild. subsp. *hockii* and *Thunbergia hockii* De Wild. subsp. *parvicapsula* Champl. (Figure 4a and 4b). In fact, *T. hockii* subsp. *hockii* was harvested in districts IV, V, IX, X and XI and T. *hockii* subsp. *parvicapsula* in districts V and XI. However, the potential spatial distribution map predicts a probability of presence in districts IV, IX and X. They have been harvested in the same habitats (clear forest, savanna, cropping sites, forest fallow) between 600 and 1800 m. The most important environmental variables for potential spatial distribution, according to Maxent, are bio_17 (Precipitation of Driest Quarter) for *T. hockii* subsp. *hockii* and bio_19 (Precipitation of Coldest Quarter) for *T. hockii* subsp. *parvicapsula*. This pair of subspecies has the same habitats and appears in the same phytogeographic territories. It presents a case of ecological vicariance.

Geographic vicariance

An example of a geographic vicariance, through the phytogeographic territories defined by Robyns (1948), is presented by the couple *Brachystephanus congensis* Champl. subsp. *congensis* Champl. and *Brachystephanus congensis* Champl. subsp. l*atipaniculatus* Champl (Figure 4c and 4d). On one hand, *B. congensis* subsp. *congensis* was harvested in districts III and IV. It has been harvested in swamp forests, in forest galleries. The potential distribution map shows presence in Districts I and II toward the borders of Congo Brazzaville and Angola. As well, a very small extension in District V and XI was observed. Its ecological niche is influenced by bio_18 (Precipitation of Warmest Quarter), according to Maxent. On the other hand, *B. congensis* subsp. *latipaniculatus* was harvested in District VI and IX. It was harvested in the forest and on the water's edge. The potential distribution map shows a probability of presence in districts VII, VIII and X up to the borders of the Republic of Central Africa, Sudan and Uganda. The environmental variable that influences its potential spatial distribution, according to Maxent, is bio_15 (Precipitation Seasonality). These two species were harvested in similar environments, but in different phytogeographic territories. Thus, they present a case of geographic vicariance.

Vicariance at the genus level through the phytogeographic entities of White (1979, 1986)

Regarding the phytogeographic entities defined by White (1979, 1986) and at the genus level, 43 pairs of cases with ecological vicariance and seven pairs, cases of geographic vicariance were observed.

Ecological vicariance

Through the phytogeographic entities defined by White (1979, 1986), an example of ecological vicariance case is presented here, within the genus *Thunbergia* Retz. with the couple *T. oblongifolia* Oliv. and *T. marunguensis* Champl. (Figure 5a and 5b). In fact, these two species were harvested in the phytogeographic entity II. Harvesting was carried out in the same environments (light forest, savannah, marsh, prairie), at altitudes between 600 and 2000 m. The most important environmental variable for their potential spatial distribution is bio_17 (Precipitation of Driest Quarter). These two species were harvested in the same environments and are circumscribed in the same phytogeographic territories. Consequently, they present a case of ecological vicariance.

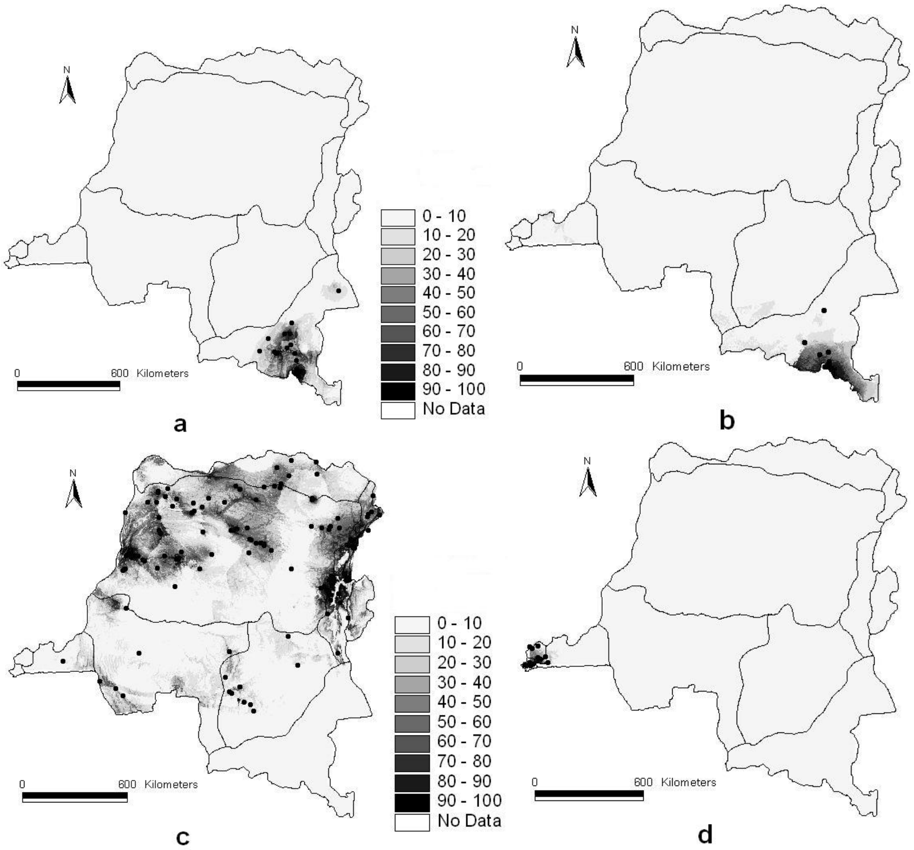

Figure 3. An example of ecological vicariance, through the phytogeographic territories defined by Robyns (1948), within the genus *Blepharis* Juss. with the couple: (a) *B. katangensis* De Wild., (b) *B. menocotyl* Milne-Redh. An example of a case of geographic vicariance, through the phytogeographic territories defined by Robyns (1948), within the genus *Pseuderanthemum* Radlk. with the couple: (c) *P. ludovicianum* (Büttn.) Lindau, (d) *P. lindavianum* De Wild. & T.Dur. The black dots represent the places of harvest, the spots represent the potential presence (the darker the greater the likelihood of presence), the lines are the boundaries of the phytogeographic districts of Robyns (1948)

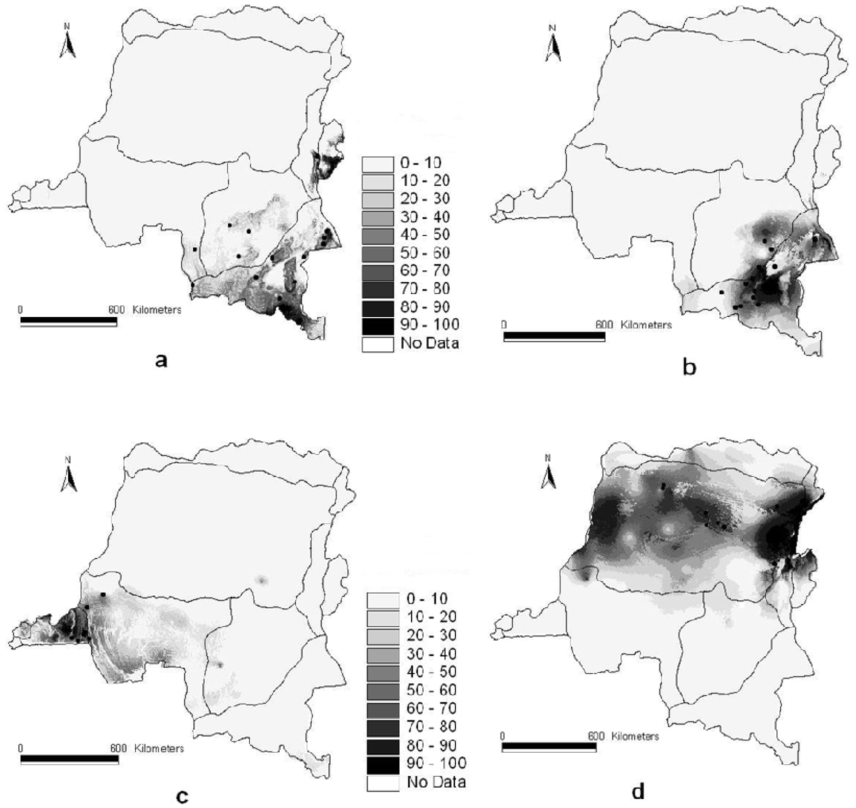

Figure 4. An example of ecological vicariance, through the phytogeographic territories defined by Robyns (1948), with the couple: (a) *Thunbergia hockii* De Wild. subsp. h*ockii*, (b) *Thunbergia hockii* De Wild. subsp. p*arvicapsula* Champl. An example of a case of geographic vicariance, through the phytogeographic territories defined by Robyns (1948), with the couple: (c) *Brachystephanus congensis* Champl. subsp. c*ongensis*, (d) *Brachystephanus congensis* Champl. subsp. *latipaniculatus* Champl. The black dots represent the places of harvest, the spots represent the potential presence (the darker the greater the likelihood of presence), the lines are the boundaries of the phytogeographic districts of Robyns (1948)

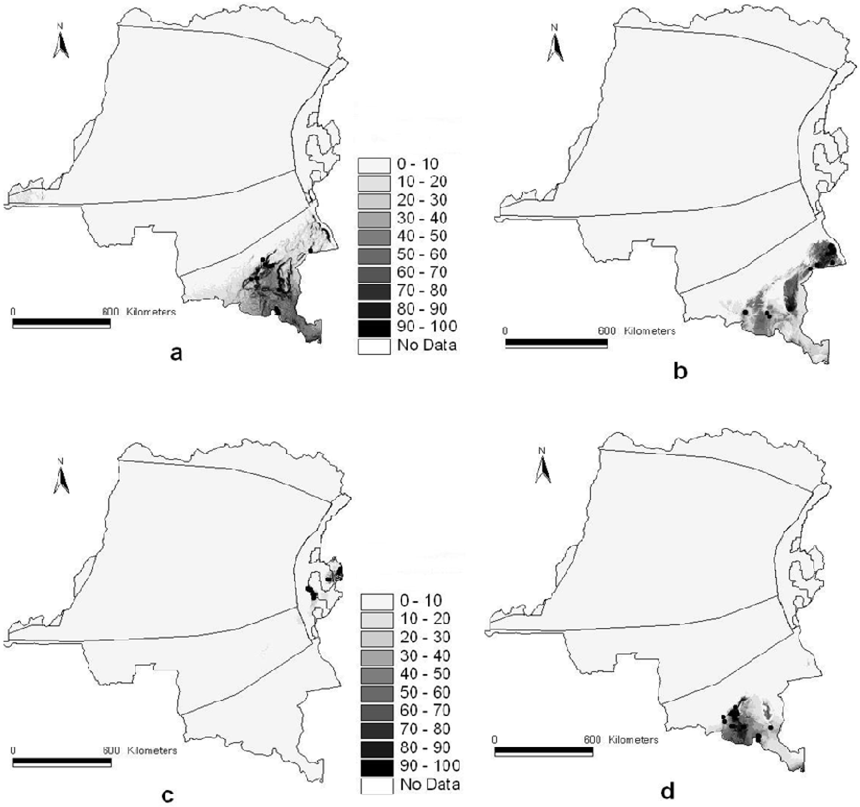

Figure 5. An example of ecological vicariance, through the phytogeographic entities defined by White (1979, 1986), within the genus *Thunbergia* Retz. with the couple: (a) *Thunbergiaoblongifolia* Oliv., (b) *Thunbergia marunguensis* Champl. an example of a case of geographic vicariance, through the phytogeographic entities defined by White (1979, 1986), with the couple: (c) *Barleria grandicalyx* Lindau, (d) *Barleria velutina* Champl. Black dots represent harvesting sites, spots represent the potential presence (the darker the greater the likelihood of presence), the features are the boundaries of White's phytogeographic entities (1979, 1986)

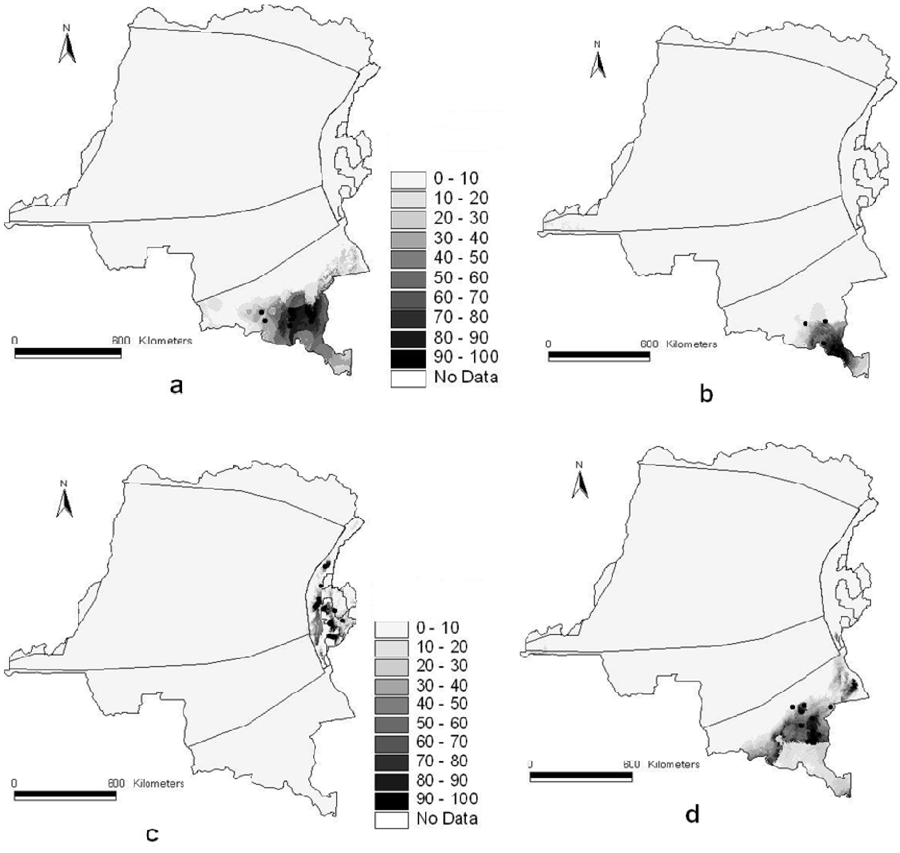

Figure 6. An example of ecological vicariance, through the phytogeographic entities defined by White (1979, 1986), with the pair: (a) *Lepidagathis scariosa* Nees subsp. *scariosa*, (b) *Lepidagathis scariosa* Nees subsp. *parvifolia* Champl. An example of a case of geographic vicariance, through the phytogeographic entities defined by White (1979, 1986), with the couple: (c) *Anisosepalum humbertii* (Mildr.) Hossain subsp. *humbertii*, (d) *Anisosepalum humbertii* (Mildr.) E. Hossain subsp. *zambiense* Champl. Black dot represents harvest location, spot represents potential presence (the darker the likelihood of occurrence), lines are the boundaries of the White's Phytogeographic Districts (1979, 1986)

Geographic vicariance

An example of geographic vicariance, through the phytogeographic entities defined by White (1979, 1986), within the genus *Barleria* L. is presented by the couple *B. grandicalyx* Lindau and *B. velutina* Champl. (Figure 5c and 5d). On one hand, *B. grandicalyx* was harvested in the phytogeographic entities VIII and XII. It was harvested in savannas, steppes and rocks at altitudes between 800 and 1450 m. Its ecological niche is influenced by bio_16 (Precipitation of Wettest Quarter), according to Maxent. *Barleria velutina*, on the other hand, was harvested in the phytogeographic entity II. It was harvested in the forest, at altitudes between 1225 and 1500 m. The environmental variable that influences its potential spatial distribution, according to Maxent, is bio_6 (Min Temperature of Coldest Month). These two species were harvested in similar environments, but in different phytogeographic territories. Thus, they present a case of geographic vicariance.

Vicariance at the subspecies level through the phytogeographic entities of White (1979, 1986)

Regarding the phytogeographic entities defined by White (1979, 1986) and at the species level, five couples with cases of ecological vicariance and a couple, cases of geographic vicariance were observed.

Ecological vicariance

An example of ecological vicariance, through the phytogeographic entities defined by White (1979, 1986), is presented by the couple *Lepidagathis scariosa* Nees subsp. *scariosa* and *Lepidagathis scariosa* Nees subsp. *parvifolia* Champl (Figure 6a and 6b). Indeed, these two species were harvested in the phytogeographic entity II. They were harvested in the same habitats (light forest, savanna), at altitudes between 1000 and 1500 m. The most important environmental variables for the potential distribution, according to Maxent, are bio_17 (Precipitation of Driest Quarter) for *L. scariosa* subsp. *scariosa* and bio_7 (Temperature Annual Range) for *L. scariosa* subsp. *parvifolia*. This pair of subspecies has the same habitats and is the same phytogeographic entities. Consequently, it presents a case of ecological vicariance.

Geographic vicariance

An example of geographic vicariance, through the phytogeographic entities defined by White (1979, 1986), is presented by the couple *Anisosepalum humbertii* (Mildr.) E. Hossain subsp. *humbertii* and *Anisosepalum humbertii* (Mildr.) Subsp. *zambiense* Champl (Figure 6c and 6d). In fact, *A. humbertii* subsp. *humbertii* was collected in the phytogeographic units VIII and XII, at altitudes between 1500 and 2700 m. It has been harvested in rainforest, forest galleries and marshes and on rocks. The environmental variable influencing its ecological niche is bio_10 (Mean Temperature of Warmest Quarter) according to Maxent. Whereas, *A. humbertii* subsp. *zambiense* was harvested in the phytogeographic entity II. It was harvested in forest galleries, savanna, temporary pools and swamp forests, at altitudes between 1400 and 1800 m. The most significant environmental variable for its potential spatial distribution, according to Maxent, is bio_17 (Precipitation of Driest Quarter). These two subspecies have been harvested in similar environments, but in different phytogeographic territories. So, they present a case of geographic vicariance.

DISCUSSION

The database highlighted the degree of exploration through the phytogeographic territories defined by Robyns (1948) and White (1979, 1986), in DR Congo, Rwanda and Burundi. These observations with the Acanthaceae reflect the recent status of floristic knowledge in Central Africa. Some phytogeographic territories are more floristically known than others. The phytogeographic territories in which there has been intense activities of harvesting are those hosting the major centers of activity and research centers. Outside these zones, other highly diversified phytogeographic territories in natural vegetation are not explored or are only very partially explored. This is the case for the districts of Kasai and Lower Katanga according to Robyns (1948) or Guinean-Congolese / Zambezian regional transition zone (White 1979, 1986). These findings are consistent with those of Hepper (1979), which states that in DR Congo, Rwanda and Burundi there are well-known regions, medium-known regions and poorly known regions. The areas, either partially or non-sampled, identified in this study, were also recognized as subsampled in other studies (Léonard 1968, Gibbs Russell et al. 1984, Campbell and Hammond 1989, Bürger 2001, Küper et al. 2006). Botanical surveys are very unevenly distributed. Some regions, and naturally the most accessible ones, are overrepresented. Others are not at all. These are usually localities with difficult access but whose botanical interest is generally very large (Pascal and Ramesh, 1993). Despite these barriers, some species were harvested almost throughout the study area. These are species that have a wide ecological amplitude. They are capable of adapting to diverse edaphic and abiotic factors. This is the case, for example, with *Whitfieldia elongata* and *Nelsonia smithii*. On the other hand, the spatial distribution of other species does not exceed the limits of the phytogeographic territories. These species are likely to have a more restricted ecological amplitude. This is the case for example of *Thunbergia pynaertii*. (in the regional center for endemic Guinean - Congolese), *Hygrophila pilosa* (in the regional center of Zambezian endemism) and *Justicia exigua* (in the Afromontane regional center of endemism and in the regional Mosaic of the lake Victoria). Other species, although abundantly harvested in a territory, have some samples in neighboring phytogeographic territories. This is the case of *Lankesteria elegans*. These could be termed transitional species. According to Schnell (1971), many species have had a much larger area but have not been able to adapt to relatively rapid climatic changes, which may explain the presence of some species in restricted areas.

Two types of vicariance were found in this study at the genus and species level: ecological vicariance and geographic vicariance. Ecological vicariance concerns species that are not geographically isolated but can evolve into distinct species. When a geographic barrier (river, mountain, valley, ocean, glacier) cuts the range of a species into several zones, it is a geographic vicariance. In each zone, each population evolves independently of the others, leading to the appearance of a new species. The phenomenon of vicariance is an evolutionary process giving rise to speciation, a phenomenon leading to the individualization of a new species entirely, passing through forms hardly distinct by morphological nuances, others of varietal value or under-specific (Lebrun 1960). Under these conditions, the cases of ecological vicariance described in this study could be cases of sympatric speciation: this is the case of the couple *Thunbergia hockii* subsp. *hockii* and *T. hockii* subsp. *parvicapsula* (Figure. 4a and 4b). Also, cases of geographic vicariance could be cases of allopatric speciation: this is the case of the couple *Anisosepalum humbertii* subsp. *humbertii* and *A. humbertii* subsp. *zambiense* (Figure. 6c and 6d). Two populations with allopatric speciation occupy disjointed areas (Tassy 1991). This phenomenon can be accentuated to give cases of peripatric speciation or speciation by founder effect (Excoffier 1999).In this type of speciation, a small number of individuals founds a new population outside the allotment area of the original species, for instance following the colonization of an island near the coast. This new small population can evolve rapidly into a new species. This is the case of the couple *Pseuderanthemum ludovicianum* and *P. lindavianum* (Figure. 3c and 3d).

In the case of ecological vicariance, even if the ecological niches of certain species exceed the limits of the phytogeographic territories considered in this study, they are not superimposed, they are juxtaposed. This is the case of the couple *Brachystephanus congensis* subsp. *congensis* and *B. congensis* subsp. *latipaniculatus* (Figure. 4c and 4d). The speciation centers highlighted in this study are the Upper Katanga district (Robyns 1948) or the Zambezian regional endemism center (White 1979, 1986), the Lakes Edward and Kivu districts and the Ruanda-Urundi district (Robyns 1948) or regional Afromontane endemism center including the lake Victoria Regional Mosaic (White1979, 1986). This may explain the specific richness in these two areas. Thus, the specific richness of the Acanthaceae flora of DR Congo, Rwanda and Burundi follows the subdivisions of Lebrun (1960, 1976) and Ozenda (1982). In this work, it appears that the great center of speciation of the African flora is located in the Zambezian Region and more precisely in the area of the floral element Bangweolo-Katangais. The same results were obtained with the flora of the Eriocaulaceae of Central Africa (Kimpouni 1993). Furthermore, the Edouard and Kivu Lakes district, the Ruanda-Urundi district (Robyns 1948) or the Afromontane regional endemism center, including the Lake Victoria regional mosaic (White 1979, 1986), where the Albertin rift valley East of DR Congo is situated, has also been recognized as a center of high floristic diversity (hotspots) Küper et al. 2004, Mittermeier et al. 2004, Myers et al. 2000). The phenomenon of vicariance observed in an area shows the quality in terms of biodiversity of this area (Endler 1982, Bush 1994, Schneider et al. 1999, Moritz et al. 2000, Cheviron et al. 2005, Wüter et al. 2005). These areas can be considered as zone of refuge (Chapman 1917, Maley 1987, Nores 1999, 2004, Adrian et al. 2007). This may explain the high diversity of these two areas. The importance of phytogeographic systems should therefore not be underestimated in the conservation of a species. Phytogeographic distribution data may reflect hotspots, spatial variability of species diversity, vicarious cases and thus constitute an important tool in the development of conservation policy. All this information is, of course, crucial for phytogeography work on speciation centers or zone of refuge, as well as for conservation decisions. These two aspects must be taken into account: the protection of particularly rich areas and the protection of areas with strictly confined species. The choice of areas to be protected should also take into account the present state of the region, which may have varied considerably since the collection of the samples.

Conclusion

This study highlighted the intensity of the harvest through the phytogeographic territories. The equitability index calculated through the meshes and therefore in the phytogeographic territories has shown that some have been explored more than others. The sampling effort varies greatly from one phytogeographic territory to another, from one mesh to another and from one taxonomic group to another. Analysis of actual spatial distribution maps, coupled with potential distribution maps, showed two types of vicariance: ecological vicariance and geographic vicariance. These two types of vicariance were determined through the phytogeographic territories of Robyns (1948) and White (1979, 1986), at genera and species levels. For the phytogeographic territories of Robyns (1948), 27 pairs showing ecological vicariance cases and six pairs of geographic vicariance were determined at the genus level; six pairs of ecological vicarious cases and two pairs of geographic vicarious species were determined at the subspecies level. For the phytogeographic territories of White (1979, 1986), 43 pairs of ecological vicarious cases and seven pairs of cases of geographic vicariance were determined at the genus level; Five pairs showing ecological vicariance cases and one couple with a geographic vicarious case were determined at the subspecies level. Most of these types of vicariance have been identified in the Upper Katanga District (Robyns, 1948) or Zambezian regional endemism center (White 1979, 1986), the district of Edward and Kivu Lakes and the district of Ruanda-Urundi (Robyns, 1948) or Afromontane regional endemism center including the regional mosaic of Lake Victoria (White 1979, 1986). These two areas must be taken into account by conservation decision-makers, as speciation areas are areas of high biological diversity.

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